

MINIREVIEW

ECOLOGICAL NICHE MODELS OF INVASIVE SEAWEEDS¹

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Ecological niche models (ENMs) are commonly used to calculate habitat suitability from species' occurrence and macroecological data. In invasive species biology, ENMs can be applied to anticipate whether invasive species are likely to establish in an area, to identify critical routes and arrival points, to build risk maps and to predict the extent of potential spread following an introduction. Most studies using ENMs focus on terrestrial organisms and applications in the marine realm are still relatively rare. Here, we review some common methods to build ENMs and their application in seaweed invasion biology. We summarize methods and concepts involved in the development of niche models, show examples of how they have been applied in studies on algae and discuss the application of ENMs in invasive algae research and to predict effects of climate change on seaweed distributions.

Key index words: introduced species; invasive algae; niche; niche modeling; species distribution

Abbreviations: AUC, area under the receiver operating characteristic curve; BRT, boosted regression trees; ENMs, ecological niche models; GAM, generalized additive model; GARP, genetic algorithm for rule-set prediction; GIS, geographic information system; GLM, generalized linear models; MaxEnt, maximum entropy; PAR, photosynthetically active radiation; SDMs, species distribution models; SST, sea surface temperature

The distribution of seaweed species is strongly affected by environmental factors at global (e.g., Adey and Steneck 2001, Müller et al. 2009), regional (e.g., Schils and Wilson 2006) and local scales (e.g., Bulleri et al. 2011), offering great potential to predict seaweed distributions based on environmental variables. Predictive modeling would be especially desirable for introduced and invasive seaweeds because they are more likely to establish and persist in regions that are similar to their native environment, which can be predicted with these models. As

such, niche models can help identify areas with suitable habitat outside the native range, assess whether introductions are likely to be successful, anticipate critical routes and arrival points, and predict the extent of potential spread following an introduction. The models can thus inform decisions about preventive and control actions, and can cut management costs by optimizing surveying effort according to the predicted habitat suitability for the species being monitored.

Generally speaking, three factors are known to affect species distributions: abiotic conditions (A), biotic factors (B) and movement (M) – composing what is known as the “BAM diagram” (Fig. 1; Soberón and Peterson 2005, Peterson et al. 2011). Temperature can be considered the principal abiotic condition shaping the geographic boundaries of seaweeds (Lüning et al. 1990, Eggert 2012). Two aspects play a central role: temperature-dependent effects on performance (e.g., photosynthesis, growth, reproduction) and temperature tolerance, i.e., survival limits (Eggert 2012). The role of other abiotic factors is more evident at smaller geographic scales, where seaweeds' niches are defined by bathymetry, substrate type, available light, etc. Among the biotic factors, competition and grazing are the main factors shaping the distribution and abundance of seaweeds, especially at the community scale (see Edwards and Connell 2012). Movement refers to the area that is accessible for the species on an ecological timescale. This area could be limited, for example by biogeographical barriers or a lag in postglacial recolonization, and is mainly determined by the seaweed's dispersal strategies (Arrontes 2005). The intersection of these three factors defines the native geographic distribution of the species (Soberón and Peterson 2005).

Ecological niche models (ENMs) – and the related species distribution models (SDMs) or habitat suitability models – are based on the relationships between abiotic habitat features and species' occurrence. They characterize the aspects of the niche that determine the species' distribution to produce habitat suitability maps. Some authors make a distinction between ENMs and SDMs based on the purpose and methodology used (e.g., Peterson et al. 2011) while others suggest that the use of

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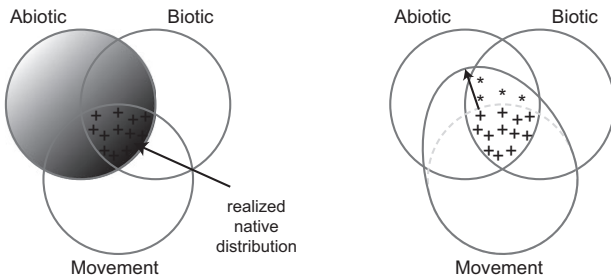


FIG. 1. Representation of the species niche as the BAM Venn diagram, with B representing biotic interactions, A representing abiotic factors (habitat suitability), and M representing movement. The species only occurs where all three conditions are met, hence the realized distribution corresponds to the intersection of the BAM diagram. When a species is introduced outside its native range, the movement ellipse is modified, resulting in an expanded realized niche (right hand side). Inspired by figures from Soberón and Peterson (2005) and Rödder and Lötters (2009).

the more neutral term SDM would be preferable (e.g., Elith and Leathwick 2009, McInerny and Etienne 2012a), but in practice these terms are commonly used interchangeably. Here, the term ENM is used to refer to all correlative distribution models, as all these methods estimate a subset of the conditions within which a species can survive and reproduce (i.e., the niche; Warren 2012).

Which facets of the species' niche are going to be modeled is an essential question without a straightforward answer, as the "niche" concept itself is still under discussion (Chase and Leibold 2003, Araújo and Guisan 2006, Godsoe 2010, McInerny and Etienne 2012b). Joseph Grinnell was the first to describe a species' ecological niche in terms of habitat and climatic requirements, a concept now known as the Grinnellian niche (Grinnell 1917). For Charles Elton, niche would rather be the ecological and functional role of a species in a community (Elton 1927). Hutchinson considered the niche as the set of biotic and abiotic conditions under which a species is able to persist and maintain population sizes (Hutchinson 1957). Further distinction is made between the fundamental niche, i.e., the set of all environmental conditions under which a species can reproduce and survive, and the realized niche, i.e., the subset of the fundamental niche actually occupied by the species, which is often constrained by biological interactions and dispersal limitation. The foundations of ENMs are rooted in Grinnell's and Hutchinson's ideas, but there are conflicting views on what models truly characterize (Araújo and Guisan 2006, Kearney 2006, Soberón 2007, Jimenez-Valverde et al. 2008). What correlative models estimate is a portion of the species' fundamental niche, encompassing an area between the realized species distribution and the abiotic niche (A) of the BAM diagram (Fig. 1, represented by a gradient). How much of the shaded region is cov-

ered by the ENM depends on methodological and species-specific factors (Jimenez-Valverde et al. 2008, Peterson et al. 2011).

