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Staying ahead of invaders: using species distribution modeling to predict alien species' potential niche shifts

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ABSTRACT: Early detection and rapid response are essential to prevent invasive species from thriving in marine environments following their introduction. Species distribution models (SDMs) are widely used to predict the potential distribution of invasive species, providing excellent tools for the design of strategies to prevent or mitigate impacts of non-native species. Niche shifts are among the major drawbacks in the use of SDMs, leading scientists to formulate inaccurate predictions. In this work, we tested the performance of 3 different SDMs (Bioclim, Mahalanobis distance and Maxent) to predict the distribution of a niche-shifting invasive species using native data only. As a model organism, we used the neurotoxic sea-slug *Pleurobranchaea maculata*, which was recently introduced into the southwestern Atlantic, where it has undergone a niche shift. Our results show that Maxent outperforms the other modeling techniques in predicting the invasive distribution, but that Bioclim provides the most accurate outputs, minimizing over- and underpredictions. Our study strongly suggests that niche decomposition can provide important evidence for the underlying causes of niche shifts, aiding our understanding of why they occur and how they can be addressed by SDMs. This approach will improve the interpretation of SDMs in order to predict the potential spread of invasive species worldwide.

KEY WORDS: *Pleurobranchaea maculata* · Invasive species · Species distribution · SDM · Ecological niche · Niche shift · Neurotoxins

1. INTRODUCTION

The introduction of marine invasive species has accelerated in the past few decades by an increasing trend of trade and transportation across oceans and continents (Hulme 2009, Katsanevakis et al. 2016). Biological invasions are among the major causes of biodiversity loss worldwide, leading to important impacts at the social, economical and human health levels (Vitousek et al. 1997, Sala et al. 2000). Since the eradication of marine invasive species is virtually impossible (Hayes et al. 2005, Katsanevakis et al. 2013, Werschkun et al. 2014), prevention, early detection and rapid response strategies are the best management alternatives to avoid their impacts (Gallien et al. 2010, Jiménez-Valverde et al. 2011a). For these strategies to be effective, limited resources and efforts must focus on specific vectors, pathways, species and locations (Hayes et al. 2005, Inglis et al. 2006). Species distribution models (SDMs) provide spatially explicit information to support decisions directed at preventing and managing biological invasions (Peterson 2003, Franklin 2010, Guisan et al. 2013, Leidenberger et al. 2015, Goldsmit et al. 2018).

The most commonly used SDMs are based on correlational techniques (correlative SDMs, hereafter referred to simply as SDMs), and rely on assumptions that have motivated criticism on their predictive ability. Firstly, the 'quasi-equilibrium' assumption requires occurrence data to be in equilibrium with the environment (i.e. the species occupies all of the suitable areas and is absent from the unsuitable areas within a given range) (Guisan & Thuiller 2005, Gallien et al. 2010). In the case of invasive species, especially during the early phase of the invasion, this assumption is rarely met. Second, when models are transferred in space or time, niches are assumed to remain conserved in the original (i.e. native in the case of invasive species) and the novel (i.e. invasive) ranges. Recent insights into these issues have shown that SDMs perform well under non-equilibrium situations (Barbet-Massin et al. 2018), but there is little understanding of how models perform when transferred in space under a scenario in which niches are not conserved.

The tendency to retain ancestral ecological requirements is termed 'niche conservatism' (Wiens & Graham 2005), and implies that the environmental conditions where a species occurs in the invaded range are similar to those occupied by the species in its native range. Niche shifts occur when niches are not conserved, and an increasing amount of evidence suggest that shifts are not uncommon during biological invasions (Broennimann et al. 2007, Fitzpatrick et al. 2007, Schwindt et al. 2009, Callen & Miller 2015, Rodrigues et al. 2016). However, in most cases, these shifts do not refer to fundamental but to realized niche shifts. The fundamental niche (FN) is the set of combinations of environmental variables for which population growth rate of a species is positive (Soberón & Nakamura 2009), and depends exclusively on the species' ecological requirements; thus, it is expected to be highly invariant within short to moderate (tens to hundreds of years) time spans (Peterson 2011). The realized niche (RN) represents a subsample of the FN that exists in a given region and time and is used by the species after biotic interactions are taken into account (Fig. 1a) (Soberón & Nakamura 2009). Shifts in the RN can be driven by changes in the type and/or intensity of biotic interactions or in dispersal limitations. The relative frequency and importance of these factors in niche shifting are highly debated, and the prevailing idea is that biotic interactions do not determine the distribution of a species at a macro-ecological scale (Pearson & Dawson 2003), although contrasting evidence may suggest the opposite (Araújo & Luoto 2007).
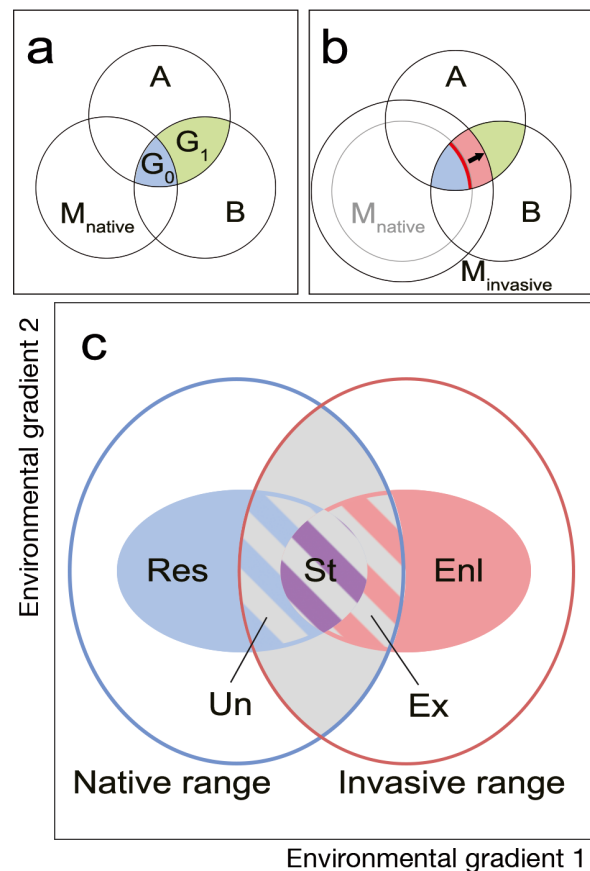

Fig. 1. (a) 'BAM' diagram (Soberón & Peterson 2005) showing the factors that constrain the distribution of a species, where B represents biotic interaction constraints, A represents abiotic or environmental constraints, also regarded as the fundamental niche, and M represents movement (or dispersal) constraints, which depend on geographical and historical limitations. The species occurs within the realized distribution (G_0), where all of these constraints are favorable, and G_1 denotes the invasible area, which is the unoccupied portion of the potential distribution. (b) When a species is introduced into a novel environment, the movement constraints for the potential niche (red line) are relaxed and the species can explore a new set of environmental conditions and biotic interactions that were previously unavailable, resulting in a realized niche shift. (c) Schematic representation of niche shift components within the environmental space, following Guisan et al. (2014) and showing the distinction between niche expansion and enlargement and between niche restriction and unfilling. Five different components can be distinguished: niche stability (St): proportion of the native niche (blue oval) overlapping with the exotic niche (red oval); niche expansion (Ex): proportion of the invasive niche non-overlapping with the native niche but within the analog conditions (grey area, conditions that are similar in native and invaded ranges); niche unfilling (Un): proportion of the native niche that does not overlap with the invasive niche within the analog conditions; niche restriction (Res): proportion of the native niche non-overlapping with the invasive niche outside the analog conditions; niche enlargement (Enl): proportion of the invasive niche non-overlapping with the native niche, outside the analog conditions

Relatively less controversial are the effects that dispersal limitations have on the RN of a species on a broad spatial scale. These limitations imply physical and/or historical constraints to the range of environmental conditions that a species can explore (Barve et al. 2011, Acevedo et al. 2012), restricting the RN to the available climatic conditions within those limits. When a species is introduced into a novel range, the dispersal constraints fall down, and the accessible area increases. This increment may allow the species to explore both environmental conditions and biotic interactions that were previously unavailable to the species in the native area (Fig. 1b). Under this scenario, RN shifts are expected even when the FN remains conserved, driven by the environmental conditions that emerge in the invaded range (i.e. novel environments). In a similar vein, environmental conditions found in the native range may no longer be available in the invaded one, leading to the occurrence of niche shifts. Thus, when a species is introduced into a novel region, different components of the niche can provide clues to understanding the relationship between the environmental availability and the RN of the species in each range (Fig. 1c).

