



## Impacts of climate change on geographical distributions of invasive ascidians

Zhixin Zhang<sup>a</sup>, César Capinha<sup>b</sup>, Dirk N. Karger<sup>c</sup>, Xavier Turon<sup>d</sup>, Hugh J. MacIsaac<sup>e,f</sup>,  
Aibin Zhan<sup>g,h,\*</sup>

<sup>a</sup> Graduate School of Marine Science and Technology, Tokyo University of Marine Science and Technology, Konan, Minato, Tokyo, 108-8477, Japan

<sup>b</sup> Centro de Estudos Geográficos, Instituto de Geografia e Ordenamento do Território - IGOT, Universidade de Lisboa, Rua Branca Edmée Marques, 1600-276, Lisboa, Portugal

<sup>c</sup> Swiss Federal Research Institute WSL, 8903, Birmensdorf, Switzerland

<sup>d</sup> Centre for Advanced Studies of Blanes (CEAB, CSIC), Blanes, Catalonia, Spain

<sup>e</sup> School of Ecology and Environmental Science, Yunnan University, Kunming, China

<sup>f</sup> Great Lakes Institute for Environmental Research, University of Windsor, Windsor, Ontario, Canada

<sup>g</sup> Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China

<sup>h</sup> University of Chinese Academy of Sciences, Chinese Academy of Sciences, Beijing, China

### ARTICLE INFO

#### Keywords:

Benthos  
Biological invasion  
Climate change  
Habitat  
Management strategy  
Species distribution model

### ABSTRACT

Ocean warming associated with global climate change renders marine ecosystems susceptible to biological invasions. Here, we used species distribution models to project habitat suitability for eight invasive ascidians under present-day and future climate scenarios. Distance to shore and maximum sea surface temperature were identified as the most important variables affecting species distributions. Results showed that eight ascidians might respond differently to future climate change. Alarmingly, currently colonized areas are much smaller than predicted, suggesting ascidians may expand their invasive ranges. Areas such as Americas, Europe and Western Pacific have high risks of receiving new invasions. In contrast, African coasts, excluding the Mediterranean side, are not prone to new invasions, likely due to the high sea surface temperature there. Our results highlight the importance of climate change impacts on future invasions and the need for accurate modelling of invasion risks, which can be used as guides to develop management strategies.

### 1. Introduction

Biological invasions have been recognized as one of the most serious threats to global biodiversity and have resulted in substantial ecological changes, health effects, and economic impacts (Pimentel et al., 2005; Ehrenfeld, 2010; Simberloff et al., 2013; Scheele et al., 2019). Invasive species can negatively impact native communities through competition and predation (Ehrenfeld, 2010; Simberloff et al., 2013; Zhan et al., 2015). In addition, they are capable of transmitting parasites and pathogens that cause fatal diseases and declines of native species (e.g., Kozubíková et al., 2009; Scheele et al., 2019). Marine ecosystems are extremely susceptible to biological invasions owing to several factors, notably intensive human activities such as global shipping and both direct and indirect effects of climate change (Stachowicz et al., 2002; Molnar et al., 2008; Olenin et al., 2011). Approximately 90% of global

trade relies on ships, transferring organisms *via* biofouling and ballast water among coastal waters (Molnar et al., 2008; Kaluza et al., 2010; Goldsmit et al., 2018). Additionally, ocean warming has affected large marine ecosystems worldwide (Lyman et al., 2010; Rhein et al., 2014). According to the IPCC Fifth Assessment Report, for example, the upper 75 m of the global ocean has warmed at a rate of about 0.11 °C per decade from 1971 to 2010 (Rhein et al., 2014). Owing to a combination of species' range shifts derived from climate change and arrivals of new species, changes in marine communities are often detected in coastal regions (Stachowicz et al., 2002; Perry et al., 2005; Cheung et al., 2009; Raitos et al., 2010; Sorte et al., 2010). Previous studies have confirmed that native and invasive species have different responses to environmental stressors; often, but not always, invasive species exhibit broader ecological tolerance, thus ocean warming can result in superior performance of the latter over the former (Stachowicz et al., 2002; Braby and

\* Corresponding author. Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China.

E-mail addresses: [zhanaibin@hotmail.com](mailto:zhanaibin@hotmail.com), [azhan@rcees.ac.cn](mailto:azhan@rcees.ac.cn) (A. Zhan).

<https://doi.org/10.1016/j.marenvres.2020.104993>

Received 16 December 2019; Received in revised form 14 April 2020; Accepted 15 April 2020

Available online 21 April 2020

0141-1136/© 2020 Elsevier Ltd. All rights reserved.