As mentioned above, ENMs rely on a statistical relationship between the species occurrence (and sometimes its absence) and macroecological variables (i.e., geographic information system [GIS] maps of climatic, physical and other environmental factors) to infer the environmental conditions that the species typically favors (Fig. 2). Therefore, ENMs are correlative approaches and describe patterns, not mechanisms of species distribution. Mechanistic (or process-based) distribution models, on the other hand, are based on direct measurements of species' ecophysiological responses to environmental conditions. The geographic areas where the species would be able to live can then be mapped by applying the model to geographically explicit data sets of the relevant macroecological variables (Kearney and Porter 2009). Mechanistic models are also often applied to address questions focusing on demographic processes at the community or local scales (e.g., dispersal, growth). While mechanistic models may lead to predictions more closely approximating the fundamental niche, the correlative approach has practical advantages because the required data are much easier to obtain. This review focuses on correlative ENMs, but we also mention some mechanistic studies that have contributed to our knowledge about the ecological niche of invasive seaweeds.

ENMs have received much attention in the last decade. Many studies applying ENMs, however, are restricted to terrestrial habitats and applications in the marine realm are still rare in comparison (Robinson et al. 2011). This review covers the main ENM techniques that can be applied to study seaweed invasions. We outline the concepts and methods needed to build basic niche models, show examples of how correlative and mechanistic models have been applied to study the niche of seaweeds and discuss the possibilities for further research using ENMs.

BUILDING NICHE MODELS

The modeling process can be divided into 3 main steps (Fig. 2): (i) assemble and process the input data (i.e., occurrence records and predictor data sets); (ii) build the model using one of the available algorithms (e.g., generalized linear model [GLM], maximum entropy [MaxEnt]) then evaluate it; and (iii) map the prediction into the geographic space.

GIS data sets. GIS play a central role in storing, mapping and manipulating spatial data for a wide range of goals. They have been used to characterize seaweed populations from satellite or aerial imagery (De Oliveira et al. 2006, Theriault et al. 2006) but also play a central role in storing the data needed to build correlative niche models. ENMs rely on GIS

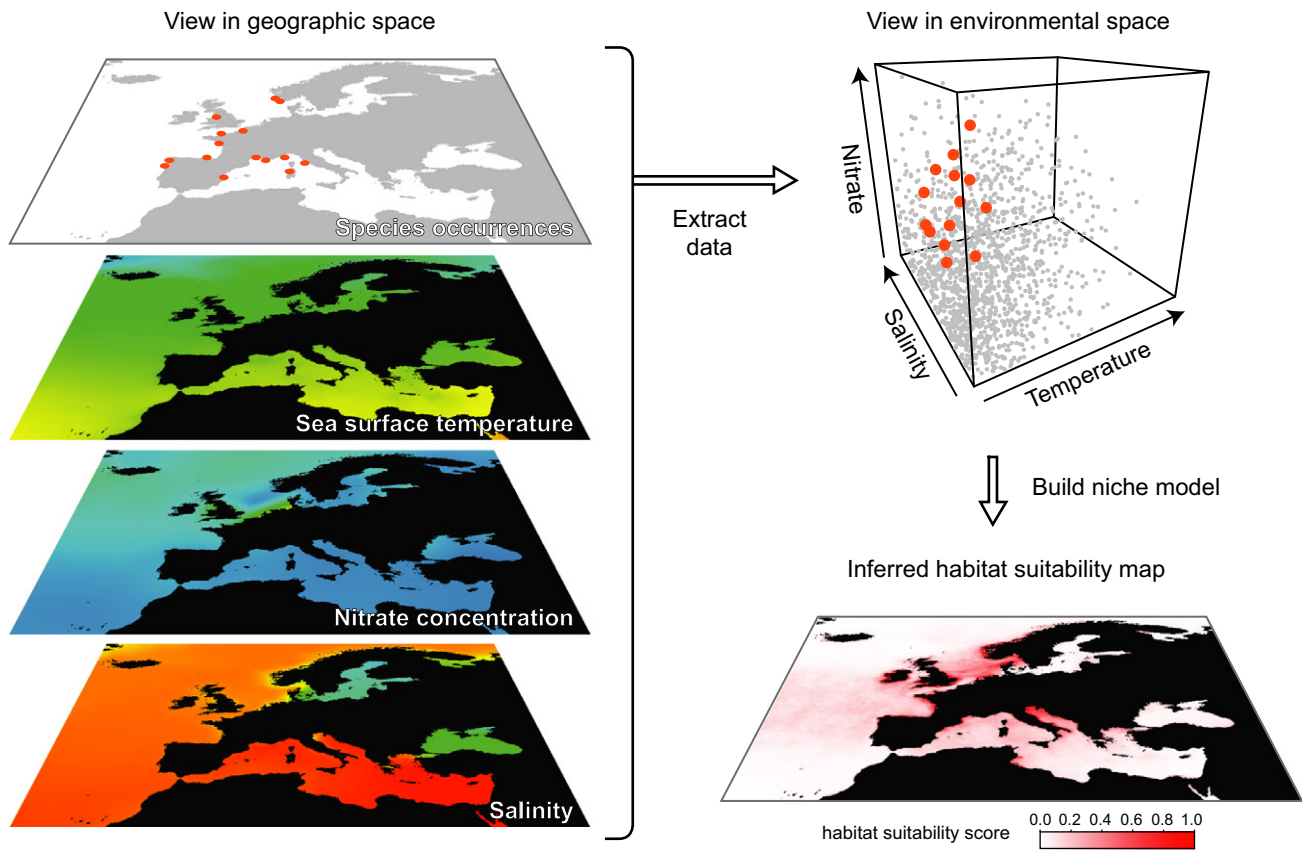


FIG. 2. Schematic overview of the process of ecological niche modeling. The environmental conditions where species occur are extracted from GIS environmental data sets using the geographic coordinates of species occurrences. Based on the information about the species' environmental preferences, a model is then optimized. The model and the environmental maps can subsequently be used to predict the habitat suitability of every location on the map. Inspired by a figure from Elith and Leathwick (2009).

data sets describing the environment, for example, maps of sea surface temperature (SST) and nutrient concentrations, which serve as predictor variables in the model (Fig. 2). The data sets are typically raster layers, meaning that they are composed of a geographic grid of square pixels in which each pixel represents the value of the variable at that geographic location (Pauly and De Clerck 2010). The size of the pixels defines the spatial resolution of the raster (also called grain size), and typically ranges from a few meters to >100 km depending on the data source.