The grey side-gilled sea slug *Pleurobranchaea maculata* (Quoy & Gaimard, 1832) is a good candidate to evaluate model performance under a niche shift scenario. Native to New Zealand and southeastern Australia, this species has recently reached the shores of Argentina (Farías et al. 2015, 2016, Battini 2016) and has spread along the coast at a rate of ca. 330 km yr^{-1} (Farías et al. 2016). This slug is an opportunistic scavenger and predator of a diverse group of soft-bodied marine invertebrates (Ottaway 1977, Willan 1984, Bökenhans et al. 2019), and no predators are known so far other than cannibalistic interactions (Bökenhans et al. 2019), which may contribute to self-regulating the population both in the native and the invaded range. In 2009, high levels of tetrodotoxin (TTX) were detected in individuals of *P. maculata* that were washed up onto beaches of New Zealand, killing several dogs (McNabb et al. 2010). Further research identified *P. maculata* as the source of TTX, and proposed the occurrence of bioaccumulation through the food chain (Wood et al. 2012a,b, Khor et al. 2014, Salvitti et al. 2015a,b). Although it remains unclear why or how the prevalence of TTX varies among native populations of *P. maculata*, ongoing research has recently revealed that invasive slugs from Argentina accumulate both TTX and other locally available neurotoxins (Farías et al. 2015, N. Farías unpubl. data); thus, there is a clear need for coastal scientists and environmental managers to better understand its ecological behavior within the invaded region. In this study, we compared the performance of 3 different SDM techniques to predict the invasive realized distribution of niche-shifting *P. maculata* based on native data only, and discuss their implications for anticipating its potential distribution around the globe.

2. METHODS

2.1. Occurrence data

We obtained occurrence data for *Pleurobranchaea maculata* from both native and invaded ranges (Broennimann & Guisan 2008, Jiménez-Valverde et al. 2011a) through the Global Biodiversity Information Facility (www.gbif.org), the Ocean Biogeographic Information System (www.iobis.org) and specific scientific literature (from Google Scholar, PubMed, Scielo, Scopus and Aquatic Sciences and Fisheries Abstracts [ASFA]), by searching for '*Pleurobranchaea maculata*', '*Pleurobranchaea maculate*' (a common misspelling) and '*Pleurobranchaea novaezelandiae*' Cheeseman, 1879, a formerly used synonym. When a record lacked coordinates but the description of the sampling location was sufficiently accurate, we georeferenced it using Google Earth Pro version 7.3.2.5491. In order to maximize the accuracy of our study, we intentionally excluded records from eastern Asia due to unresolved taxonomical uncertainties between *P. maculata* and *P. japonica* Thiele, 1925 (Jensen 1998) (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m612p127_supp.pdf). To avoid overestimating the evaluation parameters, we corrected for spatial autocorrelation among the environmental predictors for the occurrence data by removing the records that were at a distance of less than 60 km apart, as it was the minimum distance at which Mantel r was nonsignificantly different from 0. Mantel correlograms were constructed using the 'ecodist' package (Goslee & Urban 2017) in R. After correcting for spatial autocorrelation, we obtained 79 occurrences (60 native and 19 invasive) which we used for the SDMs.

2.2. Environmental predictors

We considered environmental predictors directly affecting the survival and reproduction of *P. maculata*. Temperature and salinity are the most important abiotic environmental variables directly affecting

survival, reproduction, metabolism and distribution of marine invertebrates (Gibson & Chia 1995, Zacherl et al. 2003, Compton et al. 2007, 2010, Verween et al. 2007, Bosch et al. 2018). We considered mean depth, sea temperature (annual mean and range), salinity (annual minimum and range), current velocity (annual maximum and range) and dissolved oxygen (annual minimum and range) (Table 1). As monthly minimum and maximum and annual mean values were very highly correlated for temperature, salinity and dissolved oxygen, we selected the most important variable according to preliminary model runs to avoid redundancy. We derived the environmental predictors from the Bio-Oracle database (Assis et al. 2018), as 5 arcmin raster layers, at the average benthic depth (average depth within each cell).

2.3. RN shift of *P. maculata*

In order to characterize native and invasive niches of *P. maculata* and identify potential signs of niche shift, we followed the 'centroid shift, overlap, unfilling and expansion' (COUE) scheme (Broennimann et al. 2012, Guisan et al. 2014). Based on the environmental predictors, we conducted a principal component analysis using environmental data extracted from occurrence data and the available climate (PCA-env). We restricted the native available climate using a criterion based on large marine ecosystems (LMEs, available at https://www.st.nmfs.noaa.gov/ecosystems/lme/index), and extracted data from the LMEs that contained records of *P. maculata* and from LMEs immediately adjacent to these, masked to a depth of 300 m, which is the maximum depth recorded for *P. maculata* (Wood et al. 2012b). For the selection of the background in the invaded range, we accounted for the maximum potential dispersal range

by generating a buffer area for each point with a radius given by the product of the estimated dispersal rate of 330 km yr^{-1} (Farías et al. 2016) and the number of years since that record was observed (Barve et al. 2011). Finally, we masked the resulting area to the maximum depth recorded for *P. maculata* and used that area as the invasive background.

Based on PCA-env, we tested for niche similarity and calculated niche components using the 'ecospat' package (Broennimann et al. 2018) in R. Prior to the calculation, we slightly modified the original script (see the Supplement), so that it provided the following parameters: niche expansion, unfilling, stability, enlargement and restriction (Fig. 1c), both range specific (relative to native or exotic ranges) and for the pooled ranges. Both enlargement and restriction were previously recognized but undefined (Guisan et al. 2014), and were not previously included in the analyses. These 2 parameters refer to the portions of the invasive and native niches, respectively, which do not overlap with the available climate in the other range, and must therefore be discriminated from expansion and unfilling, which we set aside to define portions of each niche in the analog climates. Niche similarity tests whether the overlap between the native and exotic niches is greater than expected by chance (Broennimann et al. 2012). For the calculation, artificial niches are created by shifting the center of the entire observed density of occurrences within 1 range, and comparing the overlap between simulated niches and the observed niche in the other range. Niche overlap is estimated using Schoener's *D* (Schoener 1970, Warren et al. 2008, Broennimann et al. 2012), which compares the amount of overlap and varies between 0, when no overlap is observed, and 1, when both niches overlap completely. A significant *D* means that the niche in one range is less similar to the niche in the other range than expected by chance

Table 1. Environmental predictors used to model the potential distribution of *Pleurobranchaea maculata*, derived from the Bio-ORACLE database (Assis et al. 2018) at a spatial resolution of 20 arcmin. 'No.' refers to the numbers used in Fig. 2b. Variables refer to annual maximums, minimums, means and ranges for the 2010–2014 period, except for bathymetry

No.	Variable name	Description	Units
1	Bathymetry	Average depth of the seafloor	m
2	CurrVel max	Maximum sea water velocity at the mean bottom depth	m s^{-1}
3	CurrVel range	Range of the sea water velocity at the mean bottom depth	m s^{-1}
4	DissOx min	Minimum dissolved oxygen concentration at the mean bottom depth	mmol m^{-3}
5	DissOx range	Dissolved oxygen concentration range at the mean bottom depth	mmol m^{-3}
6	Salinity min	Minimum sea water salinity at the mean bottom depth	PSS
7	Salinity range	Range of the sea water salinity at the mean bottom depth	PSS
8	Temp. mean	Mean sea water temperature at the mean bottom depth	°C
9	Temp. range	Range of the sea water temperature at the mean bottom depth	°C

(Broennimann et al. 2012). For each test, we performed 100 simulations in order to compute the probability of the observed D. Niche stability, expansion, enlargement, unfilling and restriction were calculated to account for the distinct components of niche shift (Guisan et al. 2014).