Somero, 2006; Fields et al., 2006; Sorte et al., 2010; Anacleto et al., 2014). For instance, Stachowicz et al. (2002) demonstrated that, compared with native ascidians, ocean warming was expected to facilitate earlier and more intense recruitment, as well as higher growth rates, of introduced ascidians, which might lead to changes in benthic community structure. Sorte et al. (2010) found that introduced species had higher thermal tolerance, survival, and growth than native species in a marine fouling community, and suggested that introduced species were likely to dominate the fouling community with ocean warming. Considering the great susceptibility of marine habitats to biological invasions jointly caused by high propagule pressure (i.e., introduction effort) as a result of shipping activities and warming, it is important to identify potential distributions of marine invaders under present and future climate conditions for implementation of management strategies at early invasion stages.

A large number (>80 species globally) of ascidians (Chordata, Tunicata) are notorious invasive species, affecting marine ecosystem functioning, local biodiversity, and industries such as aquaculture and fisheries owing to their superior competitive ability, growth rate, and broad environmental tolerance (Blum et al., 2007; Lambert, 2007; Shenkar and Swalla, 2011; Aldred and Clare, 2014; Zhan et al., 2015). Ascidians generally have limited natural dispersal ability, with recent large-scale spread primarily attributed to human-mediated activities such as shipping and mariculture (Lambert, 2001; Marins et al., 2010; Zhan et al., 2015). Thus far, few studies have been conducted to map areas susceptible to ascidian invasions (but see Herborg et al., 2009; Locke, 2009; Madariaga et al., 2014; Lins et al., 2018). Additionally, despite the recognition that climate change may favour invasions by ascidians (Stachowicz et al., 2002; Sorte et al., 2010; Rius et al., 2014), its effects on ascidian distributions have received relatively little attention (but see Dijkstra et al., 2011, 2017; Goldsmit et al., 2018). The objective of the present study is to investigate the impacts of climate changes on habitat suitability of eight globally distributed invasive ascidians: *Botrylloides violaceus*, *Botryllus schlosseri*, *Ciona savignyi*, *Didemnum vexillum*, *Microcosmus squamiger*, *Molgula manhattensis*, *Styela clava*, and *Styela plicata*. We chose these invasive ascidians as they have wide ranges of distribution, high availability of occurrence data, and great impacts on recipient ecosystems (Zhan et al., 2015). To analyse the impact of climate changes on the potential distribution of these invaders, we used ensemble species distribution models (SDMs). SDMs are a powerful tool to estimate species habitat suitability by capturing the relationship between species distribution data and environmental predictor variables (Guisan and Thuiller, 2005; Guisan et al., 2017). Recently, SDMs have been used to examine climate change impacts on marine species, including invasive species (e.g., Assis et al., 2018a; Buonomo et al., 2018; Goldsmit et al., 2018; Moraitis et al., 2018; de la Hoz et al., 2019). For instance, Goldsmit et al. (2018) used SDMs to predict that eight aquatic invasive species in the Canadian Arctic could experience poleward gains in habitat suitability and potential distribution.

Here, we aim to substantially expand current knowledge about the present-day and future global distributions of the aforementioned invasive ascidians. Specifically, we (1) constructed ensemble SDMs for each ascidian species by using species distribution data and marine predictor variables; (2) evaluated relative contribution of each predictor variable to ascidian distributions to identify critical variables regulating ascidian distributions; and (3) predicted habitat suitability for each ascidian species under present and projected future climatic scenarios. Results of our study have important implications for prioritizing resource allocation for the prevention and control of invasive ascidians under a changing climate.

## 2. Materials and methods

### 2.1. Study area and species occurrence records

Several previous studies have highlighted that the extent of the study area can influence the outcome of SDMs (VanDerWal et al., 2009; Barve et al., 2011), thus it is important to carefully choose the spatial reach of the analysis (Lins et al., 2018). Ascidians are mainly distributed in near-shore waters (Shenkar and Swalla, 2011; Zhan et al., 2015), thus as in Lins et al. (2018) we considered only areas within the Exclusive Economic Zone (i.e., within 370 km of the coast).

Georeferenced occurrence records of each ascidian species were collected from the literature and multiple online databases, including the Global Biodiversity Information Facility (<http://www.gbif.org>) (GBIF.org, 2019), the Ocean Biogeographic Information System (<http://iobis.org>) (OBIS, 2019), the NBN Atlas (<https://nbnatlas.org>) (NBN Atlas, 2019), the USGS Biodiversity Information Serving Our Nation (<https://bison.usgs.gov>) (U.S. Geological Survey, 2019), the Atlas of Living Australia (<http://www.ala.org.au>) (Atlas of Living Australia, 2019), and the Archive for Marine Species and Habitats Data ([www.dassh.ac.uk](http://www.dassh.ac.uk)). All above online databases were accessed on November 20, 2019. Previous studies have identified the problem posed by sampling bias in species occurrence records and the need to reduce it (Syfert et al., 2013; Boria et al., 2014). In order to match with the spatial resolution of marine predictor variables (see section 2.2 for details), we randomly selected only one occurrence record per 5 arcminute grid cells (approximately 9.2 km by 9.2 km at the equator). After this data cleaning procedure, a total of 3189 occurrence records (ranging from 77 to 1367 records per species; Table 1; Supporting Information Figs. S1a–S8a) were retained for downstream analyses.

