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Modelling suitable estuarine habitats for *Zostera noltii*, using Ecological Niche Factor Analysis and Bathymetric LiDAR

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ABSTRACT

Predicting species distribution and habitat suitability is of considerable use in supporting the implementation of environmental legislation, protection and conservation of marine waters and ecosystem-based management. As other seagrasses, *Zostera noltii* has declined worldwide, mainly due to human pressures, such as eutrophication and habitat loss. In the case of the Basque Country (northern Spain), the species is present only in 3 out of 12 estuaries. From the literature, it is known that at least 6 of these estuaries were formerly vegetated by this seagrass. Consequently, efforts to monitor and restore (potential) habitats have been enhanced. Therefore, we aim: (i) to determine the main environmental variables explaining *Zostera noltii* distribution, within the Basque estuaries based upon the Oka estuary; (ii) to model habitat suitability for this species, as a wider applicable management-decision tool for seagrass restoration; and (iii) to assess the applicability and predicted accuracy of the model by using internal and external validation methods. For this purpose, Ecological Niche Factor Analysis (ENFA) has been used to model habitat suitability, based upon topographical variables, obtained from bathymetric Light Detection And Ranging (LiDAR); sediment characteristics variables; and hydrodynamic variables. The results obtained from the ecological factors of the ENFA (Marginality: 1.00; Specialization: 2.59) indicate that the species habitat differs considerably from the mean environmental conditions over the study area; likewise, that the species is restrictive in the selection of the range of conditions within which it dwells. The main environmental variables relating to the species distribution, in order of importance, are: mean grain size; redox potential; intertidal height; sediment sorting; slope of intertidal flat; percentage of gravels; and percentage of organic matter content. The model has a high predicted accuracy (Boyce index: 0.92). Model validation using an independent dataset in the Bidasoa estuary has shown the applicability but also the limitations in extrapolating the habitat suitability model to select suitable transplantation areas in other estuaries with similar morphological and biogeographical characteristics. ENFA-technique, applied with an accurate selection of environmental predictors, could be a promising tool for predicting seagrass habitat suitability which could assist on seagrass conservation and restoration programs worldwide.

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1. Introduction

Seagrasses constitute important coastal habitats worldwide, being good indicators of environmental health (Short et al., 2006). Seagrass beds are among the most valuable ecosystems in the world (Costanza et al., 1997). In spite of this, their habitat is being lost and fragmented overall (Duarte, 2002; and Hughes et al., 2009); eutrophication is affecting them (Dennison et al., 1993; Short and Burdick, 1996; and Krause-Jensen et al., 2008), whilst the rates of decline have increased in recent years, with seagrass beds even disappearing in some areas (Kirkman 1997; Boudouresque et al., 2000; Green and Short 2003; Short et al., 2006; and Waycott et al., 2009). Consequently, this decline has led to restoration programmes worldwide (Park and Lee, 2007; Busch et al., 2010; Diekmann et al., 2010; and Rodríguez-Salinas et al., 2010).

One of the European estuarine seagrasses is *Zostera noltii* Hornemann 1832. This species is distributed widely within the coastal zones from the southern coasts of Norway to the Mediterranean Sea, the Black Sea, the Canary Islands, with the southern limit on the Mauritanian coast (Vermaat et al., 1993; Philippart, 1995; Auby and Labourg, 1996; Milchakova, 1999; and Pérez-Llorens, 2004).

Abbreviations: ENFA, Ecological Niche Factor Analysis; LiDAR, Light Detection and Ranging; HS, Habitat Suitability; TPI, Topographical Position Index; *M*, marginality; *S*, specialization.

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The different habitats of *Z noltii* are included in the European Habitats Directive's (92/43/EEC) list of sites of Community importance. *Z. noltii*, as a species, was not considered to be endangered and has not been protected under this legislation. However, in addition to the Habitats Directive, the Oslo-Paris Convention (OSPAR), for the protection of the marine environment of the North East Atlantic, prepared recently an initial list of threatened and/or declining species and habitats, in which *Zostera* beds are included (Tullrot, 2009). Moreover, according to the European Water Framework Directive (WFD, 2000/60/EC), this angiosperm has a high relevance as one of the five biological quality elements (phytoplankton, macroalgae, angiosperms, benthos and fishes) to be included in the ecological quality assessment in estuarine waters (Borja, 2005).

Zostera noltii has been reported to occur along most northern Spanish estuaries (Laborda et al., 1997), and there are also historical references about its presence along the Basque Country estuaries (Bubani, 1897; and Lázaro Ibiza, 1920), but nowadays is present only in 3 (Oka, Lea and Bidasoa) of the 12 main estuarine ecosystems (Fig. 1). It is the only seagrass present in the region (Uribe-Etxebarria et al., 2006; Otxoa et al., 2007; Borja et al., 2008; and Garmendia et al., 2010). The general degradation in quality of Basque estuaries over the last two centuries, due to human pressures (Borja et al., 2006), can explain the decline (from 6 to 3 vegetated estuaries) and loss of this species within the region (Sílván and Campos, 2002). However, a natural recovery is unlikely (Garmendia et al., 2010).

Taking into account that the water quality in these estuaries has been improving in recent years (Borja et al., 2009a; and Tueros et al., 2009), together with the fact that the species is important in terms of ecological quality assessment, a restoration programme is being considered to be undertaken in those Basque estuaries in which it is not present (Garmendia et al., 2010). To achieve successful results in the restoration, it is necessary to determine the most favourable environmental conditions for the species development (Moore and Short, 2006; and van Katwijk et al., 2009), i.e. the most suitable habitats which, in most cases, have been determined using conceptual models (van Katwijk et al., 2000; Gilkerson, 2008; and van der Heide et al., 2009).