The spatial scale in ENMs includes both the spatial resolution of the raster and its extent (i.e., the covered area; Guisan and Thuiller 2005). The spatial scale affects the results obtained with ENMs and is an important choice that has to be made depending on the purpose of the study and data availability (Elith and Leathwick 2009, Pauly et al. 2011b). Studies aiming to understand microhabitat and ecological variables that vary over small geographic distances (e.g., substrate or wave exposure) should use rasters that are fine enough to reflect these properties (e.g., Martínez and Viejo 2012). Models using coarser resolution data and continental to global

extents are more appropriate to study the potential distribution of a species as determined by macroecological niche dimensions and to predict worldwide distributional shifts in response to global climate change (Verbruggen et al. 2009). A comparative study of seaweed ENMs with variables at finer (100 m) and coarser (9 km) scales indicates that models at both scales perform well for homogeneous habitats, but that a coarse scale can lead to overprediction in spatially heterogeneous areas (Pauly et al. 2011b). Further information about the importance of spatial scale in niche models can be found in the literature (e.g., Elith and Leathwick 2009, Austin and Van Niel 2011 and references therein). Far less documented is the extra complexity added to ENMs of seaweeds due to their ecological peculiarities. Seaweeds generally grow along a fairly narrow coastal area, where the determinants of their distribution, like depth, temperature and nutrients, can vary substantially at very small geographic scales. This is particularly important for studies aiming to characterize introduction hotspots, as many alien marine species arrive and proliferate in human-modified areas like harbors, where the environmental conditions are substantially different

from the surrounding areas. The benefits versus drawbacks of high and low resolution imagery in such applications has to be evaluated. Another shortcoming for marine ENMs is the scarce availability of environmental data along a vertical dimension. The majority of the available data refer to values at the surface of the ocean. While this information suffices to depict macroecological patterns of shallow-water seaweeds (Tyberghein et al. 2012), it may fail to represent the niche of deep-water species if no information about environmental variations along the vertical profile is provided.

Environmental rasters are commonly derived from satellite imagery (e.g., SST) or interpolated in situ measurements (e.g., nutrients). NASA (<http://oceancolor.gsfc.nasa.gov/>), NOAA (<http://www.nodc.noaa.gov/>) and several other agencies provide remotely sensed environmental data. The rasters are usually provided in different file formats and spatial resolutions, making the assembly of a uniform data set a cumbersome task. To improve that situation, a number of projects have compiled data from diverse sources and provide them as rasters with a homogeneous resolution and format (Table 1). AquaMaps, for example, is a tool for generating occurrence predictions based on their environmental preferences (Kesner-Reyes et al. 2012). Bio-ORACLE was designed with global-scale niche modeling of shallow-water organisms in mind (<http://www.bio-oracle.ugent.be/>) and has been used to model the distribution of seaweeds (Tyberghein et al. 2012, Verbruggen et al. 2013). MARSPEC is a high-resolution data set also designed for niche model implementation (Sbrocco and Barber 2013). Although it does not include nutrients/energy proxies, it incorporates a series of fine-scale bathymetry rasters, which could prove informative for seaweeds ENMs, especially in heterogeneous habitats. When modeling coastal species, it is also possible to combine the use of oceanographic and terrestrial variables. For example, Waltari and Hickerson (2013) built ENMs with marine predictors (MARSPEC) and terrestrial rasters (WorldClim) to distinguish between Pleistocene persistence versus recolonization in North Atlantic coastal invertebrates.

Species occurrence data. Occurrence records consist of georeferenced localities (latitude/longitude) where the species has been found. Localities where the species does not occur, called absence records, can also be incorporated into models. When reliable absence records can be obtained, which is usually not the case (Loiselle et al. 2003), it is recommended to use them to improve predictions of species distributions (Brotons et al. 2004, Royle et al. 2012). An alternative to absences derived from field surveys is to randomly select localities where the species has not been found, the so-called pseudo-absence data (Peterson et al. 2011). Absence and pseudo-absence records should only include environmentally unfavor-

TABLE 1. Comparison between freely available marine environmental data sets (adapted from Tyberghein et al. 2012).

	WOD 2009 ¹	OceanColor ²	Hexacoral ³	AquaMaps ⁴	Halpern ⁵	Bio-ORACLE ⁶	MARSPEC ⁷
Resolution	30–60 arcmin (~55–110 km)	2.5–5 arcmin (~4–9Km)	30 arcmin (~55 km)	30 arcmin (~55 km)	0.5 arcmin (~1Km)	5 arcmin (~9Km)	0.5–10 arcmin (~1–20 km)
Uniform landmask ⁸	Yes	No	Yes	No	No	Yes	Yes
Data set suitable for fine-scale coastal studies	No	Yes	No	No	Yes	Yes	Yes
Multiple depth levels ⁹	Yes	No	Yes	Yes	No	No	Yes
Uniform file format	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Equal-area grids available	No	No	No	No	Yes	Yes	Yes
Nutrients/energy proxies ¹⁰	Yes	Yes	Yes	Yes	Yes	Yes	No

¹WOD2009 (Boyer et al. 2009).

²OceanColor (Feldman and McClain 2010).

³Biogeoinformatics of the Hexacorals (Fautin and Buddemeier 2008).

⁴AquaMaps (Kesner-Reyes et al. 2012).

⁵Global Mapping of Human Impacts to Marine Ecosystems (Halpern et al. 2008).

⁶Bio-ORACLE (Tyberghein et al. 2012).

⁷MARSPEC (Sbrocco and Barber 2013).

⁸Uniformity of landmask across all data layers in the package.

⁹Layers provided at different subsurface depths.

¹⁰ASCII raster grid format. Photosynthetically available radiation, nitrate, phosphate, chl, diffuse attenuation, solar radiation, particles (e.g., POC) and other variables that can be related to energy or nutrients supply.

can be related to energy or nutrients supply.

able localities when the goal is to detect the species potential (rather than actual) distribution (Jimenez-Valverde et al. 2008). In practice, however, it is difficult to determine whether absences result from inadequate surveying, seasonality, from other factors other than environmental ones influencing the species distribution (e.g., non-equilibrium, dispersion limitations), or because the habitat is in fact unfavorable. While using absence/pseudo-absence data extracted from regions further away from the species realized distribution (intersection of the BAM diagram in Fig. 1) yield model predictions nearer the species fundamental niche, it also undesirably increases overprediction (Chefaoui and Lobo 2008, Jimenez-Valverde et al. 2008). Recently, new methods have been proposed to help obtaining balanced pseudo-absence information for invasive species niche models (Senay et al. 2013).

ENMs designed for invasive species are frequently based on presence-only data. Species occurrence information is often gathered from field observations, publications, herbarium collections, or public databases like the Ocean Biogeographic Information System (<http://www.iobis.org/>) and the Marine Mediterranean Invasive Alien Species Database (<http://www.mamias.org/index.php>). Samples lodged in herbaria can usually be easily georeferenced, either automatically with marine gazetteers (e.g., VLIMAR) or manually with tools such as Google Earth (Verbruggen et al. 2009, Pauly et al. 2011a), provided of course that the sampling locality is specified in enough detail on the herbarium sheet.