### 2.2. Current and future marine predictor variables

Habitat suitability of marine organisms can be accurately predicted by a few variables (Belanger et al., 2012; Bosch et al., 2018; Goldsmit et al., 2018). Given the information available under present and future scenarios, 20 predictor variables were considered: water depth, distance to the shore, and annual mean and range values (minimum values, maximum values, maximum values - minimum values, average of the minimum and maximum values per year) of sea surface temperature,

**Table 1**

Predictive performance of ensemble species distribution models for eight ascidian species and suitable habitat ranges of each species under present-day climate. Number of presences represents the number of presence records for each species used to develop species distribution models. TSS: true skill statistics; AUC: area under the receiver operating characteristic curve. The predictive abilities are expressed as mean values  $\pm$  standard error. The range of suitable habitat is represented by the number of raster cells (i.e., 100 km<sup>2</sup>) predicted to be suitable for each species.

Species	No. of presences	AUC	TSS	No. of raster cells
<i>B. violaceus</i>	333	0.992 ( $\pm 0.000$ )	0.952 ( $\pm 0.001$ )	14,192
<i>B. schlosseri</i>	1367	0.991 ( $\pm 0.000$ )	0.947 ( $\pm 0.000$ )	21,393
<i>C. savignyi</i>	93	0.999 ( $\pm 0.000$ )	0.991 ( $\pm 0.001$ )	4089
<i>D. vexillum</i>	252	0.995 ( $\pm 0.000$ )	0.961 ( $\pm 0.002$ )	22,106
<i>M. squamiger</i>	77	0.997 ( $\pm 0.001$ )	0.969 ( $\pm 0.004$ )	5525
<i>M. manhattensis</i>	368	0.993 ( $\pm 0.000$ )	0.951 ( $\pm 0.001$ )	30,815
<i>S. clava</i>	521	0.995 ( $\pm 0.000$ )	0.961 ( $\pm 0.000$ )	20,780
<i>S. plicata</i>	178	0.992 ( $\pm 0.001$ )	0.956 ( $\pm 0.002$ )	17,237

salinity, and current velocity (see Assis et al., 2018b for details; Supporting Information Fig. S9). Water depth and distance to the shore were obtained from the Global Marine Environment Datasets (<http://gmed.auckland.ac.nz>) (Basher et al., 2014), while the other 18 environmental variables were downloaded from Bio-ORACLE v2.0 (<http://www.bio-oracle.org>) (Assis et al., 2018b). Present marine environmental predictors from Bio-ORACLE v2.0 represent average values for the period 2000–2014 (Assis et al., 2018b). Collinearity of predictor variables can severely influence the parameter estimates in a regression framework (Dormann et al., 2013). We therefore estimated collinearity of the 20 predictor variables by calculating Pearson's correlation coefficients ( $r$ ) and selected only one among highly correlated variables (i.e.,  $|r| > 0.7$ , Dormann et al., 2013) (Supporting Information Fig. S9). Empirical studies have examined the physiological tolerance of ascidians to extreme environmental conditions, such as low salinity and high temperature (e.g. Thiyagarajan and Qian, 2003; Dijkstra et al., 2008; Jiang et al., 2008). Based on multicollinearity analyses and available empirical evidence, nine predictor variables (i.e. water depth, distance to shore, maximum values of temperature, range values of temperature, minimum values of salinity, range values of salinity, range values of current velocity, maximum values of current velocity, and minimum values of current velocity) were used to develop SDMs. Water depth and distance to the shore were included in our analyses since SDMs would fail to accurately reflect the known distribution patterns of ascidians without these two variables (Supporting Information Figs. S1c–S8c).

Future projections of the seven environmental predictor variables retained for 2050s (2040–2050) and 2100s (2090–2100) under four greenhouse gas emission scenarios [i.e., representative concentration pathway (RCP), RCP26, RCP45, RCP60, and RCP85] were also obtained from Bio-ORACLE v2.0 (Assis et al., 2018b). Thus far, there is no available dataset for future water depth and distance to the shore; therefore, in this study, we assume that the two geographical variables, water depth and distance to the shore, will remain constant under future conditions. Although we acknowledge that climate change is expected to result in sea-level rise and the two geographical variables will change accordingly in the future, our SDM projections can still provide useful information about ascidian invasion risks. For the purpose of reducing uncertainties, 3 atmosphere-ocean general circulation models (i.e., CCSM4, HadGEM2-ES, MIROC5) were considered and their average values were used to represent future climate conditions (Assis et al., 2018b).