However, habitat suitability (HS) can be determined also using a species distribution model. Different statistical and mathematical techniques have been applied to generate such models (Guisan and Zimmermann, 2000). Amongst these approaches, envelope-based approaches, like Ecological Niche Factor Analysis (ENFA), are considered particularly advantageous, since it requires only data on species presence, not on absence (Braunisch et al., 2008). The ENFA approach creates HS maps; by assessing habitat requirements from the distribution data and subsequently calculating for the whole area to what extent each pixel meets these requirements (Hirzel et al., 2002). This modelling method has been applied more frequently to

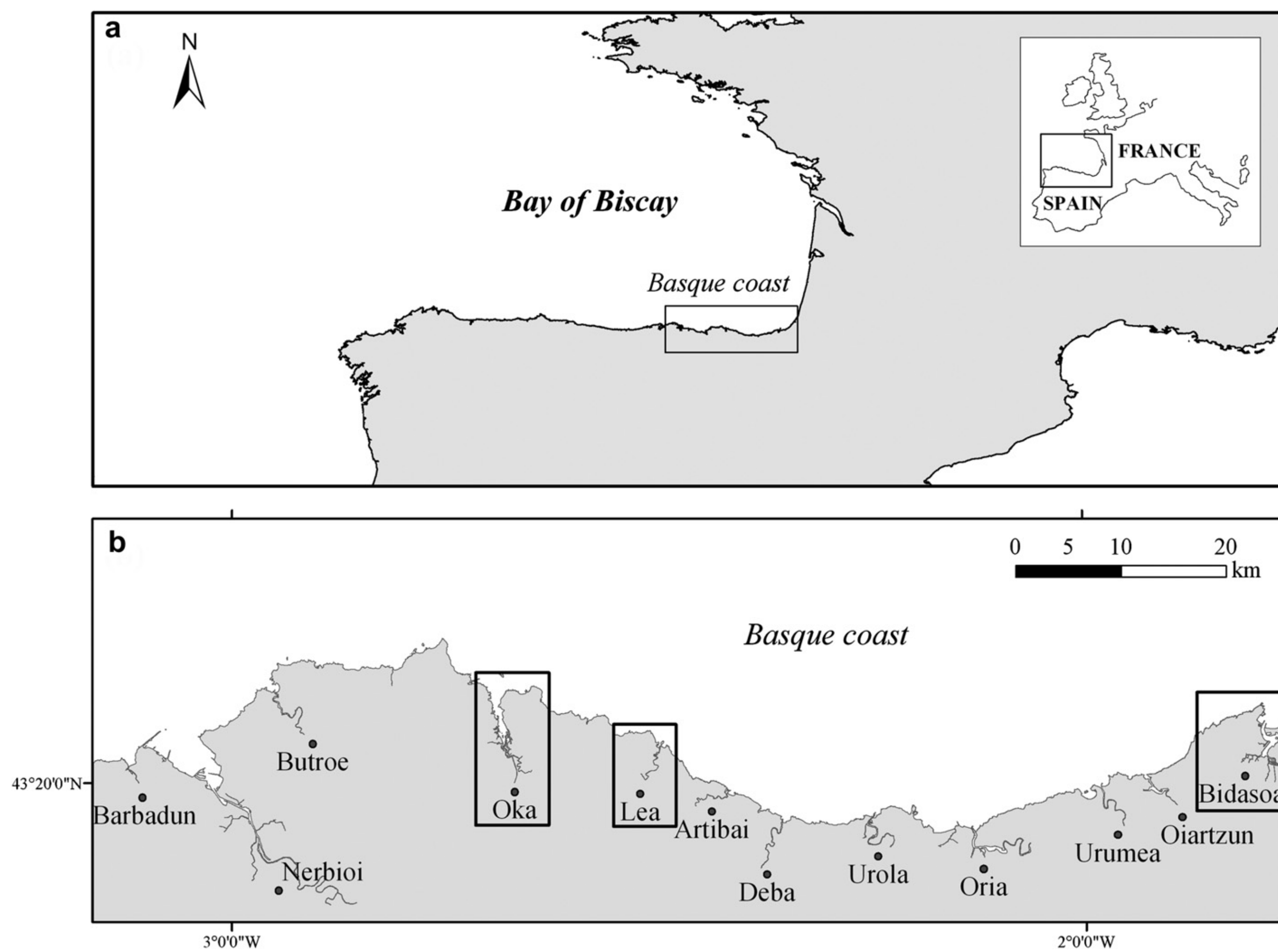

Fig. 1. (a) The Basque Country coast lying within the Bay of Biscay. (b) Map showing the 12 main estuarine ecosystems of the Basque coast, highlighting the three estuaries (Oka, Lea, Bidasoa) with *Zostera noltii* populations.

terrestrial habitats (Estrada-Peña and Venzal, 2007; and Viña et al., 2008). However, recently, it has been used also in the marine environment, modelling corals, odontocetes, Northern Gannet seabird and European lobster habitats (Bryan and Metaxas, 2007; Praca and Gannier, 2008; Skov et al., 2008; and Galparsoro et al., 2009), but it has not been applied to seagrass systems yet. Based up on Hutchinson's (1957) ecological niche concept, the ENFA compares, in the multidimensional space of ecological variables, the distribution of the localities where the focal species was observed, to a reference set describing the whole study area (Hirzel et al., 2002). *Zostera noltii*'s niche is associated with a narrow range of terrain elevation, defined mainly by submersion duration (Borja et al., 2004a). Under this context, the use of new tools, such as the airborne bathymetric LiDAR (Light Detection And Ranging), becomes highly relevant to obtain an extended and accurate coverage of the area studied, together with some environmental variables (Wedding et al., 2008; Costa et al., 2009; and Chust et al., 2010a).

Hence, the objectives of this investigation are: (i) to determine the main environmental variables explaining *Zostera noltii* distribution, using ENFA modelling, bathymetric LiDAR information and data on hydrodynamic and sediment properties; (ii) to map habitat suitability for this species within the Oka estuary, Basque Country; and (iii) to assess the applicability and predicted accuracy of the model by using internal and external validation methods. Henceforth, it is expected that the ENFA-technique could be applied as a promising to tool for seagrass conservation and restoration programs worldwide, contributing to the ecological status improvement of the coastal areas.