Even though occurrence data are becoming ubiquitous, their quality is often hard to assess and has to be checked in several ways (Vandepitte et al. 2015). The first concern is the uncertainty of the occurrence records (Graham et al. 2007a). The accuracy of the occurrence coordinates should be consistent with the spatial resolution of the layers, and imprecise records should be excluded from the model. The localities also ought to be double-checked. A common error is to attribute an erroneous positive or negative sign to a coordinate, resulting in locations on the wrong hemisphere (Pauly and De Clerck 2010). Visualizing the records is a useful strategy, but we also recommend other screening methods such as verifying whether the records fall within the maritime boundaries of the country they are listed under. An additional point, which is likely to be particularly problematic for seaweeds, is misidentification (Lozier et al. 2009). Macroalgae are often misidentified in collections and high levels of cryptic diversity add to the uncertainty surrounding identifications. Records based on superficial morphological identification are therefore inappropriate in many cases. Taxonomic issues are problematic especially when harvesting information from public biodiversity data sets, since those identifications are difficult or impossible to check.

ENM algorithms. The mathematical function or, more broadly, the methodology applied to estimate the species' niche as a function of the predictor variables is referred to as the modeling algorithm (Peterson et al. 2011). Many algorithms have been used for ENM applications, and we refer to the literature for a more in-depth overview of what is available (reviewed by, e.g., Franklin and Miller 2009, Peterson et al. 2011). The algorithms differ mainly on their mathematical principles and on the type of input data (e.g., presence-only, presence-absence, presence-background data). Many conventional algorithms are regression-based, like Generalized linear models (GLMs), Generalized additive models (GAMs), Multivariate adaptive regression splines and boosted regression trees (BRT). These models are suitable when presence and absence records are available. Algorithms that do not require absence data include envelope methods (BIOCLIM, Busby 1991), support vector machines (Drake et al. 2006) and MaxEnt models (Phillips et al. 2006). When absence data are not available, some algorithms (e.g., MaxEnt, GARP, Stockwell 1999) can incorporate into the model (random or target) background or pseudo-absence records (Phillips et al. 2009).

Building reliable ENMs. Many choices need to be made in the process of building niche models, and these can have a profound impact on the resulting model. Hence, in order to make models with good predictive power, a number of precautions need to be taken. A first consideration is to avoid confounding factors. Modeling algorithms implicitly assume that the input data are independent, but typically they are not. There are two common types of spurious correlations in ENMs: geographic bias in the occurrence (and background) records leading to spatial autocorrelation (Segurado et al. 2006) and multicollinearity among predictor variables (Graham 2003).

Geographic biases in occurrence records usually originate from the fact that some areas are more likely to be sampled than others. For example, locations near population centers are more likely to be sampled than remote areas. This geographically skewed representation also leads to environmental biases for the presence records, which can lead to model misspecification (Segurado et al. 2006, Phillips et al. 2009, Wolmarans et al. 2010, Verbruggen et al. 2013). The effects of sample bias can be mitigated by using similarly biased background data (Phillips et al. 2009, Elith et al. 2011) or density-based occurrence thinning (Hijmans 2012, Verbruggen et al. 2013, Aiello-Lammens et al. 2015). For presence-only models, biases in the background data also have strong effects on model performance (Acevedo et al. 2012). Generally speaking, background points are picked at random from the entire study area, so the extent of the study area essentially determines the background data. If the study area does not fully represent the species' geographic

range, the importance of factors operating at large scales (e.g., climate) may be underestimated (Barve et al. 2011). On the other hand, if the study area is overly large, the algorithm may fail to characterize smaller scale niche features (Lobo et al. 2010). Furthermore, excessively large backgrounds inflate model evaluation scores (e.g., area under the curve [AUC]) while adding no information to the model (Acevedo et al. 2012). It has been argued that the most suitable background is one that includes “the parts of the world that have been accessible to the species via dispersal over relevant periods of time” (Barve et al. 2011). Model realism for seaweeds could be enhanced, among other options, by restricting background points to coastal pixels (Pauly et al. 2011a), to areas where other seaweeds have been found (Phillips et al. 2009), or through trend surface analysis (Acevedo et al. 2012).

Multicollinearity among several environmental predictors is expected: mean SST, for example, correlates with maximum and minimum SST, and diffuse attenuation can be correlated with chl *a*. These relationships can lead the model to produce erroneous response curves to variables that do not reflect the species physiological tolerances. Predictors that have no ecophysiological significance for the species can also be correlated with occurrence records simply because predictor variables vary geographically and species have limited distribution ranges. This results in models based on correlations that do not reflect the species’ niche. This sort of correlation is usually dealt with by selecting a suitable subset of predictor variables. Many studies have addressed the consequences of the choice of these variables (Röder et al. 2009, Austin and Van Niel 2011, Verbruggen et al. 2013). Furthermore, only a subset of the available predictor variables is generally relevant for any given species and context. Prior knowledge of the species’ physiological requirements can be used to pre-select potentially relevant variables (e.g., Araújo and Luoto 2007, Elith et al. 2010, Verbruggen et al. 2013). Multicollinearity among predictors can also be reduced by building models on the main axes resulting from principal component analysis (Pauly et al. 2011a), eliminating closely correlated variables based on Pearson correlations (Elith et al. 2010), selecting a subset of variables that yields strong predictions (i.e., with higher AUC values; Verbruggen et al. 2013), or a combination of these. Studying the response curves inferred by the model for each predictor also hints to whether it behaves in a biologically meaningful way in the model.

Besides avoiding spatial biases in the input data, it is also important to use a model that is sufficiently complex to capture the major environmental influences on the species’ distribution but that does not overfit the data. Overfitting occurs when models have too many parameters in relation to observations (i.e., occurrence records), therefore, reducing

complexity to fit smoother response curves is recommended (Rodda et al. 2011, Warren and Seifert 2011). A general rule of thumb for regression models is that you need at least 10 samples for every parameter in the model (Burnham and Anderson 2002). The commonly used program MaxEnt automatically activates/deactivates features depending on how many samples are available, and it can be further adjusted using the regularization settings (Phillips et al. 2008, Warren and Seifert 2011). High evaluation scores for test data (e.g., AUC_{test}) have been used to indicate adequate model performance rather than overfitting, but these are sensitive to the background as mentioned above. Several other procedures, including information criterion-based approaches (e.g., Akaike’s information criterion) are also available to select models with an appropriate complexity (Burnham and Anderson 2002, Hastie et al. 2009, Warren and Seifert 2011).