### 2.3. Modelling procedures

A variety of SDM algorithms have been developed so far, but inter-algorithmic variation is still the highest source of uncertainty in future projections of species ranges (Thuiller et al., 2019). Therefore, we used an ensemble modelling approach, which is acknowledged as preferable to the application of a single algorithm, owing to its ability to combine results of different models and account for prediction uncertainties (Araújo and New, 2007; Guisan et al., 2017). We considered ten modelling algorithms with their default settings in the “biomod2” R package: artificial neural network (ANN), classification tree analysis (CTA), flexible discriminant analysis (FDA), generalized additive model (GAM), generalized boosting model (GBM), generalized linear model (GLM), multiple adaptive regression splines (MARS), maximum entropy (Maxent), random forest (RF), and surface range envelop (SRE) (Thuiller et al., 2014; Guisan et al., 2017). Several of these algorithms utilize presence-absence (1–0) data. True absence data is often difficult to acquire, thus we randomly generated 10,000 pseudo-absence points within the study area, representing the environmental conditions that are available to the species (Barbet-Massin et al., 2012; Thuiller et al., 2014; Guisan et al., 2017). A five-fold cross-validation scheme was applied to estimate predictive performances of the ten SDM algorithms: each algorithm was trained using 80% of the data and tested using the remaining 20% (Thuiller et al., 2014; Guisan et al., 2017). To account

for slight differences in the predictions caused by stochasticity in some of the algorithms, this procedure was repeated ten times for each algorithm. Predictive abilities of different algorithms were evaluated by two criteria: true skill statistics (TSS) (Allouche et al., 2006) and area under the receiver operating characteristic curve (AUC) (Swets, 1988). The TSS values range from  $-1$  to  $1$ , where a value  $\leq 0$  indicates that the model gives a random prediction, and a value of  $1$  indicates a perfect model performance (Landis and Koch, 1977). The AUC scores range from  $0$  to  $1$ , with values  $< 0.5$  indicating performance worse than random, a value of  $0.5$  indicating predictions no better than random discrimination, and  $1$  representing perfect discrimination (Swets, 1988; Allouche et al., 2006). Algorithms with TSS  $> 0.75$  and AUC  $> 0.90$  were further considered in this study (Landis and Koch, 1977; Swets, 1988). The relative contribution of each predictor variable on ascidian distribution was assessed by a randomisation approach (Thuiller et al., 2014; Guisan et al., 2017). The response curves of the most important marine environmental predictor were also determined (Thuiller et al., 2014; Guisan et al., 2017). Committee averaging ensemble models were developed by using all data, which in turn were used to map the habitat suitability of ascidians under present and future climate scenarios. The committee averaging method represents the level of agreement among binary predictions of suitability from the different single algorithms (Thuiller et al., 2014; Guisan et al., 2017). In order to establish a threshold for declaring an area as suitable habitat, the continuous predictions of habitat suitability, which ranged from  $0$  to  $1$ , were converted into binary maps by selecting probability thresholds maximizing the TSS (Jiménez-Valverde and Lobo, 2007; Thuiller et al., 2014; Guisan et al., 2017). Thus, we did not adopt a fixed threshold value, but rather sought to find an optimal threshold for each species. The coefficient of variation across single SDM predictions was calculated to estimate uncertainty among model outputs (Thuiller et al., 2014; Guisan et al., 2017). Previous studies have demonstrated that species dispersal capability can influence SDM projections (Guisan et al., 2017). These eight highly invasive ascidians can be easily transported by human activities and we mainly focus on predicting the areas susceptible to their invasions. Therefore, in this study, we estimated habitat suitability of ascidians and interpreted results assuming no limitations to their future dispersal (also known as unlimited dispersal ability hypothesis) – a widely used hypothesis: species have unlimited dispersal ability thus can occur in climatically suitable areas. To estimate range sizes of suitable habitat, projections in geographic coordinate system were transformed to the Lambert Cylindrical Equal Area projection with a grid cell resolution of  $10$  km by  $10$  km. All analyses were carried out in R 3.4.3 (R Core Team, 2017).