2. Material and methods

2.1. Study area

The study area is the intertidal zone of the Oka estuary, located within the Urdaibai Biosphere Reserve (declared in 1984). This estuary is situated on the Bay of Biscay coast, in the north of the Iberian Peninsula (Fig. 1). The main hydromorphological characteristics have been described in Borja et al. (2006). The Oka estuary is one of the most biologically diverse and best conserved of the Basque Country, together with the Bidasoa estuary (Borja et al., 2004a). Therefore, it is considered under a wide range of national and international protection and conservation frameworks; consequently, it has been investigated extensively (Castro et al., 2004). Within the estuary, there are several plant species listed in the *Catalogue of Threatened Fauna and Flora in the Basque Country* (Otxoa et al., 2007), including *Zostera noltii*. The Oka estuary encompasses the environmental conditions of 7 out of the 12 Basque estuaries (i.e. the environmental conditions in Oka estuary are representative of those along the entire Basque coast); since they are classified in the same type as 'estuaries with extensive intertidal flats', within the WFD (Borja et al., 2004b).

2.2. Zostera noltii occurrence data

Data on *Zostera noltii* distribution within the Oka estuary were obtained from Otxoa et al. (2007) and Garmendia et al. (2010). Additional field sampling was carried out in June 2009 where, besides confirming the data summarized in these studies, new locations were acquired with a Magellan MobileMapper GPS. From the collected georeferenced outline points, polygons were digitalized, to create the species presence GIS layer.

2.3. Environmental data

As can be seen in Table 1, eco-geographical variables from 3 different variable groups were collected: (i) topographical; (ii) sedimentological; and (iii) hydrographical. Although seagrass are well-known ecosystem engineers, as they can modify their abiotic environment (Jones et al., 1997), variables regarding to sediment characteristics have been used as independent predictors to model the HS. Henceforth, the extent to what *Zostera noltii* could contribute to sedimentation, in the intertidal habitats of the Oka estuary, is thought to be minor due to the low density of the population (Bos et al., 2007). Therefore, regarding to sediment, 7 eco-geographical variables were collected: (i) mean grain size in phi units (i.e. phi values from 14 to 4 are equivalents to mud; from 4 to −1 to sand; and from −1 to −20 to gravel); (ii) sediment sorting (variable, which measures the homogeneity of the grain size in sediment; e.g., values lower than 1.27 phi indicate very well-sorted sediment, whereas values higher than 16 phi indicate extremely poorly sorted (Folk, 1974)); (iii) percentage of gravels; (iv) percentage of sands; (v) percentage of silts; (vi) percentage of organic matter content; and (vii) redox potential. Data from each variable were analysed for 171 georeferenciated sampling sites. Sediment grain size analysis was developed following the methodology explained by Holme and McIntyre (1971). Organic matter content was estimated by measuring the weight loss caused by ignition (difference between dry weight at 105 °C and burned weight at 550 °C has been taken as an index of organic matter content). Redox potential data were taken on the field using a platinum electrode ORION 977800, with internal reference, connected to a CRISON digital 501 pH-meter/milivoltmeter. The samples were collected both within the seagrass bed and in unvegetated sites within the estuary. *Kriging* interpolation method was applied in order to obtain a GIS layer for each sediment characteristics variable. Tidal current velocity data (for rising and ebbing phases of the tide) were obtained from Solaun et al. (2009b).

In turn, although nutrients are important variables for seagrass growth (Cabaço et al., 2009), the HS modelling for extended areas requires information from a high number of locations within the study area. Since the information for this study is based upon hundreds of points, it is impossible to get information for nutrients from all locations. Moreover, the distribution of the species is intertidal, and the variability of the water column there is too high. Series of data from nutrients in 3 stations within the estuary, sampled seasonally between 1995 and 2011, are available, and the nutrient concentration in this period is not very high (10–50 μmol L^{-1} of dissolved inorganic nitrogen) (Borja et al., 2008, 2009a).

Table 1
Classification of variable groups, names of the eco-geographical variables (EGV), sources and types of data used in the present study. Variables in bold are those used in the analysis; the others not in bold, were removed, due to high correlation between variables. Key: TPI, Topographical Position Index.

Variable group	EGV	Source	Type of data
Topographic characteristics	**Intertidal height** **Slope** **Orientation** **Small-scale TPI** Broad-scale TPI **Rugosity**	Chust et al., 2010a	Derived from bathymetric LiDAR data (horizontal resolution grid: 2 × 2 m)
Sedimentologic characteristics	**Mean grain size** **Sediment sorting** **% of gravels** % of sands % of silts **% of organic matter** **Redox potential**	Garmendia et al., 2010; Solaun et al., 2009a; Field sampling 2009	Interpolated data (171 sampling points)
Hydrographical characteristics	Velocity of rising tide **Velocity of ebb tide**	Solaun et al., 2009a	Modelled data

2.4. LiDAR-derived topographic height

Height data were obtained from a high-resolution Digital Elevation Model (DEM), derived from data fusion between airborne bathymetric and topographic LiDAR data (Chust et al., 2010a). The DEM of the Oka estuary had a 2 m horizontal spatial resolution in the terrestrial zone (with a vertical accuracy of 0.15 m) and 4 m within the subtidal. During the summer of 2010, control points were established with a Trimble R6 GPS receiver system (differential GPS, with Real-Time Kinematic (RTK) technologies) in flat, hard, well-defined surfaces and free of objects, to validate the DEM orthometric heights. The vertical root mean square error ($RMSE_z$) (Poulter and Halpin, 2007), computed between the DEM and 16 acquired field control points, was 0.18 m, this is within the range of expected error for a LiDAR dataset. Based upon the DEM, different extensions from ArcGis 9.2 software (ESRI®) were used to generate the topographic features: (i) '*3D Analyst*' extension was used to generate intertidal height, slope of intertidal flat and orientation (i.e. aspect) features; and (ii) *Benthic Terrain Modeler* (BTM) (version 1.0) (Wright et al., 2005) extension was used to generate Rugosity index and Topographic Position Index (TPI), both at small-scale and broad-scale (TPI value provides an indication of whether any particular pixel forms part of a positive (e.g., crest) or negative (e.g. trough) feature, of the surrounding terrain (Wilson et al., 2007)).