Afterwards, the model needs to be evaluated. The goal of model evaluation is to justify the acceptance of a model for its intended purpose (Araújo and Guisan 2006). The evaluation methodology is intensively debated in literature (e.g., Anderson et al. 2003, Peterson et al. 2008, Hijmans 2012), and there is probably no single best approach. A common evaluation process is to check whether the model is able to predict independent occurrence data. Usually, the original occurrence data are subdivided into training and test data sets, the former being used to infer the model and the latter to verify whether or not the resulting model predicts high habitat suitability for test localities where the species is known to occur (or low suitability in case absences are available). Because the species presence (or sometimes absence) at the test localities is known with some degree of certainty, this approach can be used to quantitatively measure the model’s performance. The most common metric used to evaluate ENMs is the AUC of the receiver operating characteristic (Pearce and Ferrier 2000). AUC values range from 0 to 1 and models yielding scores for the test data set (AUC_{test}) above 0.5 can be interpreted as better than random predictions. The training and test data are usually obtained by randomly splitting the available occurrence records in two groups (commonly 70%–30% or 50%–50% training and test records). The occurrences can also be divided into training and test data multiple times independently, and the evaluation can proceed through bootstrap, jackknifing or *k*-fold cross-validation (Peterson et al. 2011, Hijmans 2012). As usual, care must be taken to avoid spatial biases when splitting the occurrence data into training and test data sets. In the case of invasive species, a common practice is to calibrate the model with (training) occurrences from the native range and evaluating it according to its ability to predict (test) records of the species in the invaded area (e.g., Richardson and Thuiller 2007). This approach, however, may

reduce the overall predictive power of the model due to the likely expansion of the realized Grinnellian niche after transportation (Fig. 1). This issue was tested for the invasive *Caulerpa racemosa* and the best performing model was found to be the one trained and evaluated using distribution records from both native and invaded areas (Verbruggen et al. 2013). Despite the perils of training models in regions that are likely violating the equilibrium assumption (specially in cases of recent introduction), the invaded area provides valuable information about the species tolerance to climatic conditions that may not be present in the native range. Therefore, reducing sampling bias with one of the methods cited above followed by random assignment of all occurrence records to training and test sets tends to yield better models (Broennimann and Guisan 2008, Jimenez-Valverde et al. 2011). It is useful to note that the use of AUC has been criticized for being sensitive to all kinds of choices made in the modeling process (Lobo et al. 2008, Jiménez-Valverde 2012), but to our knowledge no good alternatives have been proposed. Clearly, field-testing the model's predictiveness is to be preferred because this is truly independent test data (e.g., [Graham et al. 2007b](#)), but this is not always feasible.

Finally, it is important to note that the modeling process is not carried out in a linear way. Instead it is an iterative process in which changes are being made to the model setup and analysis settings, followed by optimization and evaluation of the model until a reliable result is obtained.

Issues for introduced species. Besides these general recommendations for building reliable ENMs, there are a few particularities that have to be taken into consideration for introduced species.

First, a central assumption of ENM that is likely to be violated for introduced species is that the species being modeled is in equilibrium with its environment, in other words its occurrence in the study region is determined by the environment and not other factors. Naturally, the distributions of introduced species are highly constrained by colonization time lags and dispersion limitations (Vaclavik and Meentemeyer 2012). In early stages of invasion, models are more likely to underpredict the potential distribution when they are calibrated with occurrence records from the invaded area (Vaclavik and Meentemeyer 2012). Seaweeds tend to thrive in disturbed habitats like harbors, but their expansion into natural habitats may be slower. Thus, the stage of invasion and the absence of equilibrium of the species in its new environment should be taken into consideration when defining training and test data sets and when evaluating the outputs of ENMs ([Elith et al. 2010](#), [Jimenez-Valverde et al. 2011](#)).

Second, the predictions made from ENMs assume that the species retains its niche (Peterson et al. 1999, Wiens and Graham 2005). Niche conservatism

has a very central position in invasion biology applications because one assumes that a species is only able to invade areas with similar ecological conditions to that found in their native range (Peterson 2003). That a species' niche can shift after invasion was clearly demonstrated for an invasive weed (*Centaurea maculosa*), for which the authors observed a mismatch between the predicted potential distribution of native and invasive ranges (Broennimann et al. 2007). Subsequently, shifts have been found for many invasive species, including the cane toad (Tingley et al. 2014), fire ant (Fitzpatrick et al. 2007), tiger mosquito ([Medley 2010](#)), earth mite ([Hill et al. 2012](#)) and several plant species (Alexander and Edwards 2010). The seaweed *C. taxifolia*, which lives at different depths in its native and invaded areas (Klein and Verlaque 2008, Katsanevakis et al. 2010b), could be a niche-shifter at micro-habitat scales.

An obvious question when observing such niche shifts is whether they are situated at the level of the fundamental niche or are simply a matter of changes in the realized niche. Modification of the fundamental niche is certainly possible in introduced species, as rapid evolution in several traits has been observed in introduced populations (e.g., Gordon et al. 2009, Phillips 2009, see Whitney and Gabler 2008 for a review). Shifts in the realized niche, however, are probably more common and often constitute the most parsimonious explanation for observed niche shifts, simply because expansion of the movement ellipse is expected to correspond to an expansion of the realized niche (Fig. 1). These two scenarios are not mutually exclusive and both may contribute to the observed niche shifts. Interestingly, in several cases where niche shift was observed, the models were able to correctly predict the locations of introduction (Broennimann et al. 2007, Fitzpatrick et al. 2007, Medley 2010), suggesting that, even for niche-shifting species, modeling tools can be useful to predict areas at risk.

Solutions to issues typical of introduced species are not straightforward, but a few general recommendations have been made (Jimenez-Valverde et al. 2011). One commonly used option is to use occurrence records from both the native and invaded regions simultaneously to build the ENM. This has the advantage of using records that are likely to be in equilibrium with the environment in the native range while also including samples from the invaded range that may provide information about expansions of the realized niche. When feasible, combining mechanistic and correlative methods can help to discriminate realized versus fundamental niche shifts in invaded regions (e.g., Tingley et al. 2014). Other recommendations include using only predictors that are linked directly to the physiological requirements of the species and careful evaluate the model to avoid overfitting (Jimenez-Valverde et al. 2011).

TABLE 2. Studies applying niche models to investigate algal niche features or distributions.