## 3. Results

### 3.1. Predictive accuracy of SDMs and contribution of predictor variables

AUC and TSS results demonstrated that predictive abilities of SDMs varied among different modelling algorithms and that all algorithms except GAM, Maxent and SRE had good predictive performance for all eight ascidian species (Supporting Information Tables S1 and S2). Therefore, the seven best-performing algorithms, including ANN, CTA, FDA, GBM, GLM, MARS, and RF, were selected to evaluate variable contribution and to construct ensemble SDMs. The ensemble SDMs exhibited high predictive power for all eight ascidians as evidenced by the high AUC ( $> 0.99$ ) and TSS ( $> 0.94$ ) values (Table 1). Results of relative contributions of the nine predictor variables to the potential distributions of ascidians suggest that despite the fact that the eight ascidian species have different environmental requirements, distance to the shore, maximum sea surface temperature, and water depth were identified as the three most important variables for all species tested (overall means of contribution =  $0.468$ ,  $0.327$ , and  $0.300$ , respectively), followed by range of sea surface temperature and minimum sea surface salinity (mean contribution across species:  $0.143$  and  $0.079$ ,

respectively); range of current velocity, minimum current velocity, maximum current velocity, and range of sea surface salinity consistently contributed least to the distributions (mean contribution = 0.008, 0.016, 0.014, and 0.028, respectively; Fig. 1). Response curves of the most important marine environmental predictor (i.e. maximum sea surface temperature) also indicate that the eight ascidians have different environmental requirements (Supporting Information Fig. S10).

### 3.2. Habitat suitability under present-day climates

The coefficient of variation of species habitat suitability predicted by single SDMs demonstrated that variability in species occurrence probability within suitable ranges was relatively small and significantly lower than that within unsuitable ranges (Supporting Information Figs. S1b–S8b). The eight ascidians were predicted to have different ranges of suitable habitat under present-day climates: *M. manhattensis* has the largest suitable habitat followed by *D. vexillum*, *B. violaceus*, and *S. clava*, while suitable ranges of *C. savignyi* and *M. squamiger* were predicted to be the smallest (Table 1). Interestingly, the eight ascidians exhibited important differences in the distribution of suitable areas. For example, in Europe, the suitable habitats of *B. violaceus* and *D. vexillum* were predicted to occur mainly along coastal areas of Atlantic side of the north Iberian Peninsula, Atlantic coast of France, the United Kingdom, Ireland, Belgium, Netherlands Denmark, and Norway, whereas coastal areas of the Mediterranean Sea were most suitable for *M. squamiger* (Supporting Information Figs. S1a–S8a). It is important to note that under present-day conditions, these species have not yet fully occupied their predicted suitable habitats (Supporting Information Figs. S1a–S8a). For instance, *B. violaceus*, *D. vexillum*, and *S. clava* have not been reported in the South America, though southern coastal Argentina and Chile present suitable habitats for these species (Supporting Information Figs. S1a, S4a, S7a). According to our predictions, a number of coastal regions have high susceptibility to invasions by the studied ascidians, including the coastal areas of China, Japan, Australia, New Zealand, North America, southern South America, the Mediterranean Sea, and the Atlantic coast of Europe. In contrast, invasion risk of ascidians in Africa was much lower than that in the regions mentioned above (Supporting Information Fig. S1a–S8a, S11; Table 2).

**Table 2**

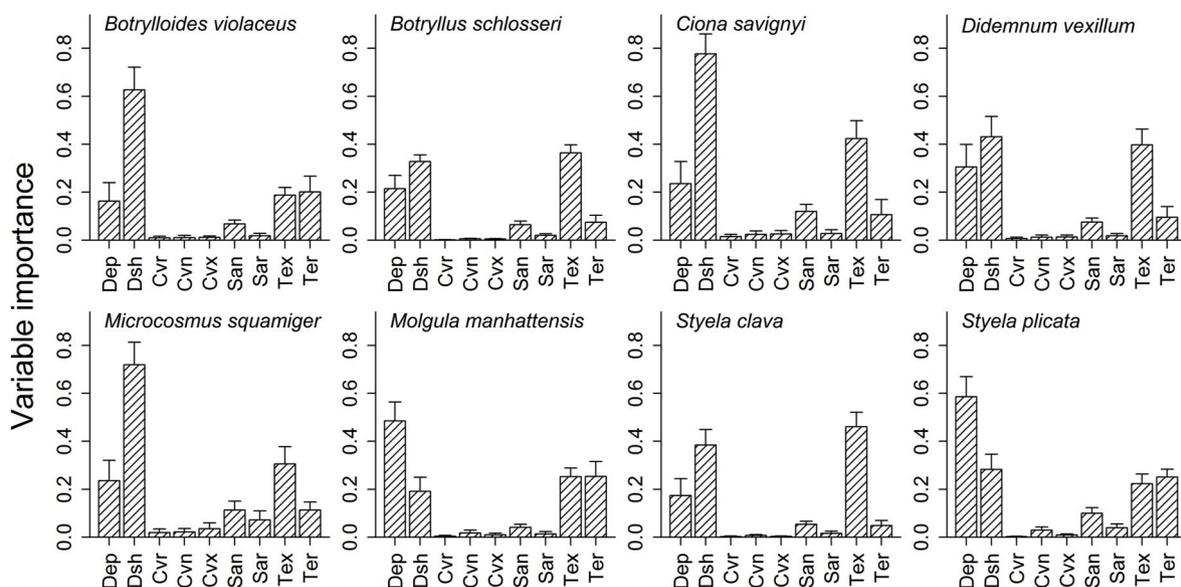
Suitable habitat ranges of each species under present-day climate and range size change (percentage values in parentheses) under RCP45 in 2050s. Four regions (i.e. Americas, Europe, Western Pacific, and Africa) were divided as shown in Supporting Information Fig. S12. Range size change was calculated as: (suitable range under RCP45 in 2050s – present-day suitable range)/present-day suitable range. Suitable habitat range is represented by the number of raster cells (i.e., 100 km<sup>2</sup>) predicted to be suitable for each species.