2.5. Ecological Niche Factor Analysis (ENFA) and habitat suitability map

The ENFA approach, developed by Hirzel et al. (2002), computes suitability functions, by comparing the species distribution in the eco-geographical variables space. This approach determines the relationships between variables and establishes combinations of these variables, to produce uncorrelated factors. The first factor is defined as the 'Marginality' (*M*) of the species' niche; this describes the mean of a variable when the species is present ('species mean'), in relation to the mean of the variable in the whole study area ('global mean') distribution (Bryan and Metaxas, 2007). It is defined as 'the absolute difference between the global mean and the species mean' for each environmental variable (Hirzel et al., 2002) and is calculated as:

$$m_i = \frac{|m_{G_i} - m_{S_i}|}{1.96\sigma_{G_i}} \quad (1)$$

where m_i is the *M* for a particular environmental variable, m_{G_i} is the global mean of the variable, m_{S_i} is the mean of the variable in species' range and σ_{G_i} is the standard deviation of the global distribution for the variable (Bryan and Metaxas, 2007). Then, combining the *M* of individual environmental variables, ENFA computes an overall global *M* (Hirzel et al., 2002; and Reutter et al., 2003). *M* ranges generally between 0 and 1, with larger values indicating that the species is not equally represented in all the environments.

The second factor is defined as Specialization (*S*), which indicates how restricted the species' niche is, in relation to the study area ('global' area); it is defined as 'the ratio of variance in the global distribution to that in the species distribution' of the environmental variable (Hirzel et al., 2002; and Reutter et al., 2003). It is calculated as:

$$\lambda_i = \frac{\sigma_{G_i}}{\sigma_{S_i}} \quad (2)$$

where λ_i is the *S* for a particular environmental variable and; σ_{S_i} and σ_{G_i} are the standard deviation of the variable, within the species' range and global, respectively. As for the *M* factor, the *S* for individual environmental variables are combined to compute an overall global *S*. *S* ranges from 1 to ∞, with the niche becoming narrower as *S* increases. Tolerance, which is the inverse of *S*, ranges from 0 to 1, with a larger coefficient indicating a wider niche for a particular species (Reutter et al., 2003).

In order to apply ENFA, *Zostera noltii* location data (Fig. 2), as well as environmental data (Table 1), were incorporated into BioMapper 4.0 software (www2.unil.ch/biomapper/) as a raster-based grid file, with a horizontal resolution of 2 m, and the same extent. Subsequently, a covariance matrix was calculated for all the eco-geographical variables, in order to identify the highly-correlated variables (Table 1); as such, to remove those which had a high correlation (values above 0.7) from later analysis, as they are considered redundant. After removing the correlated variables, ENFA was applied to obtain *M* and *S* factors values.

Subsequently, the HS map was produced from the ENFA results using the median algorithm. This algorithm assumes that the median value for the environmental variable, within the species distribution, is approximately the same as in the study area; it makes no assumptions, based up on the density of the observation/sampling points (Hirzel et al., 2002; and Hirzel and Arlettaz, 2003). A global *M* value for all of the environmental factors was generated for each cell, computing the weighted mean of all partial suitabilities. The HS map ranges between 0 to 100 global suitability values, rescaled using the isopleth method.

2.6. Validation of the habitat suitability model

Two validation methods were applied in order to validate the HS model: (i) validation by cross-validation method within the Oka estuary, hence, resampling the same dataset that generates the model (therefore, called 'internal validation'); and (ii) validation by model extrapolation to another estuary (i.e. Bidasoa), hence, using an independent dataset from that used for generating the model (therefore, called 'external validation'). The internal model validation was achieved through the Jack-knife Area-Adjusted Frequency Cross-Validation procedure, implemented in the BioMapper software and following the method described by Boyce et al. (2002). By this method, the presence points of the species were partitioned into ten subsets of equal sizes. Nine of them were used to calibrate the HS map, whilst the last one was used to evaluate the result. By replicating this process 10 times, each subset was used, in turn, for validation purpose. As such, a confidence interval, the Boyce Index, was produced (ranging between 0 and 1); this indicates the predicted accuracy of the habitat model (Skov et al., 2008). A value lying close to 1 shows high confidence of the model, whilst 0 indicates the worst confidence. This index provides predicted-to-expected ratio curves, which offer further insights into the model quality: robustness, HS resolution and deviation from randomness. Such information assists in reclassifying the predicted maps, into meaningful HS classes (Hirzel et al., 2006).

In order to undertake the external validation, the HS model generated for the Oka estuary was extrapolated to the Bidasoa estuary (Fig. 1). Eco-geographical variables were obtained from Borja et al. (2008) and Chust et al. (2009, 2010b), except the velocity of ebb tide variable that was not available. Species presence data was obtained from Silván and Campos (2002) and Garmendia et al. (2010). Thus, observed presence data were compared with the predicted HS map. In particular, two external validation tests were undertaken: (i) ENFA-based HS model taking into account all available eco-geographical variables from the Bidasoa estuary; and (ii) ENFA-based HS model with the variables which most explain *M* and *S* factors.

3. Results

Eleven eco-geographical variables were used to compute the ENFA (Table 1). The overall *M* was 1.00, whilst the overall *S* was 2.591, with a Tolerance of 0.386. These results indicate that *Zostera noltii* habitat differs considerably from the mean environmental

Fig. 2. (a) Distribution of the presence areas of *Zostera noltii* within the Oka estuary, with insets of the (b) Arketas and (c) Murueta locations.

conditions over the study area; likewise, that it is restrictive in the selection of the range of conditions within which it dwells.

Five factors were retained for the later HS map production, accounting for 90% of the explained variance. The first selected axis, or the *M* factor (which maximizes the absolute difference between global mean and the species mean), explained 34% of the variability. The other 4 selected factors (*S* factors) explained, respectively, 27%, 19%, 6% and 4% (Table 2).

The environmental variables that most determined the presence of *Zostera noltii* (variables with the highest *M* values), in order of

Table 2
Variance explained by the first five (out of 11) ecological factors, and coefficient values (in cursive) for the 11 used eco-geographical variables (EGV). EGVs are sorted by decreasing absolute value of coefficients on the Marginality factor. Positive values on this factor mean that the species prefers locations with higher values on the corresponding EGV than average location in the study area, and vice versa. Signs of coefficient have no meaning on the Specialisation factors. The amount of specialisation accounted for is given in parentheses. Key: Spec., Specialization factor; Mean, Mean grain size; Redox pot., Redox potential; Inter. height, Intertidal height; TPI_small, small-scale Topographical Position Index; % Org. matt., Percentage of organic matter content; V. ebb tide, Velocity of ebb tide.