2.4. Modeling workflow

In order to compare the performance of the models, we used native data to calibrate the SDM and invasive data to test them. For each run of each model, we randomly split both native occurrence and background data in half, and used one half to calibrate the SDM and the other to generate an environmental niche model (ENM) based on the scores of the PCA-env. Invasive data were also included in the ENM, and in order to maintain the native to invasive data ratio, we only used half of the invasive data to calibrate the ENM. We then thresholded the global projection of the SDM into a binary presence/absence map and projected it on the ENM using the scores of the PCA-env. In the environmental space, we estimated niche dynamics between native or invasive niches and the output of the SDM. Assuming the species is in a quasi-equilibrium state within the native range but not necessarily in the invasive one, SDM should simultaneously (1) maximize the overlap with the native niche, while minimizing underprediction or overprediction, and (2) maximize the overlap with the invasive niche. To compare the performance of the modeling techniques, we estimated 3 parameters derived from the modified COUE scheme: model accuracy (A), model predictability (P) and overfitting (O), which were calculated as follows:

$$A = S_N \times (S_N + E_N + U_N + RE_N)^{-1} \qquad (1)$$

$$P = S_I \times (S_I + U_I)^{-1} \qquad (2)$$

$$O = (E_N + EN_N) \times (E_N + EN_N + S_N)^{-1} \qquad (3)$$

where S is stability, E is expansion, U is the unfilling, EN is the enlargement, and RE is the restriction, computed for the native (N) or invasive (I) ranges compared to model predictions. Note that the quasi-equilibrium assumption is not required in the invaded range, and that we did not consider enlargement in Eq. (1) because areas where enlargement occurred do not *a priori* represent commission errors. However, to account for the effect of enlargement, we computed model overfitting, which we defined as the proportion of enlargement and expansion relative to stabil-

ity. Model projections in novel environments are considered unreliable (Guisan et al. 2014), so we compared the performance of the models using a restricted projection, which was constrained to non-novel environments, or an unrestricted one, which was projected worldwide. To restrict model projections, we performed multivariate environmental similarity surface (MESS) analyses during each run of the models (Elith et al. 2010), and restricted the projections to areas with positive MESS values. The MESS estimates the similarity between the environmental conditions in the entire projected area and those in the calibration range. Negative MESS values indicate environmental conditions that differ from those used to calibrate the model. For the second series of analyses, the model was projected to the global extent. The extent of the projected models was included in the ENM to calculate niche components.

2.5. SDMs

We modeled the potential distribution of *P. maculata* using 3 different algorithms: Bioclim, Mahalanobis distance and the maximum entropy method (Maxent). We performed Maxent models with the whole set of background data (Maxent) and with an equal number of presences and absences (Maxent_0.5), in order to maintain a prevalence (i.e. presence to pseudoabsence ratio) of 0.5 (Lobo et al. 2008). Both Bioclim and Mahalanobis distance are presence-only methods, which are preferred when reliable absence data are unavailable and the aim is to model potential distributions because they do not require absence or pseudoabsence data (Jiménez-Valverde et al. 2011a) and are thus free of assumptions about contingent absences (i.e. absence due to disturbance, sampling bias, geographical or historical constraints). Maxent does require pseudoabsences, but outperforms other methods when using few occurrences (Pearson et al. 2007) and when models are transferred into novel environments when appropriate thresholds are used (Peterson et al. 2007). We sampled background data using an environmental systematic sampling design that maximizes its environmental coverage (Hattab et al. 2017). To delimit the background-sampling extent, we followed the same criteria as mentioned for the PCA-env. We sampled 600 background points that represented a 10-fold increase relative to native occurrence data. We included these background data to estimate the MESS for Bioclim and Mahalanobis distance methods. We ran the models using the 'dismo' package (Hijmans

et al. 2017) in R. As threshold selection directly influences modeling output when projecting binary maps, we compared model performance using 4 recommended threshold criteria: minimum and tenth percentile training presence threshold, maximum sum of sensitivity and specificity (Liu et al. 2013) and the 'Boyce' threshold, which is estimated as the suitability level at which the predicted to expected ratio is equal to 1 (Hirzel et al. 2006).

We ran 10 replicates of each algorithm and threshold criteria to compute model performance. We compared accuracy, predictability and overfitting among algorithms, threshold levels and projection restriction using generalized linear models with a beta distribution. Predictability values were transformed prior to the analyses using $(x \times (n-1) + 0.5) / n$ transformation, where n is the sample size (Smithson & Verkuilen 2006). We compared the differences among algorithms or threshold levels using simultaneous tests for general linear hypotheses, performed using the 'multcomp' package (Hothorn et al. 2017) in R. When the interaction between algorithm and restriction was significant, we compared threshold levels and projection restriction for each algorithm. We ran the models in the 'betareg' package (Zeileis et al. 2018) in R, and used the minimum Akaike's information criterion (AIC) for model selection.

2.6. Final potential distribution models

For the final model, we used the best performing alternatives derived from the previous section and modeled the global potential distribution of *P. maculata* using both native and invasive data. We ran the models as previously described and evaluated them by using the Boyce index (Boyce et al. 2002), which is the best evaluation parameter for presence-only SDMs (Boyce et al. 2002, Hirzel et al. 2006, Petitpierre et al. 2012) and the area under the receiver operating characteristics (ROC) curve (AUC), which was estimated using background and calibration data for each model. For Bioclim and Mahalanobis distance, we determined the influence of each environmental predictor as the drop in the Boyce index value when the values of the respective predictor were randomly permuted. For Maxent models, we determined the variable importance using the permutation importance parameter, which is computed as the drop in the AUC values when the values for each predictor are randomly permuted on training presence and background data (Phillips et al. 2006).

3. RESULTS

3.1. RN shift

The first 2 axes of the PCA-env accounted for 54.8% (PC1 = 39.2%, PC2 = 15.6%) of total variation (Fig. 2). The invasive background showed a broader range of environmental conditions than the native background, and it shifted towards areas with a greater variability in dissolved oxygen, temperature and salinity, as shown by the background centroid shift vector (Fig. 2). Only a small fraction (11%) of the pooled niches corresponded to stability, which represented 8% of the native niche and 15% of the invasive niche. The larger fractions of the pooled niches corresponded to unfilling (58%) and enlargement (28%), while there was no expansion and only a small portion (3%) corresponded to restriction. The native and invasive niches were more similar than expected by chance, as a niche similarity test showed that niche overlap was greater than expected for randomly created niches with the same pattern but different centroid position (Schoener's D = 0.13, p = 0.11).
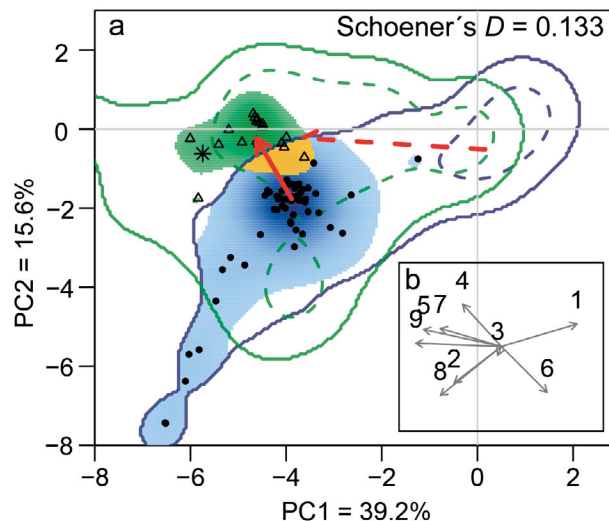