Reference	Organism	Invasive	Modeling algorithm	Scope
Assis et al. 2014,	<i>Fucus vesiculosus</i>	No	Correlative: MaxEnt, BRT, MARS	North Atlantic
Báez et al. 2010,	<i>Undaria pinnatifida</i>	Yes	Correlative: LBR	N Spain
Bulleri et al. 2011,	<i>Caulerpa cylindracea</i>	Yes	Correlative: Mixed GLM	NW Mediterranean
Burfeind et al. 2013,	<i>Caulerpa taxifolia</i>	Yes	Mechanistic	Australia
Crockett and Keough 2014,	<i>Caulerpa longifolia</i> ,	No	Correlative: BRT	Port Phillip Bay, Australia
Gardon et al. 2008,	<i>C. remotifolia</i> , <i>C. sedoides</i>	Yes	Correlative: MLRM	Florida, USA
Gorman et al. 2012,	<i>Caulerpa</i>	No	Correlative: GAM	Bay of Morlaix, France
Graham et al. 2007b,	<i>unitalicize</i>	No	Mechanistic	Global
Graham et al. 2010,	<i>Macrocystis pyrifera</i>	No	Mechanistic	California, USA
Hall and Cox 1995,	<i>Hydrodictyon reticulatum</i>	Yes	Correlative: GLM	New Zealand
Jueterbock et al. 2013,	<i>Ascophyllum nodosum</i> ,	No	Correlative: MaxEnt	North Atlantic
	<i>Fucus serratus</i> , <i>F. vesiculosus</i>			
Katsanevakis et al. 2010a,	<i>Caulerpa cylindracea</i>	Yes	Correlative: GAMLSS	Zakynthos, Greece
Katsanevakis et al. 2010b,	<i>Caulerpa racemosa</i> varieties	Yes	Correlative: GAM	Saronikos, Greece
Martínez and Viejo 2012,	<i>Ascophyllum nodosum</i> , <i>Pelvetia canaliculata</i> , <i>Fucus vesiculosus</i> , <i>F. serratus</i> ,	No	Correlative: GLM	NW Iberia
	<i>Himanthalia elongata</i> ,			
Martínez et al. 2014,	<i>Himanthalia elongata</i> ,	No	Hybrid	NW Iberia
	<i>Bifurcaria bifurcata</i>			
Neiva et al. 2014,	<i>Pelvetia canaliculata</i>	No	Correlative: MaxEnt, BRT, MARS	NE Atlantic
Pauly et al. 2011a,	<i>Trichosolen</i>	Blooms	Correlative: MaxEnt	Global
Pauly et al. 2011b,	<i>Halimeda discoidea</i> ,	No	Correlative: MaxEnt	Regional: Oman
	<i>Nizamuddinia zanardinii</i> ,			
	<i>Tolypiocladia glomerulata</i>			
Raybaud et al. 2013,	<i>Laminaria digitata</i>	No	Correlative: NPPEN	NE Atlantic
Sandman et al. 2013,	<i>Fucus vesiculosus</i> , <i>Cladophora glomerata</i> , <i>Ceramium tenuicorne</i>	No	Correlative: GAM	Baltic Sea
Tyberghein et al. 2012,	<i>Codium fragile</i> subsp. <i>fragile</i>	Yes	Correlative: MaxEnt	Global
Verbruggen et al. 2009,	<i>Halimeda</i>	No	Correlative: MaxEnt	Global
Verbruggen et al. 2013	<i>Caulerpa cylindracea</i>	Yes	Correlative: MaxEnt	Global

MaxEnt, maximum entropy; MLMR, multiple logistic regression model; GLM, generalized linear mode; GAM, generalized additive model; GAMLSS, generalized additive models for location, scale and shape; BRT, boosted regression trees; NPPEN, non-parametric probabilistic ecological niche model; MARS, multivariate adaptive regression splines; LBR, logistic binary regression.

INVASIVE SEAWEED ENMS

ENMs have not been extensively used to predict habitat suitability of invasive seaweeds or macroalgae in general (Table 2). Most of the work has focused on siphonous green algae, kelps and furoids. Nonetheless, the available examples span across different spatial scales and represent correlative as well as mechanistic approaches, which we will present in more detail below. Because there are few examples, our overview includes examples of invasive as well as non-invasive seaweed species. At the end, we address the particularities of using ENMs to study seaweed invasiveness under climate change.

Correlative niche models of introduced seaweeds. Correlative models have been used to investigate seaweed distributions at several geographic scales. At the small-scale end of this spectrum, the studies on

distribution and microecological preferences of *Caulerpa* invasive species constitute a well-known example. Using GAM to investigate *Caulerpa* distribution in the Saronikos Gulf (Greece), Katsanevakis et al. (2010b) found that the species shows a bimodal depth distribution pattern, with a first peak at shallow depths (<4 m.) and a second at depths between 15 and 30 m, contrasting with the species' ecology in its native range where it grows between the intertidal and 6 m depth (Klein and Verlaque 2008, Katsanevakis et al. 2010b). Using different modeling techniques, Katsanevakis et al. (2010a) and Bulleri et al. (2011) showed that *Caulerpa* takes advantage of degraded habitats. The first study concluded that dead *Posidonia oceanica* rhizome mattes, fragmented meadows and rock substrates are especially vulnerable to *Caulerpa* invasions. Accordingly, protection policies should ensure that *Posidonia*

meadows are effectively preserved (Katsanevakis et al. 2010a). The second study included differently impacted areas at various ecological scales (i.e., habitat and community), finding distinct distribution patterns according to the scale in question (Bulleri et al. 2011).

A few other invasive seaweeds have been subjected to niche modeling approaches at larger geographic scales. A correlative presence-absence model based on macroecological predictors was used to identify the factors that determine the successful establishment of *Undaria pinnatifida* in northern Spain (Báez et al. 2010). Chl concentration and photosynthetically active radiation (PAR) were suggested to best characterize the distribution of *U. pinnatifida* in the invaded area. Although the relationship between PAR and this species distribution seems odd, as this kelp has low light requirements, this variable is expected to affect the overall number of species, increasing the availability of suitable habitats (e.g., shadowing) for *U. pinnatifida* (see Báez et al. 2010 and references therein). Proximity to urban centers and temperature were also found to be related to the species' distribution, the latter being especially important when considering the optimum temperatures for the recruitment and development of sporophytes. Another interesting (although not on invasives) example is the study on *Pelvetia canaliculata* historical biogeography (Neiva et al. 2014). By combining molecular data with correlative models projections for present and past distributions of this seaweed, the authors detected a latitudinal range shift since the last glacial period. Understanding historical distributions of invasive seaweeds may also provide valuable information regarding their requirements for establishing in a new area.

At global scales, ENMs have been inferred for a range of seaweed species using fairly coarse-grained macroecological predictor variables (Bio-ORACLE). The potential niche of *Codium fragile* subsp. *fragile* was inferred with a MaxEnt method (Tyberghien et al. 2012). The model was based on combined presence records from the native (Japan) and one of the invaded areas (Europe), resulting in highly predictive habitat suitability maps for both ranges. It also predicted other areas where the invasive subspecies is known to occur (East coast of USA and Canada, southern Australia, Chile). The potential spread of *Caulerpa cylindracea* was also assessed at a global scale using correlative approaches (Verbruggen et al. 2013). The resulting model suggests that *C. cylindracea* can expand its range to nearby areas in southern Australia where the species has been recently introduced, as well as along the Atlantic coasts of Europe and Africa. Besides potential expansions, many other regions are predicted to have suitable environmental conditions, where *C. cylindracea* could establish if introduced, including the East Coast of the USA, parts of the Caribbean and Brazil, Southeast Africa and Japan. The products of these global-scale ENMs

can be further scrutinized by coupling data on major maritime routes (e.g., Roura-Pascual et al. 2009) to pinpoint higher introduction-risk areas and advise precautionary measures.