Marginality (34%)	Spec. 1 (27%)	Spec. 2 (19%)	Spec. 3 (6%)	Spec. 4 (4%)
Mean *0.70*	Inter. height *0.91*	Rugosity *0.97*	Slope *0.59*	TPI_small *−0.61*
Redox pot. *−0.55*	Redox pot. *0.36*	Redox pot. *−0.16*	Rugosity *−0.48*	V. ebb tide 0.54
Inter. height *0.33*	% Gravel *0.13*	Slope *−0.11*	Redox pot. *−0.44*	% Org. matt. *0.38*
Sorting *0.24*	Mean *−0.09*	Inter. height *−0.10*	Mean *−0.30*	Slope −0.26
Slope *−0.14*	V. ebb tide *0.08*	TPI_small *0.04*	% Org. matt. *0.27*	Rugosity *0.21*
% Gravel *−0.12*	% Org. matt. *0.07*	Mean *−0.03*	% Gravel *−0.24*	Redox pot. *−0.17*
% Org. matt. *−0.07*	TPI_small *−0.07*	Orientation *−0.02*	V. ebb tide *−0.10*	Mean *−0.16*
Orientation *−0.06*	Sorting *−0.04*	% Org. matt. *0.01*	TPI_small *0.04*	% Gravel *−0.09*
V. ebb tide *−0.05*	Slope *0.04*	Sorting *−0.01*	Sorting *0.03*	Inter. height *0.09*
Rugosity *−0.05*	Rugosity *0.02*	% Gravel *0.00*	Orientation *0.03*	Sorting *−0.06*
TPI_small *−0.03*	Orientation *0.01*	V. ebb tide *0.00*	Inter. height *0.03*	Orientation *−0.05*

importance, were: mean grain size (0.70); redox potential (−0.55); intertidal height (0.33); sediment sorting (0.24); slope of intertidal flat (−0.14); percentage of gravel content (−0.12); and percentage of organic matter content (−0.07) (Table 2).

For an improved interpretation of the values of the environmental variables throughout the *M* factor, the distribution of the most significant variables, for those sites where *Zostera noltii* occurs and for the overall area, were compared (Table 3). Along the *M* factor (Table 2), the positive coefficient of the mean grain size variable indicates the preference of the species for higher values than the mean values of the study area; thus, as the units for the mean grain size are fixed on phi units, it means that the species presents tendency towards more fine-grained materials. In the Oka estuary, *Z. noltii* occurs at locations of fine sand (3.76 phi) (Table 3). In terms of redox potential, the mean value associated with *Zostera noltii's* presence is −6.07 mV; this is much lower than the mean value within the overall area (192.74 mV) (Table 3). The height range occupied by the species, ranges from 0.68 to 3.54 m (referred to the local datum (zero) level) (Fig. 3), with a mean value of 2.6 m; this is an higher mean value than the corresponding one for the study area (1.41 m) (Table 3). Regarding to the sediment sorting variable, the mean value at those sites where the species dwells is very close to the mean value for the overall area; both have values around 1.5 phi, which indicates high homogeneity of the grain size. The next variable which determines the presence of *Z. noltii* within the Oka estuary is the slope of intertidal flat. The species is present at those sites that ranged within 0.01 and 8.36° (with a mean of 1.31°) (Table 3). Thus, the species is developed over flat areas, or areas with a very low slope. The mean value of the percentage of gravel content for the species locations is 0.81% (Table 3), this supports the association of the species with finer sand sediments. Regarding to the percentage of organic matter content, the species is distributed in those areas with a lower percentage of organic matter content than in the study area (10.6 % versus 17.5%) (Table 3). The remaining variables influencing the species distribution show very similar values between the presence areas and the study area, except for the velocity of ebb tide. The species selects sheltered areas with a maximum tidal current velocity of 35 cm s^{-1}. The topographic characteristics were of remarkable importance in the explanation of the species Specialization. Hence, the intertidal height was the most important, which highlights the association of this species to a narrow range of terrain elevation, which is defined mainly by tidal submersion.

The cross-validation of the model quality resulted in a Boyce index of 0.92 ± 0.09; this is indicative of the predictive power of the model, with 'best-fit' for 4 equal-area bins. The habitat suitability map was reclassified, resulting in a map which ranged between 0 and 100 and was divided into 4 different intervals of suitability: from 0 to 25 (unsuitable); from 25 to 50 (scarcely suitable); from 50 to 75 (moderately suitable) and from 75 to 100 (highly suitable) (Fig. 4). The percentage of the occupied area for each interval was calculated resulting, respectively, for each HS interval: 74%; 10%; 9% and 7%.

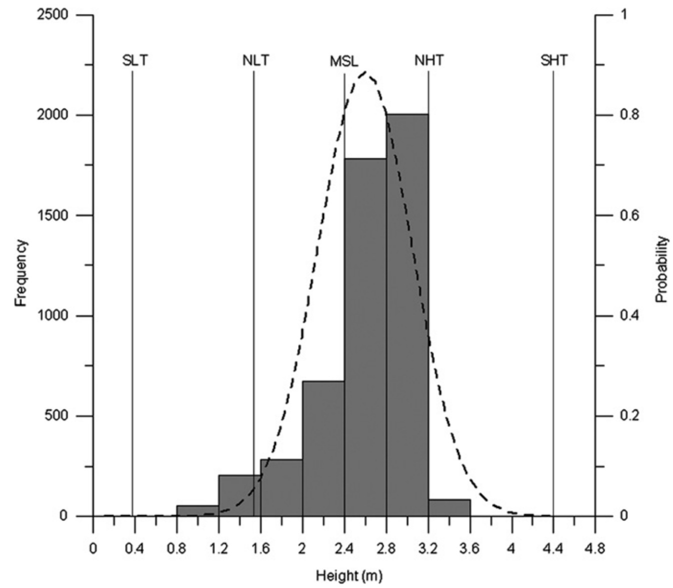

Fig. 3. Frequency histogram for the altitudinal distribution of *Zostera noltti*'s presence points within the Oka estuary. The dashed line shows the expected occurrence probability, assuming a Normal distribution based upon the mean and standard deviation value of the data. Key: SLT, observed mean Spring Low Tide; NLT, observed mean Neap Low Tide; MSL, Mean Sea Level; NHT, observed mean Neap High Tide; SHT, observed mean Spring High Tide. Note: Tidal parameters for the Bilbao I tide gauge (within the Nerbioi estuary, see Fig. 1) were obtained from REDMAR (2005).