Fig. 2. (a) PCA using environmental data (PCA-env) of the first 2 principal components (total variation explained is 54.8%) showing the 99% (solid lines) and 75% (dashed lines) percentiles of the environmental availability in the invaded (green lines) and the native (blue lines) ranges. Invasive and native niches are represented as green and blue areas, respectively, and niche overlap is represented in yellow. Red solid and dashed arrows represent niche and range centroid shifts, respectively. Native occurrences are shown as filled circles, invasive ones as open triangles and the first record in the invasive area as an asterisk. (b) Contribution of each environmental predictor to the principal components. Environmental variables are given in Table 1

3.2. Accuracy, predictability and overfitting

Bioclim models were significantly more accurate than Mahalanobis distance and both models constructed with Maxent (Table 2) at representing the native niche of *Pleurobranchaea maculata* when calibrating with native data only, achieving an accuracy of between 81 and 97 % (mean = 90 %) (Fig. 3). Accuracy was unaffected by the restriction of model projections to non-novel environments (Table 2), and there were no differences among threshold levels. Despite this greater accuracy, Bioclim models were unable to predict the invasive distribution of *P. maculata* in the southwestern Atlantic (SWA) (Fig. 4). In contrast, higher predictability was achieved by Maxent_0.5, which managed to predict the whole niche of *P. maculata* in the invaded range (Fig. 4). The effect of projection restriction on model predictability varied depending on the algorithm. Restriction had no effect on models constructed with Bioclim (Table 2) but it did when using Mahalanobis distance, Maxent and Maxent_0.5 (Table 2, Fig. 3). Threshold levels had no effect on model predictability for Mahalanobis distance or Maxent_0.5, but they did for Bioclim and Maxent. Minimum training presence threshold resulted in slightly but significantly worse predictability in the case of Bioclim, but was better for Maxent (Table 2). The higher predictive ability achieved by Maxent_0.5 came at the cost of greater model overfitting (Fig. 3), which resulted in the prediction of large suitable areas for *P. maculata* in the SWA (Fig. 4). As for predictability, restriction produced different effects on model overfitting according to the algorithm used. Projection restriction had no effect on model overfitting when using Bioclim or Mahalanobis distance, but it did when modeling with Maxent and Maxent_0.5 (Table 2). Among thresholds, minimum training presence and

Table 2. Results for beta regression models assessing the effects of modeling algorithm, restriction and threshold criteria on model accuracy, predictability and overfitting. Significance is indicated with asterisks (*p < 0.05, **p < 0.01, ***p < 0.001). When appropriate, results from comparisons using simultaneous tests for general linear hypotheses (GLH) among algorithms and threshold criteria are indicated with letters, where different letters indicate differences with a significance level of 0.05; maxSSS: maximum sum of sensitivity and specificity

| Variable	Source of variation	Estimate	z	GLH
Accuracy	Intercept	2.141	20.887***	
	Mahalanobis	−0.472	−4.626***	a
	Maxent	−0.890	−9.062***	b
	Maxent_0.5	−0.895	−9.122***	b
	Restriction	0.017	0.269	
	Boyce	−0.047	−0.510	
	MaxSSS	0.016	0.171	
	Minimum training presence	−0.113	−1.232	
Predictability	**Bioclim**			
	Intercept	−0.619	−2.799**	
	Restriction	−0.217	−1.075	
	Boyce	−0.414	−1.460	a
	MaxSSS	−0.237	−0.845	a
	Minimum training presence	−0.571	−1.995*	a
	Mahalanobis distance			
	Intercept	−0.058	−0.475	
	Restriction	−0.390	−2.230*	
	Maxent			
	Intercept	1.132	3.863***	
	Restriction	1.400	4.868***	
	Boyce	2.609	6.464***	a
	MaxSSS	0.572	1.522	b
	Minimum training presence	2.302	5.599***	a
	Maxent_0.5			
	Intercept	0.882	2.781**	
	Restriction	3.071	8.349***	
	Boyce	0.428	1.264	
	MaxSSS	0.075	0.222	
	Minimum training presence	0.390	1.151	
Overfitting	**Bioclim**			
	Intercept	−2.435	−12.441***	
	Restriction	−0.043	−0.252	
	Boyce	−0.030	−0.124	
	MaxSSS	0.000	0.000	
	Minimum training presence	0.000	0.000	
	Mahalanobis distance			
	Intercept	−2.316	−9.184***	
	Restriction	−0.027	−0.128	
	Boyce	0.024	0.082	
	MaxSSS	0.000	0.000	
	Minimum training presence	0.000	0.000	
	Maxent			
	Intercept	−1.508	−10.204***	
	Restriction	0.768	6.176***	
	Boyce	0.503	2.885**	a
	MaxSSS	0.025	0.138	b
	Minimum training presence	0.439	2.512*	a
	Maxent_0.5			
	Intercept	−1.467	−9.582***	
	Restriction	1.029	7.856***	
	Boyce	0.249	1.366	a
	MaxSSS	0.052	0.280	b
	Minimum training presence	0.245	1.347	ab
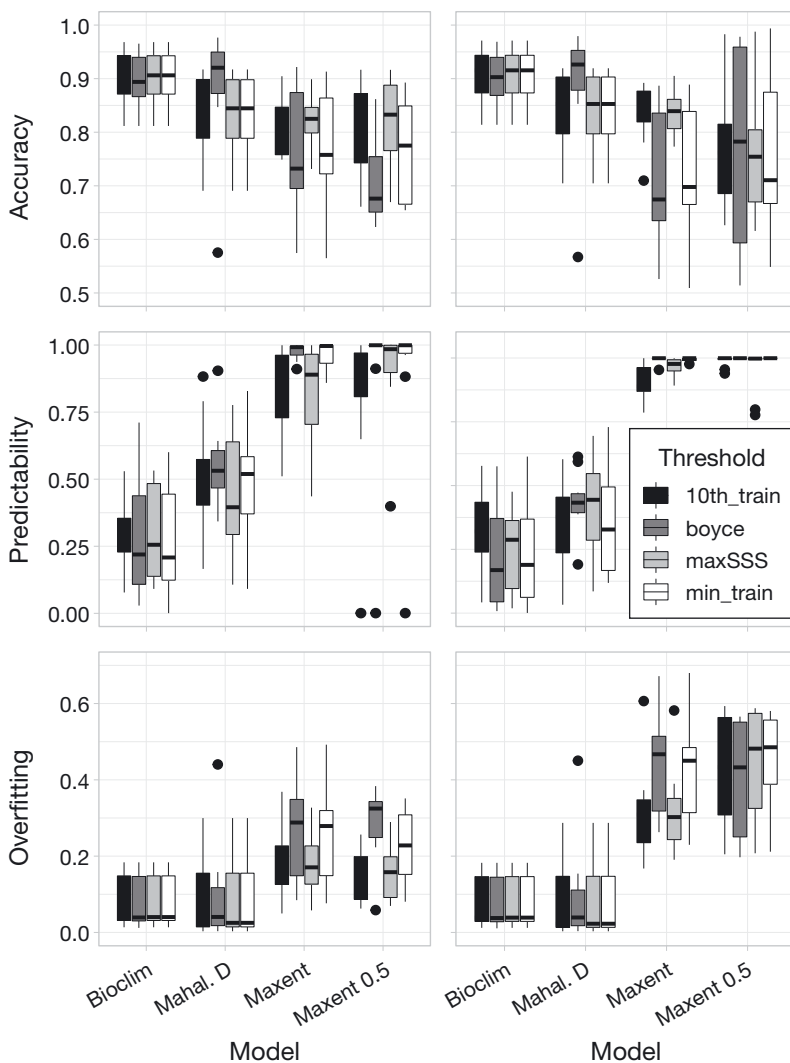
Fig. 3. Accuracy, predictability and model performance for Bioclim, Mahalanobis distance (Mahal. D), Maxent and Maxent_0.5 models calibrated using native data only and projected into non-novel environments (areas where the multivariate environmental similarity surface [MESS] is >0) (restricted), or into the entire extent (unrestricted), discriminated by threshold criteria (10th_train: tenth percentile training presence threshold, boyce: 'Boyce' threshold, maxSSS: maximum sum of sensitivity and specificity, and min_train: minimum training presence threshold). The lower and upper hinges correspond to the first and third quartiles. The lower and upper whiskers extend from the hinge to the smallest and largest value, respectively, no further than 1.5 times the interquartile range (IQR) from the hinge. Dots represent data beyond the end of the whiskers