The underlying physiological mechanisms. The relationship between experimentally measured physiological tolerances of algae and their geographic distributions has been known for a long time (e.g., Breeman 1988) but physiological data have rarely been used to generate quantitative habitat suitability maps. Nonetheless, two studies on kelps used known physiological requirements to predict the presence of kelp beds in tropical deep-water habitats (Graham et al. 2007b) and the historical extent of kelp beds in California (Graham et al. 2010). Although physiological responses to environmental variables have been studied for several notorious invasive species (e.g., Hanisak 1979, Steen 2004), this has not resulted in mechanistic models to map habitat suitability and potential spread yet.

While the application of mechanistic models is still a challenge, the response curves produced by correlative models can be used to inform experimental studies on physiological tolerances. The above-mentioned study on *C. cylindracea* (Verbruggen et al. 2013) shows the parallels of this seaweed distribution with environmental factors (Fig. 3). The species appears to do best in localities with an annual mean SST of around 20°C. The phosphate response curve, however, is counterintuitive, indicating that the species would be less likely to occur in waters with concentrations over $0.4 \mu\text{mol} \cdot \text{L}^{-1}$, while studies indicate that lower rather than higher nutrients limit seaweeds distributions. This results from the collinearity between the phosphate and SST predictors, and the fact that *C. cylindracea* has only been recorded in relatively phosphate poor waters. The global pattern of phosphate shows high concentrations in temperate and polar regions, not in the warm-temperate waters where this species occurs. While the model response curves certainly do not mirror physiological response curves, they can contribute to our understanding and offer hypotheses that can be further tested with physiological experiments. These experiments, in turn, can feed back into mechanistic niche models (see the work of Rees 2003 on nutrients uptake by seaweeds) and further improve our understanding of the physiological needs determining the species niche and distribution.

Climate change. The urge to forecast how species' invasive potential will be affected by climate change has been leading scientists to extrapolate ENMs to future climate conditions (Lee et al. 2008). Niche models can be built based on the present occurrence data and then projected into the future to predict species distributions in future climates (e.g., Martínez and Viejo 2012, Martínez et al. 2014, see Jeschke and Strayer 2008 for a review). Future climate rasters have been recently included in the

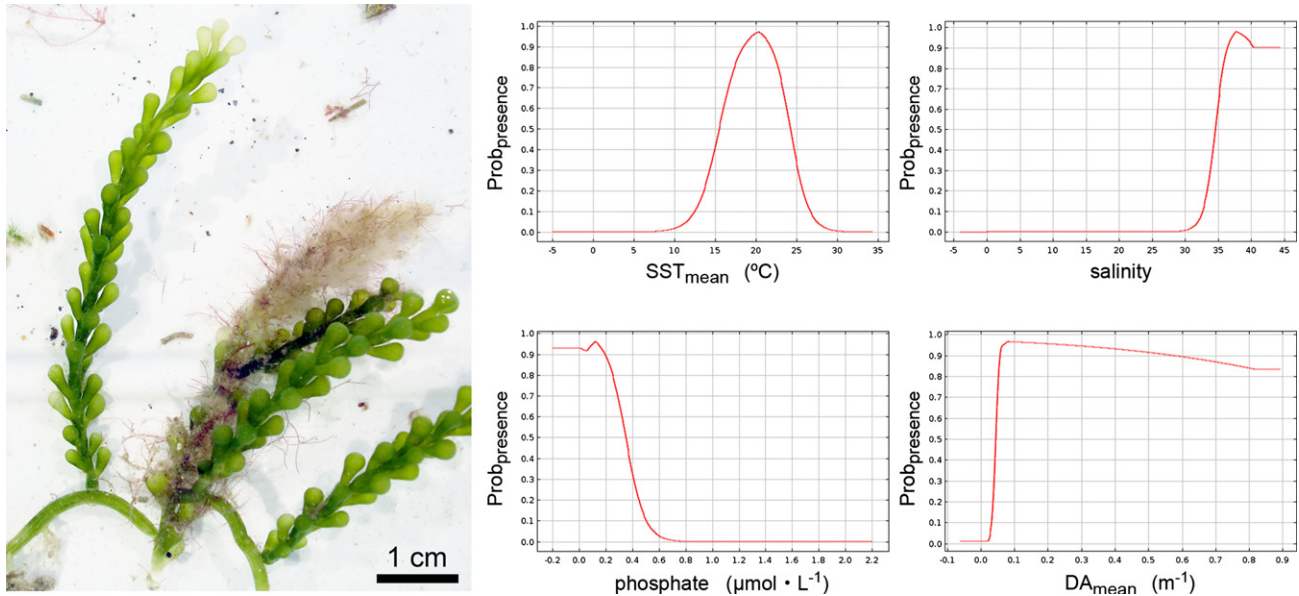


FIG. 3. Response curves to different environmental predictors estimated by a correlative niche model for *Caulerpa cylindracea* (Verbruggen et al. 2013). The model indicates higher habitat suitability in water temperatures around 20°C. Other graphs may show a counterintuitive pattern (e.g., phosphate). Although response curves produced by correlative models do not always reflect physiological tolerances, they can be used to inform experimental studies and access model behavior.

Bio-ORACLE data set (Jueterbock et al. 2013), making extrapolations to future scenarios fairly straightforward. To date, relatively few studies with marine organisms have done so (Robinson et al. 2011), and none that we are aware of have done it for invasive seaweeds. One of the few examples used correlative models to forecast the future distribution of a set of keystone fucoid species in the North Atlantic (Jueterbock et al. 2013). The models suggested that climate change would provoke substantial distribution shifts at southern distribution edges and the potential for even larger range extensions at the northern edges. More recently, another study combined thermal thresholds obtained from ecophysiological experiments, presence-absence data and future scenarios based on climatic anomalies reported in the last decades in order to predict potential niche shifts in kelps (Martínez et al. 2014). This study also highlights how the coupling of mechanistic and correlative approaches can deliver more robust predictions to forecast the effects of climate change.