Species	Present-day suitable ranges and range changes under RCP45 in 2050s			
	Americas	Europe	Western Pacific	Africa
<i>B. violaceus</i>	6359 (7.5%)	3671 (16.2%)	3928 (–4.0%)	190 (–22.1%)
<i>B. schlosseri</i>	6508 (15.9%)	8633 (–21.7%)	5610 (–3.2%)	508 (–10.8%)
<i>C. savignyi</i>	1571 (39.8%)	882 (7.1%)	1608 (–21.9%)	75 (10.7%)
<i>D. vexillum</i>	8568 (6.5%)	6762 (3.3%)	5988 (–7.0%)	411 (–11.2%)
<i>M. squamiger</i>	931 (–19.1%)	2412 (–52.5%)	1653 (–6.5%)	429 (–0.5%)
<i>M. manhattensis</i>	11,119 (12.7%)	8755 (–3.3%)	10,039 (–2.2%)	649 (–43.0%)
<i>S. clava</i>	7742 (9.3%)	6014 (–5.8%)	6269 (–14.4%)	505 (–19.6%)
<i>S. plicata</i>	5673 (–31.4%)	4041 (4.9%)	5653 (–12.8%)	1342 (–11.0%)

### 3.3. Impacts of climate changes on ascidian distributions

The eight ascidians responded differently to future climate changes (Fig. 2). The suitable habitat size of *B. schlosseri* was predicted to contract in the future except under the RCP85 scenario in 2100s; the suitable habitat sizes were expected to decrease for *M. squamiger* and *S. plicata*, but expand for the other five species under future climate conditions (Fig. 2).

Here we used the results for the 2050s under an intermediate greenhouse gas emission scenario (i.e., RCP45) as an example to illustrate potential climate change impacts on ascidian distributions. Under these plausible conditions, an extensive part of European coasts was predicted to be suitable for the eight ascidian species (Fig. 3, Table 2).



**Fig. 1.** Relative contributions of the nine predictor variables to distributions of eight ascidians. Dep: water depth, Dsh: distance to the shore, Cvr: range of current velocity, Cvn: minimum current velocity, Cvx: maximum current velocity, San: minimum salinity, Sar: range of salinity, Tex: maximum sea surface temperature, Ter: range of sea surface temperature. Data is expressed as mean values + standard error.

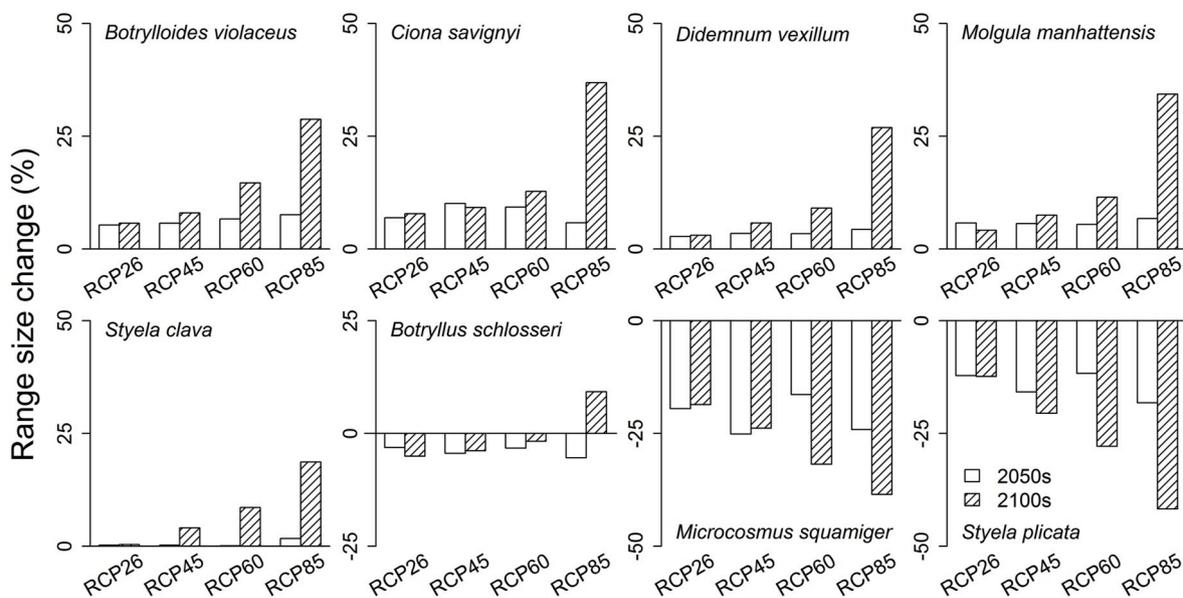


Fig. 2. Predicted changes in suitable habitat size of the eight ascidians under future climates. RCP: representative concentration pathway. 2050s: 2040–2050, 2100s: 2090–2100.