Boyce produced greater model overfitting for Maxent (Table 2, Fig. 3).

3.3. Final models

Final models were calibrated using both native and invasive data and performed based on Bioclim and

Maxent_0.5, as they were the most accurate and with the highest predictability, respectively (Fig. 5). The mean Boyce index and mean AUC evaluation parameters were, respectively, 0.75 ± 0.08 (SD) and 0.95 ± 0.01 for Bioclim, and 0.91 ± 0.05 and 0.97 ± 0.02 for Maxent_0.5 (Table 3). Bioclim predictions represented a subsample of the areas predicted as suitable by Maxent_0.5 (Fig. 5), and only a very small fraction of the entire suitable area was predicted solely by Bioclim. The hotspots for the establishment of *P. maculata* are the North and Baltic Seas, the Sea of Japan, the northwestern Atlantic and the southeastern Atlantic (Fig. 5). Variable importance differed according to the different algorithms (Fig. 6). However, temperature annual mean and range and salinity annual range were important predictors for all modeling techniques. Bathymetry was important for all algorithms except Mahalanobis distance, and for Bioclim, minimum dissolved oxygen and annual range in dissolved oxygen were also important predictors (Fig. 6).

4. DISCUSSION

Our study revealed that environmental availability played a key role in the RN shift of *Pleurobranchaea maculata* during its introduction in the SWA. Novel environmental conditions found in the invaded range, which were unavailable in the native range due to dispersal limitations, favored niche enlargement across the SWA. Indeed, when accounting for environmental availability, the invaded niche represented only a small portion of the native one. Whether niche shifts are common (Fitzpatrick et al. 2007, Gallagher et al. 2010, Mandle et al. 2010, Hill et al. 2017, Wang et al. 2017) or rare (Peterson 2011, Petitpierre et al. 2012, Strubbe et al. 2013, Liu et al. 2017, Sales et al. 2017, Ribas et al. 2018) events happening during the bioinvasion process remains a matter of debate. Frequently, behind this contrasting evidence lie conceptual differences
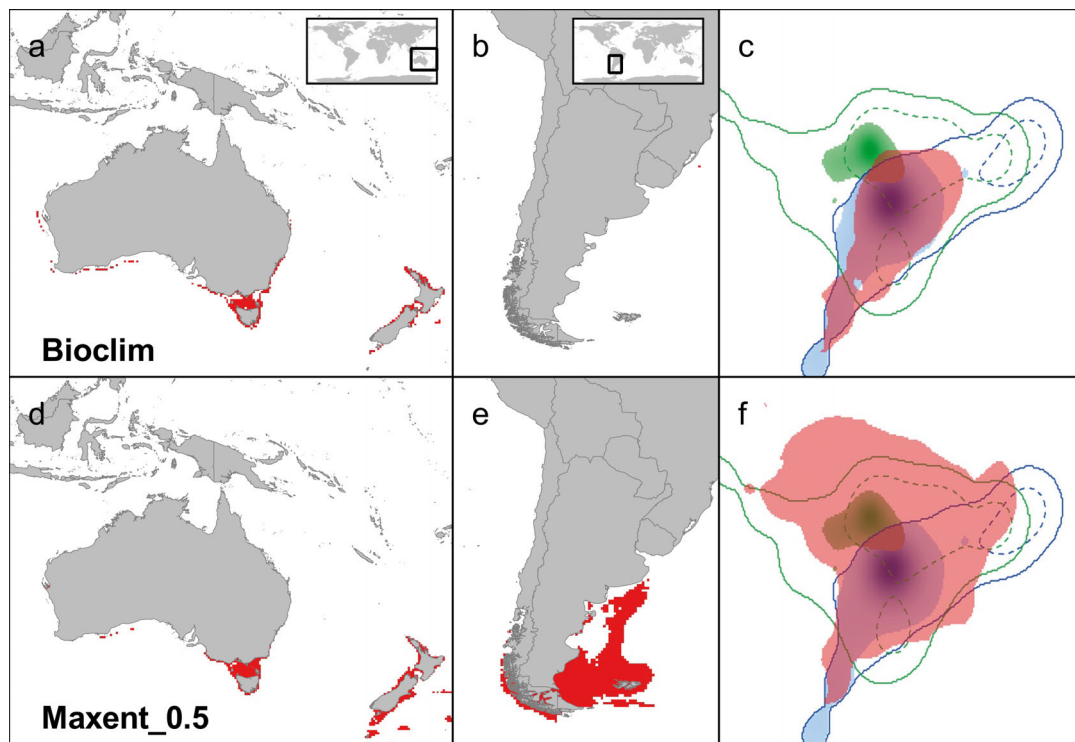
Fig. 4. Predicted habitat suitability for *Pleurobranchaea maculata* (solid red areas) based on (a,b) Bioclim and (d,e) Maxent_0.5 models, calibrated using invasive data and the maximum training sum of sensitivity and specificity as a threshold criterion, and projected in the native (a,d) and the invaded (b,e) range. (c,f) PCA using environmental data (PCA-env) showing the native (blue area) and invasive (green area) niches, the 75 and 99% percentiles of available climates in each range as (solid and dashed lines, respectively) and the predicted suitability (red area) for Bioclim and Maxent_0.5

specifically associated with environmental availability. While several studies have considered the effect of environmental availability (Petitpierre et al. 2012, Hill et al. 2017, Liu et al. 2017, Sales et al. 2017, Ribas et al. 2018), others have not (Fitzpatrick et al. 2007, Gallagher et al. 2010, Mandle et al. 2010, Wang et al. 2017), and this may reflect some of the observed differences.