Two issues need special attention when extrapolating ENMs of seaweeds to future climates. First, the assumptions of equilibrium and niche conservatism are likely to be violated when projecting models across no-analog climates, which is the case in ENMs featuring climate change (for a detailed discussion and proposals to reduce the related uncertainty see Wiens et al. 2009 and Veloz et al. 2012). The second refers to the complex interactions of the environmental factors affecting seaweeds' survival. One aspect of climate change is global warming, and tem-

perature is one of the most important factors shaping seaweeds distribution (Eggert 2012). Global warming is expected to move the distribution boundaries of seaweed species polewards (Müller et al. 2009), and large-scale analysis of herbarium records suggest that they already have (Wernberg et al. 2011, but see Huisman and Millar 2013). Another aspect of global change is the expected decrease in pH and calcium carbonate saturation, which are likely to affect photosynthesis, growth, calcification and consequent distribution of macroalgae (Harley et al. 2012, Kroeker et al. 2013). The synergistic effects of these changing environmental factors are poorly known and are likely being overlooked in models extrapolated to future climate conditions. Further research on species physiological tolerances and hybrid modeling are urgently needed to better understand and predict the effects of climate change on seaweed distributions.

CONCLUSIONS AND PERSPECTIVES

ENMs are valuable tools to forecast and manage species invasions. Several of the available examples for seaweeds indicate that both mechanistic and correlative models yield highly predictive models, reflecting the strong dependence of seaweed distributions on environmental parameters. The availability of several user-friendly data sets mapping various environmental dimensions of the marine ecosystem has made building global, coarse-grained ENMs of invasive seaweeds a much less cumbersome task. At regional and especially local scales, additional work

is needed to assemble data sets of relevant environmental variables. The work by Pauly et al. (2011b) shows that at least some of those variables can be derived from high-resolution satellite imagery in combination with ground-truthing. At local scales, microhabitat information derived directly from field observations can contribute insights into invasive species' habitat requirements.

In order to build reliable correlative ENMs, it is crucial to take the general assumptions of ecological niche modeling as well as the specific problems for introduced species into consideration. Several solutions are available to avoid potential problems resulting from spatial autocorrelation, multicollinearity, handle the issue that introduced species are not at equilibrium with the environment, and deal with the problem that the realized niche inevitably shifts to some degree in association with species' introductions.

Spatial scale can strongly influence a model's predictions. At continental and global scales, climate can be considered the dominant factor affecting species distributions, while at local scales factors like substrate, biotic interactions and anthropogenic impacts typically become more important. The various studies carried out on invasive *Caulerpa* species illustrate this very well. Although models based on temperature, salinity, nutrients and diffuse attenuation well predicted the global distribution of the species (Verbruggen et al. 2013), the degree of urbanization and heterogeneity of the seascape play a larger role at regional scales (Bulleri et al. 2011), while habitat type, depth and community composition (macrophytes and invertebrates) determines the species' success at the microhabitat level (Katsanevakis et al. 2010a,b, Bulleri et al. 2011). An ecological niche modeling study aiming to characterize algal distributions at regional scales in a heterogeneous area (Oman) obtained very different predictions with coarse macroecological predictors and more fine-grained predictors that included microhabitat aspects (Pauly et al. 2011b). Interestingly, the predictive power of the coarse-grained and fine-grained models was very similar, indicating that similarly relevant but different processes are captured by the models at different scales. The predictions at the two scales differed especially along the heterogeneous south coast of Oman, whereas the coasts of the more homogeneous Gulf of Oman had more consistent predictions between scales. Integrating effects at different scales in a single model can be achieved with hierarchical (or nested) modeling approaches (Pearson and Dawson 2003, Morin and Lechowicz 2008, Elith and Leathwick 2009). These methods incorporate data at different spatial, ecological or temporal scales, often analyzed under the same methodological perspective.

Besides the integration of different scales to capture processes acting at different levels, ENMs of invasive species could benefit from the inclusion of several other aspects of the species' invasion

biology, more specifically any knowledge we may have about the species' ecophysiology or the movement and biotic components of its niche (Fig. 1). Hybrid models – the approach coupling mechanistic and correlative methods – have recently been recommended to jointly explore these aspects (Gallien et al. 2010, Dormann et al. 2012). The coupling of dispersal models and correlative ENMs, for example, can be used to model the spread of invasive species (e.g., Williams et al. 2008). While this approach clearly has potential, a study of two nonindigenous bivalves in New Zealand yielded low predictive power (Inglis et al. 2006). As we start gaining a better understanding of invasive seaweed dispersal (Arrontes 2005, Mineur et al. 2010, Gagnon et al. 2011), perhaps such approaches will become more successful. Likewise, the distribution and density of seaweed species at a local scale is strongly influenced by biotic interactions (Scheibling and Gagnon 2006, Edwards and Connell 2012). While these effects may be difficult to capture in ENMs spanning larger geographic scales, they play a central role in predicting invasive seaweeds density (Bulleri et al. 2011). Finally, the species' ecophysiological properties clearly have an impact on its distribution and any experimental knowledge can also be used to ameliorate correlative models in various ways. For instance, the results of a mechanistic ecophysiological model of the invasive cane toad were used to define absence points for a correlative distribution model (Elith et al. 2010). Much physiological information about invasive seaweed species is available but it has not been integrated in ENMs so far. Its inclusion would be especially useful when projections need to be made outside the range of conditions observed today.

Ongoing climate change is another aspect that would be beneficial to incorporate into ENMs of invasive and non-invasive seaweeds. Changes in environmental conditions can both enable alien species to invade regions in which they could not survive before and reduce invasions in areas that become environmentally unfavorable (Stachowicz et al. 2002, Walther et al. 2009). Niche models can help to forecast the invasiveness potential of alien species in future climate scenarios. One of the main sources of uncertainty here is the lack of knowledge regarding seaweeds physiological responses to the synergistic action of changing (no-analog) environmental factors. This apparent shortcoming is quickly being minimized as data on seaweeds physiology and environmental data sets for future climates become increasingly accessible.

The fact that seaweed distributions are largely determined by environmental conditions offers great opportunity to use ENMs to study seaweed invasions. The increased availability of user-friendly marine environmental data sets and modeling software facilitates the use of ENMs. If built with attention to the relevance of variables at different

spatial scales, taking care to avoid the known sensitivities of the methods, and evaluated critically, ENMs can serve a purpose as predictive and management-guiding tools for seaweed invasions. Clearly, more work is needed to develop mapped data sets for relevant predictors at finer spatial scales, and additional effort should be spent on the inclusion of different scales and other types of information such as physiology and dispersal in the models, depending on the goal. The available studies on ENMs of invasive seaweeds and macroalgae in general clearly show the potential of the methods to make predictions at different spatial scales, which will hopefully stimulate further development of the field.

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