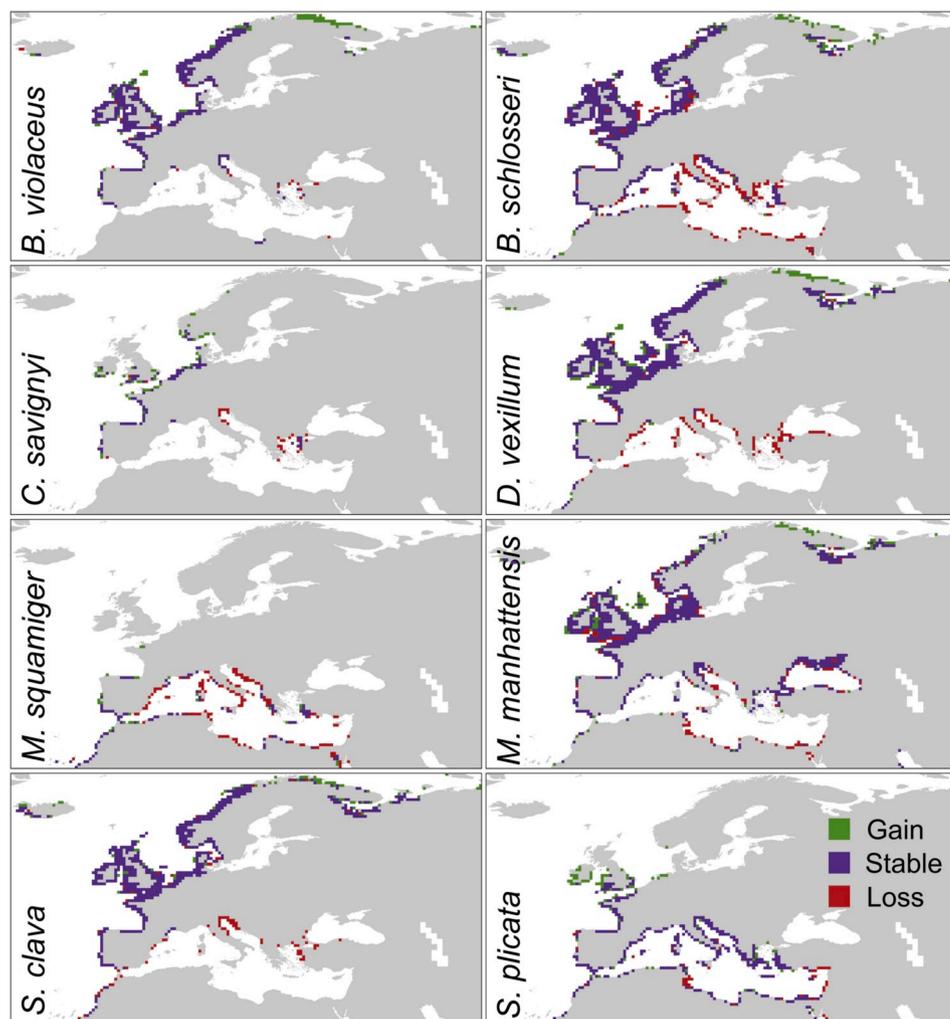


Fig. 3. Predicted range shifts of the eight ascidians in Europe in 2050s under RCP45 scenario. RCP: representative concentration pathway. 2050s: 2040–2050. Stable areas (in purple) indicate habitats that are predicted to be suitable under both present-day and future climates; loss areas (in red) show areas which are predicted to be no longer suitable in the future; gain areas (in green) represent habitats that are predicted to become suitable in the future. To improve readability, we downscaled spatial resolution from 5 arcmin to 30 arcmin. High quality figures are available from Figshare (<https://doi.org/10.6084/m9.figshare.12038619>). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

These models highlighted that the northern Atlantic coast was more susceptible to invasions, especially by *B. violaceus*, *B. schlosseri*, *D. vexillum*, *M. manhattensis*, and *S. clava* (Fig. 3, Table 2). Additional spread of *S. plicata* was forecasted to be limited to the United Kingdom, Ireland and the Netherlands. However, species range increases in Northern Europe may be offset by losses in the southern part of the continent owing to reduced suitability (Table 2). For example, suitable habitat along the Mediterranean Sea was likely to decrease under RCP45 in 2050s for all ascidians except *B. violaceus* and *S. plicata*, whose habitats were expected to remain nearly unchanged (Fig. 3).