Although there has been much improvement since the appearance of the COUE scheme used here (Guisan et al. 2014), we are convinced that further niche decomposition, including and computing niche enlargement and restriction, will continue to enhance our understanding of the role that dispersal limitations, biotic interactions and/or rapid adaptability can have on the niche changes of invasive species. The incorporation of niche enlargement and restriction is important because the causes that underlie them may differ from those producing expansion and unfilling. Niche expansion and niche unfilling are produced by (1) changes in biotic interactions, (2) the invasive species not reaching the quasi-equilibrium state within the invaded range, or

(3) sampling bias. During the early phase of invasions, species are rarely at equilibrium with the environment and therefore niche unfilling may be an important component of the observed niche shift (Sales et al. 2017), as occurred in our study. Once a species has reached the quasi-equilibrium state at the end of the expansion process, both niche expansion and unfilling can provide clues on novel biotic interactions that may favor or impair, respectively, the fitness of the invasive species in the invaded range, assuming there is no sampling bias in the occurrence records. Niche restriction and enlargement result from changes in the available environmental conditions, which do not imply changes in the species' use of the environment. Unlike expansion and unfilling, which are greatly unpredictable, enlargement and restriction depend on the relationship between the niche and the available environmental conditions in the native and the invaded range. It has been argued that species with a more restricted distribution, such as endemic species, are more likely to undergo niche shifts when introduced to a novel environment (Li et al. 2014). However, these species
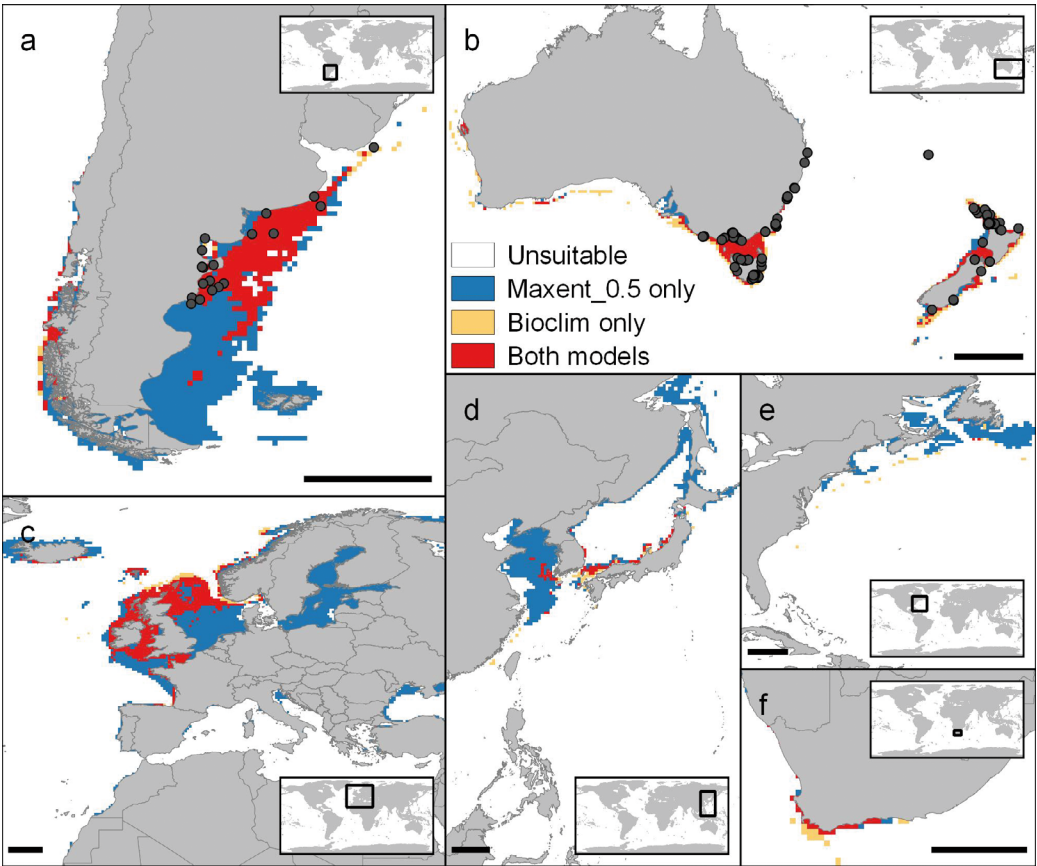
Fig. 5. Predicted habitat suitability for *Pleurobranchaea maculata* based on Maxent_0.5 (blue), Bioclim (yellow) and both algorithms (red) in the main suitable areas: (a) southwestern Atlantic (invaded range), (b) Australia and New Zealand (native range), (c) North and Baltic Seas, (d) Sea of Japan, (e) northwestern Atlantic and (f) southeastern Atlantic. Suitability is based on models calibrated using both native and invasive data and thresholded to presence/absence maps using the maximum training sum of sensitivity and specificity (maxSSS) criteria. Results are averages over 10 replicate runs for each model. Grey circles indicate the occurrence records of *P. maculata* in both the invaded and the native ranges. Black scale indicates 500 km

are more likely to have environmental rather than dispersal constraints within the native range, and then the RN accurately resembles the potential niche, and niche expansion, enlargement or unfilling are unlikely to occur.

Table 3. Boyce index and the area under the receiver operating curve (AUC) for the different modeling algorithms. Selected final models are marked in **bold**. Values are means ± SD over 10 replicate runs for each algorithm

Modeling algorithm	Evaluation parameter	
	Boyce index	AUC
Bioclim	**0.753 ± 0.083**	**0.953 ± 0.013**
Mahalanobis distance	0.727 ± 0.090	0.998 ± 0.001
Maxent	0.938 ± 0.048	0.961 ± 0.009
Maxent_0.5	**0.907 ± 0.054**	**0.965 ± 0.017**

Correlative SDMs face a very challenging scenario when niche enlargement occurs, and this is why model projections in novel environments are considered unreliable (Guisan et al. 2014). We found that model accuracy (i.e. the ability of the models to predict the distribution of a species in equilibrium with the environment) did not vary whether projections were restricted to non-novel environments or not, regardless of the algorithm used. To the contrary, predictability was higher when projections were unrestricted, but only when using Maxent, and this was associated with a greater overfitting. For presence-only methods, which show more constrained predictions than do more complex algorithms (Jiménez-Valverde et al. 2011b), predictability did not vary (Bioclim) or was slightly lower (Mahalanobis distance) when restricting the projections. In the light of these results, it is evident that the selection of
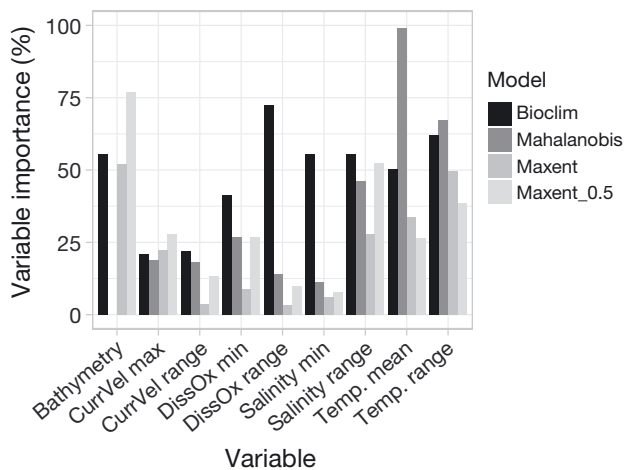
Fig. 6. Permutation test of variable importance for the different algorithms. For Bioclim and Mahalanobis distance, the percentage drop in the Boyce index estimator is shown, when values of each variable are randomly permuted for occurrence data. For Maxent and Maxent_0.5, the percentage drop in the area under the receiver operating curve (AUC) estimator is shown; random permutation was done both in occurrence and background data (Phillips et al. 2006). Environmental variables are defined in Table 1

the best modeling approach depends on the aim of the modeling procedure. Moreover, the ability of models to predict invasions within novel environmental conditions comes at the cost of generating broader predictions that may increase the probability of producing commission errors (i.e. predicting suitable conditions that are unsuitable). In the context of biological invasions, preventive strategies rely on early detection and rapid response (Gallien et al. 2010, Jiménez-Valverde et al. 2011a); hence, the use of conservative models, which maximize predictability, may be preferred. Otherwise, expansion and enlargement can lead to the underestimation of the invasion risk (Rodrigues et al. 2016). On the other hand, when a species has been introduced and all managing efforts are directed to control its local and regional spread, the use of models that maximize accuracy is recommended.