For the external validation two new HS models for the Oka estuary were computed in order to extrapolate them to the Bidasoa estuary and perform the validation based upon the collected presence areas of the species. The first model based upon 10 eco-geographical variables (all except velocity of ebb tide) with an *M* value of 0.999 and *S* value of 2.650, presented a Boyce index of 0.92 ± 0.09. An extrapolation model was built based upon this HS model and it was applied to the Bidasoa estuary, resulting in a HS map which was divided into two probability intervals (from 0 to 50 and from 50 to 100) (Fig. 5a). Although the generated extrapolation model presented a high Boyce accuracy index, when it was applied to the Bidasoa estuary the HS map for this area shown 90% of

Table 3
Distribution of the values of the 11 eco-geographical variables used in the ENFA to produce the model of habitat suitability for *Zostera noltii* in the Oka estuary. For each variable, minimum, maximum, mean values and standard deviations (S.D.) were calculated, for the presence areas and the whole of the study area. Key: TPI_small, small-scale Topographical Position Index.

	Presence areas				Study area			
	Minimum	Maximum	Mean	S.D.	Minimum	Maximum	Mean	S.D.
Mean grain size (phi)	1.47	5.91	3.76	1.20	1.28	5.92	2.23	1.12
Redox potential (mV)	−185.37	331.24	−6.07	70.13	−188.14	548.92	192.74	185.85
Intertidal height (m)	0.68	3.54	2.60	0.45	−8.18	4.56	1.41	1.83
Sediment sorting (phi)	0.59	2.23	1.72	0.44	0.43	2.35	1.62	0.22
Slope of intertidal flat (°)	0.01	8.36	1.31	0.98	0.00	47.30	1.90	2.11
Gravel (%)	0.05	8.91	0.81	0.94	0.00	17.56	1.10	1.22
Organic matter (%)	1.11	10.60	4.25	1.28	0.99	17.46	4.43	1.34
Orientation	0.00	360.00	162.08	103.71	−1.00	360.00	175.63	109.09
Rugosity	1.00	1.04	1.00	0.00	1.00	1.78	1.00	0.01
Velocity of ebb tide (cm s^{-1})	0.00	35.81	13.12	8.77	0.00	101.34	14.33	12.78
TPI_small	0.00	1.00	0.11	0.31	−5.00	5.00	0.13	0.44

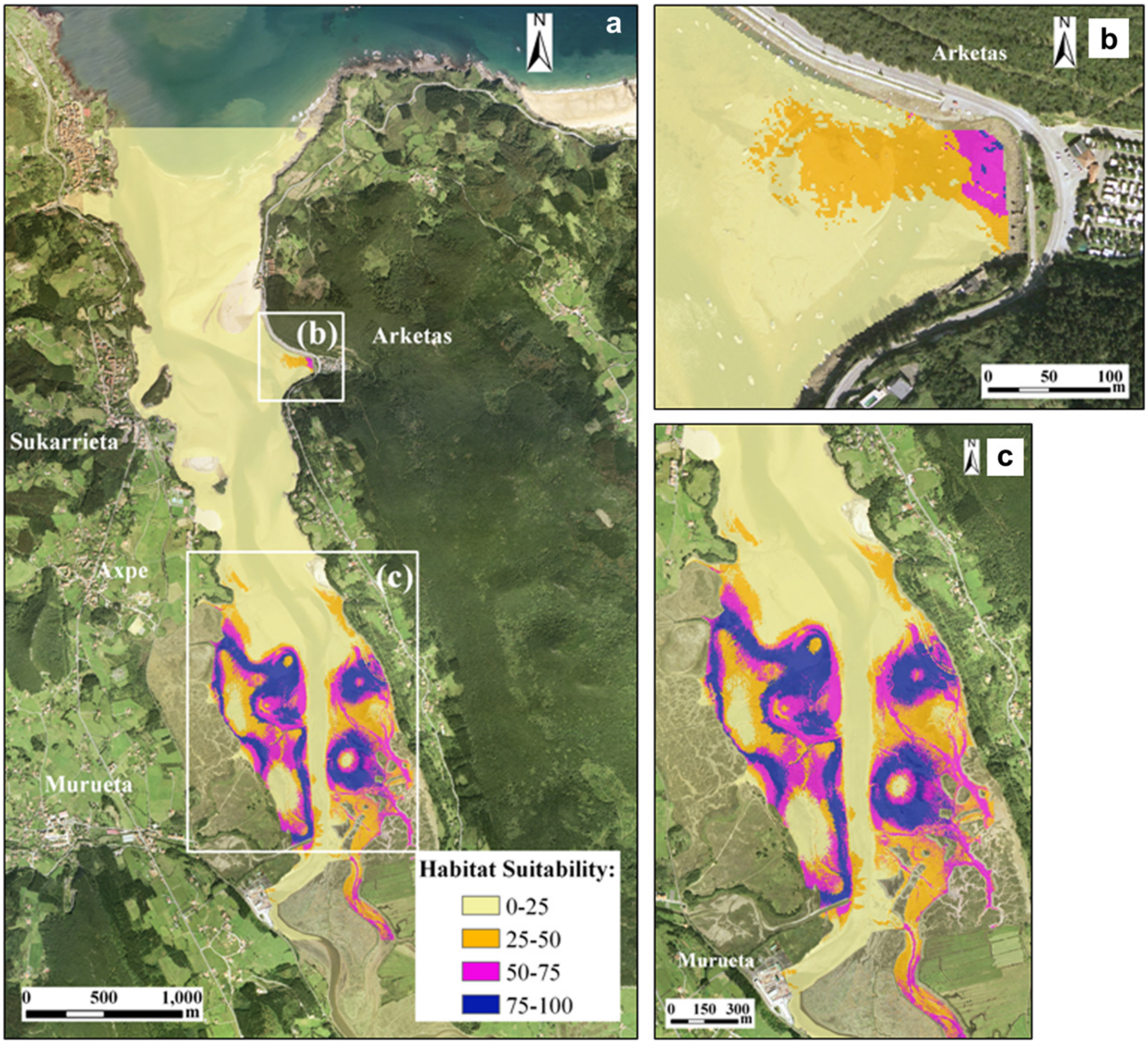

Fig. 4. (a) Habitat Suitability Map for *Zostera noltii* within the Oka estuary, with insets of the (b) Arketas and (c) Murueta locations.

no-value pixels. And when it was compared with the observed presence points, most of them were unclassified, whilst only 9% of them were predicted to be in the first interval.