In this work, we explored how novel environments affected the accuracy and predictability of different modeling approaches. Indeed, environmental availability plays a key role in the distribution of species (Martínez et al. 2017). A better understanding of the conceptual and methodological framework underlying SDMs will enhance their accuracy and reliability in predicting the potential distribution of invasive species, helping to make the measures to prevent their introduction more effective. Our results show that regions such as the North Sea, southern Africa

and the Sea of Japan have environmental conditions that resemble those that represent the RN, and therefore are regarded as suitable for the establishment of *P. maculata* by both SDMs, regardless of their accuracy and predictability levels. In other regions, such as the northwestern Atlantic, the Black Sea and the Baltic Sea, the environmental conditions are considered suitable only by the SDM with larger values of predictability (Maxent), mainly because they do not represent the current RN of *P. maculata*, but may correspond to part of their hitherto inaccessible FN. Besides the implications that the presence of TTX may represent within these areas, *P. maculata* may interfere with pre-existing ecological interactions, altering the trophic networks through predation over other invertebrates or through competition with other predators and scavengers. Many of these areas represent closed or semi-enclosed seas, but nevertheless share many marine species with the native and/or the invaded ranges that are considered invasive in some of those regions, such as *Carcinus maenas* (Linnaeus, 1758), *Undaria pinnatifida* (Harvey) Suringar, 1873, *Ascidiella aspersa* (Müller, 1776), *Ciona intestinalis* (Linnaeus, 1767), *Rapana venosa* (Valenciennes, 1846) and *Mnemiopsis leidyi* A. Agassiz, 1865, among others.

Although we have only considered physical and oceanographic variables in this work, other factors including biological interactions such as competition or predation, or the local availability of certain resources, can significantly condition the shape and extent of the RN. Particularly in the case of toxin-resistant organisms, toxin concentration and availability in the environment can be crucial for their populations to grow and reproduce successfully. The ability to resist the noxious effects of toxins often allows them to consume resources that are not available to other organisms, and the accumulation of these chemicals can also act as a predator deterrent for both adult individuals and their offspring, for prey capture and even for both intra- and interspecific signaling (Ferrer & Zimmer 2013). The recent detection of locally available neurotoxins in the exotic *P. maculata* (N. Farías unpubl. data), which were undetected in the native range, suggests that niche enlargement occurred not only at the climatic level but also in terms of other resources. The relevance of *P. maculata* as a potential vector of neurotoxins for humans, especially children, along coastal environments highlights the importance of providing new perspectives, such as those provided in this work, directed to prevent its spread locally and worldwide.

LITERATURE CITED

Acevedo P, Jiménez-Valverde A, Lobo JM, Real R (2012) Delimiting the geographical background in species distribution modelling. J Biogeogr 39:1383–1390

Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. Glob Ecol Biogeogr 16:743–753

Assis J, Tyberghein L, Bosch S, Verbruggen H, Serrão EA, De Clerck O (2018) Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. Glob Ecol Biogeogr 27:277–284

Barbet-Massin M, Rome Q, Villemant C, Courchamp F (2018) Can species distribution models really predict the expansion of invasive species? PLoS One 13:e0193085

Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A and others (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol Model 222:1810–1819

Battini N (2016) Evaluando el riesgo de intoxicación por una especie invasora: la babosa de mar moteada (*Pleurobranchaea maculata*). Rev Coleg Vet Patagónicos 3: 16–18

Bökenhans V, Fernández Alfaya JE, Bigatti G, Averbuj A (2019) Diet of the invasive sea slug *Pleurobranchaea maculata* in Patagonian coastal waters. N Z J Zool 46: 87–94

Bosch S, Tyberghein L, Deneudt K, Hernandez F, De Clerck O (2018) In search of relevant predictors for marine species distribution modelling using the MarineSPEED benchmark dataset. Divers Distrib 24:144–157

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. Ecol Model 157:281–300

Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. Biol Lett 4:585–589

Broennimann O, Treier UA, Müller-Schärer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. Ecol Lett 10:701–709

Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B and others (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. Glob Ecol Biogeogr 21:481–497

Broennimann O, Di Cola V, Petitpierre B, Breiner F and others (2018) ecospat: spatial ecology miscellaneous methods. Version 3.0. https://cran.r-project.org/web/packages/ecospat/

Callen ST, Miller AJ (2015) Signatures of niche conservatism and niche shift in the North American kudzu (*Pueraria montana*) invasion. Divers Distrib 21:853–863

Compton TJ, Rijkenberg MJA, Drent J, Piersma T (2007) Thermal tolerance ranges and climate variability: a comparison between bivalves from differing climates. J Exp Mar Biol Ecol 352:200–211

Compton TJ, Leathwick JR, Inglis GJ (2010) Thermogeography predicts the potential global range of the invasive European green crab (*Carcinus maenas*). Divers Distrib 16:243–255

Elith J, Kearney M, Phillips SJ (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342

Farías NE, Obenat S, Goya A (2015) Outbreak of a neurotoxic side-gilled sea slug (*Pleurobranchaea* sp.) in Argentinian coasts. N Z J Zool 42:51–56

Farías NE, Wood SA, Obenat S, Schwindt E (2016) Genetic barcoding confirms the presence of the neurotoxic sea slug *Pleurobranchaea maculata* in southwestern Atlantic coast. N Z J Zool 43:292–298

Ferrer RP, Zimmer RK (2013) Molecules of keystone significance: crucial agents in ecology and resource management. BioScience 63:428–438

Fitzpatrick MC, Weltzin JF, Sanders NJ, Dunn RR (2007) The biogeography of prediction error: Why does the introduced range of the fire ant over-predict its native range? Glob Ecol Biogeogr 16:24–33

Franklin J (2010) Moving beyond static species distribution models in support of conservation biogeography. Divers Distrib 16:321–330

Gallagher RV, Beaumont LJ, Hughes L, Leishman MR (2010) Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. J Ecol 98:790–799

Gallien L, Münkemüller T, Albert CH, Boulangeat I, Thuiller W (2010) Predicting potential distributions of invasive species: where to go from here? Divers Distrib 16:331–342

Gibson GD, Chia FS (1995) Developmental variability in the poecilogonous opisthobranch *Haminaea callidegenita*: life-history traits and effects of environmental parameters. Mar Ecol Prog Ser 121:139–155

Goldsmit J, Archambault P, Chust G, Villarino E and others (2018) Projecting present and future habitat suitability of ship-mediated aquatic invasive species in the Canadian Arctic. Biol Invas 20:501–517

Goslee S, Urban D (2017) ecodist: dissimilarity-based functions for ecological analysis. Version 2.0.1. https://cran.r-project.org/web/packages/ecodist/

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8: 993–1009

Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I and others (2013) Predicting species distributions for conservation decisions. Ecol Lett 16:1424–1435

Guisan A, Petitpierre B, Broennimann O, Daehler CC, Kueffer C (2014) Unifying niche shift studies: insights from biological invasions. Trends Ecol Evol 29:260–269

Hattab T, Garzón-López CX, Ewald M, Skowronek S and others (2017) A unified framework to model the potential and realized distributions of invasive species within the invaded range. Divers Distrib 23:806–819

Hayes KR, Cannon R, Neil K, Inglis GJ (2005) Sensitivity and cost considerations for the detection and eradication of marine pests in ports. Mar Pollut Bull 50:823–834

Hijmans RJ, Phillips SJ, Leathwick JR, Elith J (2017) Species distribution modeling. Package 'dismo.' Version 1.1-4. https://cran.r-project.org/web/packages/dismo/index.html

Hill MP, Gallardo B, Terblanche JS (2017) A global assessment of climatic niche shifts and human influence in insect invasions. Glob Ecol Biogeogr 26:679–689

Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecol Model 199:142–152

Hothorn T, Bretz F, Westfall P, Heiberger RM, Schuetzenmeister A, Scheibe S (2017) Package 'multcomp: simultaneous inference in general parametric models.' R-CRAN Proj Version 1.4-8. https://cran.r-project.org/web/packages/multcomp/index.html