The second model was undertaken using the 3 eco-geographical variables that most explain *M* and *S* factors (mean grain size, redox potential and intertidal height). This model, presented an *M* value of 0.945, a *S* value of 3.193 and a Boyce index of 0.85 ± 0.17. An extrapolation model was built, based upon this HS model, and it was applied to the Bidasoa estuary. The extrapolated HS map, was divided into the same two probability intervals (Fig. 5b) and, subsequently, it was compared to the observed species presence points. For this new HS map, the 70% of the species presence points was correctly classified.

4. Discussion

The results obtained from the ecological factors of the ENFA (Marginality: 1.00; Specialization: 2.59) indicate that the species habitat differs considerably from the mean environmental conditions over the study area; likewise, that the species is restrictive in the selection of the range of conditions within which it dwells.

Main environmental variables relating to the species distribution (Marginality factor), in order of importance were: mean grain size; redox potential; intertidal height; sediment sorting; slope of intertidal flat; percentage of gravels; percentage of organic matter content; and velocity of ebb tide. Thus, most suitable estuarine habitats for the species are: locations lying between areas with medium sand and medium silt type sediments, with negative redox potential, within the intertidal zone, with a lower organic matter content than in the whole study area and sheltered from high velocity currents. To a certain extent, some of these variables could, in turn, have been influenced by the seagrass itself through ecosystem engineering processes (e.g. Bos et al. 2007 and van Katwijk et al. 2010). However, from the results (i.e. low organic matter content) it seems that the extent to what *Zostera noltii* could contributed, in the study area, as an ecosystem engineer (trapping sediments and organic matter) is not very large. Nevertheless, for an improved understanding of the species ecosystem engineering capacity and to enhance the model applicability within other systems, further studies should be done removing sediment characteristics variables and comparing the results between models.

Although most previous HS studies have examined *Zostera marina* (van Katwijk et al., 2000; and Gilkerson, 2008), some of

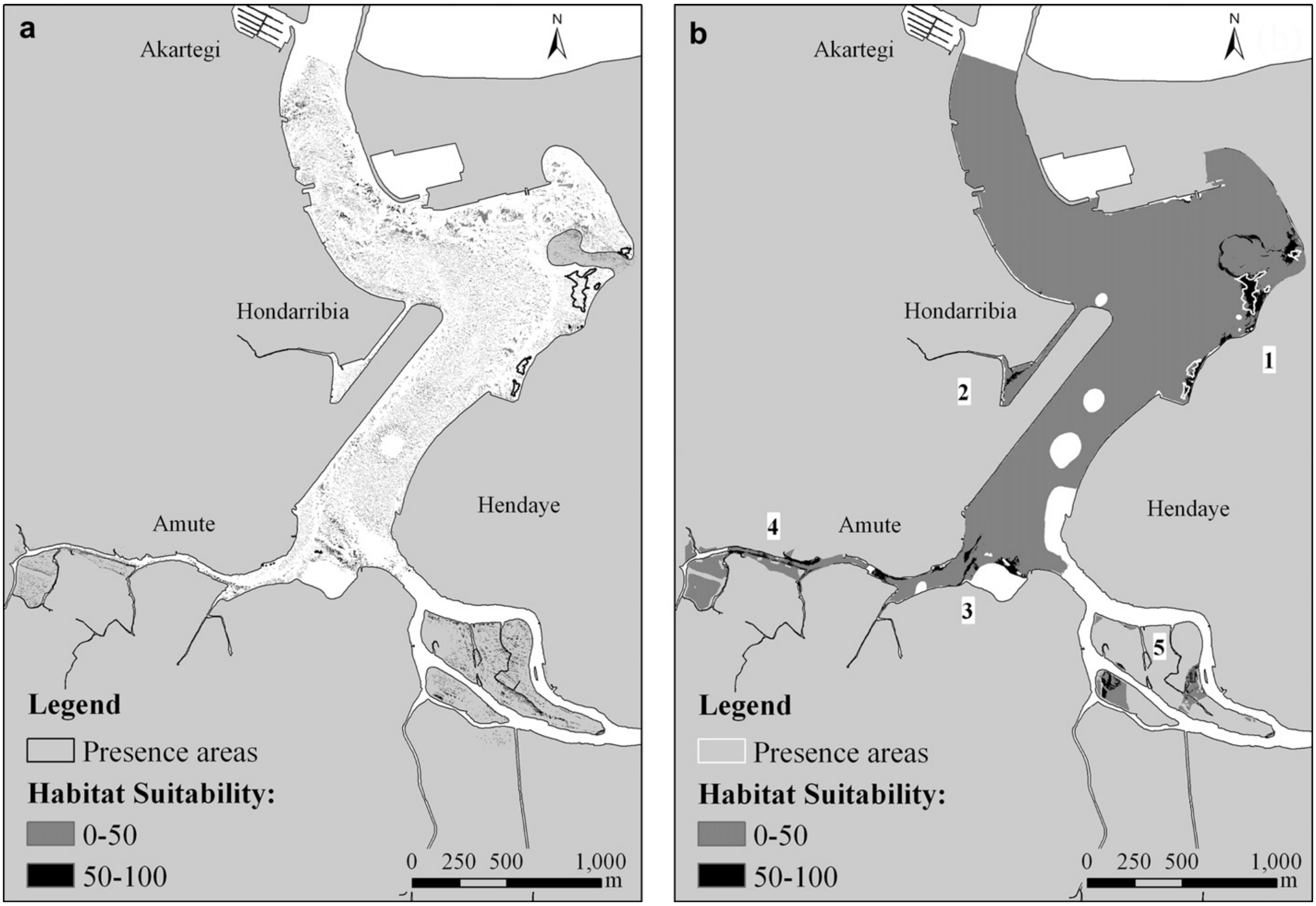

Fig. 5. Extrapolated Habitat Suitability Maps for the Bidasoa estuary, (a) based upon 10 eco-geographical variables (b) based upon 3 eco-geographical variables (for numbers in this figure, see the Discussion section).