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

Inglis GJ, Hurren H, Oldman J, Haskew R (2006) Using habitat suitability index and particle dispersion models for early detection of marine invaders. Ecol Appl 16: 1377–1390

Jensen KR (1998) Zoogeographic affinities of Hong Kong Opisthobranchia (Mollusca, Gastropoda). In: Morton B (ed) Third International Conference on the Marine Biology of the South China Sea. Hong Kong University Press, Hong Kong, p 43–55

Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragón P, Lobo JM (2011a) Use of niche models in invasive species risk assessments. Biol Invas 13:2785–2797

Jiménez-Valverde A, Decae AE, Arnedo MA (2011b) Environmental suitability of new reported localities of the funnelweb spider Macrothele calpeiana: an assessment using potential distribution modelling with presence-only techniques. J Biogeogr 38:1213–1223

Katsanevakis S, Zenetos A, Belchior C, Cardoso AC (2013) Invading European seas: assessing pathways of introduction of marine aliens. Ocean Coast Manag 76:64–74

Katsanevakis S, Tempera F, Teixeira H (2016) Mapping the impact of alien species on marine ecosystems: the Mediterranean Sea case study. Divers Distrib 22:694–707

Khor S, Wood SA, Salvitti L, Taylor DI, Adamson J, McNabb PS, Cary SC (2014) Investigating diet as the source of tetrodotoxin in Pleurobranchaea maculata. Mar Drugs 12:1–16

Leidenberger S, Obst M, Kulawik R, Stelzer K, Heyer K, Hardisty A, Bourlat SJ (2015) Evaluating the potential of ecological niche modelling as a component in marine non-indigenous species risk assessments. Mar Pollut Bull 97:470–487

Li Y, Liu X, Li X, Petitpierre B, Guisan A (2014) Residence time, expansion toward the equator in the invaded range and native range size matter to climatic niche shifts in non-native species. Glob Ecol Biogeogr 23:1094–1104

Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. J Biogeogr 40:778–789

Liu X, Petitpierre B, Broennimann O, Li X, Guisan A, Li Y (2017) Realized climatic niches are conserved along maximum temperatures among herpetofaunal invaders. J Biogeogr 44:111–121

Lobo JM, Jiménez-Valverde A, Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. Glob Ecol Biogeogr 17:145–151

Mandle L, Warren DL, Hoffmann MH, Peterson AT, Schmitt J, von Wettberg EJ (2010) Conclusions about niche expansion in introduced Impatiens walleriana populations depend on method of analysis. PLOS ONE 5:e15297

Martínez G, Arim M, Defeo O (2017) Distribution of the isopod Excirolana braziliensis on sandy beaches of the Atlantic and Pacific Oceans. Mar Ecol Prog Ser 583: 137–148

McNabb P, Selwood AI, Munday R, Wood SA and others (2010) Detection of tetrodotoxin from the grey side-gilled sea slug - Pleurobranchaea maculata, and associated dog neurotoxicosis on beaches adjacent to the Hauraki Gulf, Auckland, New Zealand. Toxicon 56:466–473

Ottaway JR (1977) Pleurobranchaea novaezelandiae praying on Actinia tenebrosa. N Z J Mar Freshw Res 11: 125–130

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Glob Ecol Biogeogr 12: 361–371

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34:102–117

Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. Q Rev Biol 78: 419–433

Peterson AT (2011) Ecological niche conservatism: a time-structured review of evidence. J Biogeogr 38:817–827

Peterson AT, Pape M, Eaton M (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30:550–560

Petitpierre B, Kueffer C, Broennimann O, Randin C, Daehler CC, Guisan A (2012) Climatic niche shifts are rare among terrestrial plant invaders. Science 335:1344–1348

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Ribas LGS, de Cássia-Silva C, Petsch DK, Silveira MJ, Lima-Ribeiro MS (2018) The potential invasiveness of an aquatic macrophyte reflects founder effects from native niche. Biol Invas 20:3347–3355

Rodrigues JFM, Coelho MTP, Varela S, Diniz-Filho JAF (2016) Invasion risk of the pond slider turtle is underestimated when niche expansion occurs. Freshw Biol 61: 1119–1127

Sala OE, Chapin FS III, Armesto JJ, Berlow E and others (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774

Sales LP, Ribeiro BR, Hayward MW, Paglia A, Passamani M, Loyola R (2017) Niche conservatism and the invasive potential of the wild boar. J Anim Ecol 86:1214–1223

Salvitti L, Wood SA, Taylor DI, McNabb P, Cary SC (2015a) First identification of tetrodotoxin (TTX) in the flatworm Stylochoplana sp.; a source of TTX for the sea slug Pleurobranchaea maculata. Toxicon 95:23–29

Salvitti LR, Wood SA, McNabb P, Cary SC (2015b) No evidence for a culturable bacterial tetrodotoxin producer in Pleurobranchaea maculata (Gastropoda: Pleurobranchidae) and Stylochoplana sp. (Platyhelminthes: Polycladida). Toxins 7:255–273

Schoener TW (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408–418

Schwindt E, Bortolus A, Idaszkin YL, Savoya V, Méndez MM (2009) Salt marsh colonization by a rocky shore invader: Balanus glandula Darwin (1854) spreads along the Patagonian coast. Biol Invas 11:1259–1265

Smithson M, Verkuilen J (2006) A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychol Methods 11:54–71

Soberón J, Nakamura M (2009) Niches and distributional areas: concepts, methods, and assumptions. Proc Natl Acad Sci USA 106:19644−19650

Soberón J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodivers Inform 2:1−10

Strubbe D, Broennimann O, Chiron F, Matthysen E (2013) Niche conservatism in non-native birds in Europe: niche unfilling rather than niche expansion. Glob Ecol Biogeogr 22:962−970

Verweeen A, Vincx M, Degraer S (2007) The effect of temperature and salinity on the survival of *Mytilopsis leucophaeata* larvae (Mollusca, Bivalvia): the search for environmental limits. J Exp Mar Biol Ecol 348:111−120

Vitousek PM, D'Antonio CM, Loope LL, Rejmánek M, Westbrooks R (1997) Introduced species: a significant component of human-caused global environmental change. N Z J Ecol 21:1−16

Wang CJ, Wan JZ, Qu H, Zhang ZX (2017) Climatic niche shift of aquatic plant invaders between native and invasive ranges: a test using 10 species across different biomes on a global scale. Knowl Manag Aquat Ecosyst 418: 1−9

Warren DL, Glor RE, Turelli M (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868−2883

Werschkun B, Banerji S, Basurko OC, David M and others (2014) Emerging risks from ballast water treatment: the run-up to the International Ballast Water Management Convention. Chemosphere 112:256−266

Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annu Rev Ecol Evol Syst 36:519−539

Willan RC (1984) A review of diets in the Notaspidea (Mollusca: Opisthobranchia). J Malacol Soc Aust 6: 125−142

Wood SA, Casas M, Taylor DI, McNabb P, Salvitti L, Ogilvie S, Cary SC (2012a) Depuration of tetrodotoxin and changes in bacterial communities in *Pleurobranchea* [sic] *maculata* adults and egg masses maintained in captivity. J Chem Ecol 38:1342−1350

Wood SA, Taylor DI, McNabb PS, Walker J, Adamson J, Cary SC (2012b) Tetrodotoxin concentrations in *Pleurobranchaea maculata*: temporal, spatial and individual variability from New Zealand populations. Mar Drugs 10:163−176

Zacherl D, Gaines SD, Lonhart SI (2003) The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletii* (Forbes, 1852). J Biogeogr 30:913−924

Zeileis A, Cribari-Neto F, Gruen B, Kosmidis I, Simas AB, Rocha AV (2018) Package 'betareg.' R-CRAN Proj Version 3.1-1. https://cran.r-project.org/web/packages/betareg/index.html