them include also references to *Z. noltii* (Bos et al., 2005; and van der Heide et al., 2009). The last authors applied principal component analysis and (multivariate) logistic regression, to predict suitable habitat for *Zostera* spp.; they determined the importance of commonly-measured environmental variables in explaining the presence and absence of the species. Hence, the identified importance of redox potential and tidal location, for *Z. noltii* within the Oka estuary, was highlighted also by van der Heide et al. (2009), in northern Europe. Although the relationship which these authors found was the reverse, they identified low redox potential sites as less suitable. This might be because their measurements were sampled outside the seagrass bed, whereas in this research have been sampled both within and outside the seagrass beds. Measures outside beds bear the risk that the environmental conditions are different with respect to inside beds and could not be representative of the species requirements. Therefore, based upon the obtained results in accuracy of the model and in the external validation, the use of this kind of variables is thought to be appropriate, as long as the ecosystem engineering effect within the system is considered to be minor.

Topographic characteristics (e.g. intertidal height, slope of intertidal flat, rugosity, etc.) had a remarkable importance in the explanation of species Specialization, this indicates that the mean value of these variables is not so different from those of the general study area, although it is very confined to a narrow range around this mean. Those variables which have been detected as important by the model, are obtained using new habitat mapping tools, such as the bathymetric LiDAR; this provides an improvement in the habitat mapping reliability in complex landscapes such as estuaries (Chust et al., 2010a). According to the model developed, *Zostera noltii* is located within low rugosity areas, at an intertidal height range of between 0.638 and 3.543 m (referred to the local datum (zero) level); this indicates that the species settles on flat areas which are uncovered at daily low tides. The height value range for the different patches of the species at the Oka estuary, lies between the lower intertidal and the upper intertidal zone. Hence, there are some patches which are only dry during the lowest tides and others which experiences dry periods daily. Almost 75% of the species presence points are located between mean sea level and the observed mean neap high tide height value (Fig. 3). The present investigation confirms the importance of a sheltered location with limited tidal current velocities on the species distribution, which has been described previously by some authors (Conover, 1968; Fonseca and Kenworthy, 1987; Schanz and Asmus, 2003; and Peralta et al., 2006). The narrow range of tidal depth associated with *Zostera noltii* meadows, which is defined mainly by tidal submersion duration, together with the existence of railways, roads and natural fixed boundaries in the margins of the Oka estuary, suggest this seagrass to be vulnerable to the predicted sea-level rise in this region (Chust et al., 2010b) since migration landward, following the rise in sea level, can be limited.

The model has a high predicted accuracy, with a Boyce index of 0.92, for the internal validation, and good external validation results. The external validation tests, using an independent dataset in the Bidasoa estuary, revealed that extrapolating an ENFA-based HS model is a difficult task and should be undertaken with caution. Although it can accurately predict species presences within the same area used for generating the model, extrapolating the model to another site can be erroneous when this is based on a relatively high number of predictor variables. The results suggest that error amplification throughout model extrapolation could cause the loss of information when a large number of variables are used. Thus, the ENFA-based HS model extrapolation should be undertaken with the minimum number of variables as possible and with the confidence that those variables are highly accurate and intercalibrated. This finding is supported by the results obtained extrapolating the model based upon the 3 eco-geographical variables that most explain *M* and *S* factors (Fig. 5b). This model was able to detect 70% of the areas in which *Zostera noltii* is currently present within the Bidasoa estuary (see numbers 1 and 3 in Fig. 5b). The model also predicted some suitable areas that are presently unvegetated, but were vegetated in the past. For example the islands in the inner part of the estuary (number 5 in Fig. 5b) presented in 1991 some populations of *Zostera noltii*, as described by Lozano and Alagón (1995); these have not been detected in recent years (Garmendia et al., 2010) but could be due to the periodic discharges of waste water in the area, which produced also degradation in benthic communities (Borja et al., 2009b). A second example is the area numbered 2, although suitable for *Zostera noltii* (Fig. 5b), the species presence was not detected in the survey carried by Garmendia et al. (2010). This zone was dredged in 2008–2009, for boat anchoring. Thus, this alteration of the substratum in the whole area can be an explanation of the absence of *Zostera noltii*, since it is well known that sediment removal is one of the most important impacts on seagrasses (Erfteneijer and Robin Lewis, 2006). Finally, the area number 4 (Fig. 5b) was recently restored from habitat degradation, and is still recovering (Marquiegui and Aguirrezabalaga, 2009).

Seagrasses are highly relevant as a biological quality element, required for the assessment of the coastal and estuarine ecological quality status, in the European Water Framework Directive (Krause Jensen et al., 2005; Foden and Brazier, 2007; and Selig et al., 2007). These plants are regarded as a useful indicator of water quality due to their sensitivity to anthropogenic pressures. Hence, any management plan to restore *Zostera noltii* beds, after removing pressures causing its decline, would benefit from tools such as the HS modelling. As such, location selection has been considered the most important phase in restoration practices (van Katwijk et al., 2009, Golden et al., 2010; Leschen et al., 2010; Orth et al., 2010; and Tanner et al., 2010). Within this conservation context, results from the external validation (Fig. 5b) give an important insight for the application of the model in other estuaries with similar morphological and biogeographical characteristics in Europe. Therefore, extrapolation must be performed (i) based upon an HS model from an area which encompasses the environmental characteristics of the areas where the model is going to be extrapolated; (ii) the environmental data have to be collected in the same way for each area; and (iii) the number of environmental variables must be limited to the most explaining ones. Thus, ENFA-technique may be a promising tool for seagrass conservation and restoration programs worldwide, and also may be a suitable tool for monitoring and predicting changes under future scenarios, such as global sea-level rise on habitat loss (Chust et al., in press), which could affect seagrass restoration decisions. Future research should focus on establishing a generic way to perform an accurate selection of environmental variables and on comparing ENFA performance with other niche models.

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