Concerning the coasts of North and South America, model predictions highlighted that large coastal regions – except for the tropics – would be suitable for all ascidians (Fig. 4, Fig. 5, Table 2). Suitable habitats of *M. squamiger* and *S. plicata* were predicted to contract under future climates (Table 2). Habitats of six species, including *B. violaceus*, *B. schlosseri*, *C. savignyi*, *D. vexillum*, *M. manhattensis*, and *S. clava*, were expected to exhibit a poleward expansion, especially along the Gulf of Alaska, Gulf of Saint Lawrence, and Patagonia (Figs. 4 and 5). Most ascidians were projected to encounter suitable habitat only north of the Tropic of Cancer in the northern hemisphere (Fig. 4) and south of the Tropic of Capricorn in the southern hemisphere (Fig. 5); north of the Tropic of Capricorn, all species except *M. squamiger* and *S. plicata* were expected to experience suitable habitats only on the west coast, if at all (Fig. 5).

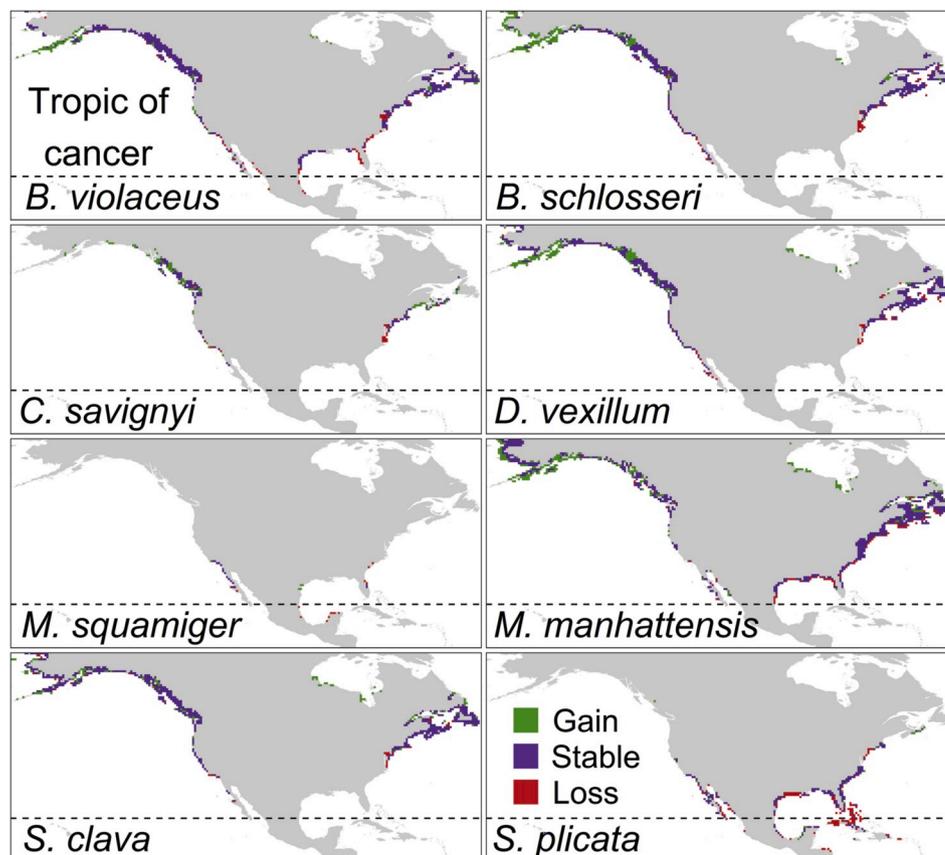
The coasts of China, Korea, and Japan were predicted under future climate change scenarios to be suitable habitats for all eight ascidians (Fig. 6). These species will generally lose habitat suitability in southern East Asia and, owing to climate changes, all these species except *M. squamiger* would extend their habitats farther north in Hokkaido in Northern Japan (Fig. 6). The coasts of Australia were predicted to be suitable for all ascidians except *C. savignyi*; the coasts of New Zealand were expected to remain susceptible to invasions by all ascidians in 2050s, with little expected changes in patterns (Fig. 7). *B. violaceus*,

*M. squamiger*, *M. manhattensis*, and *S. plicata* habitat might expand to include Tasmania and adjacent coastal mainland Australia, as well as the South Island of New Zealand (Fig. 7). In addition, *B. violaceus*, *B. schlosseri*, and *S. plicata* would experience loss of suitable habitats in some regions of Northern Australia (Fig. 7).

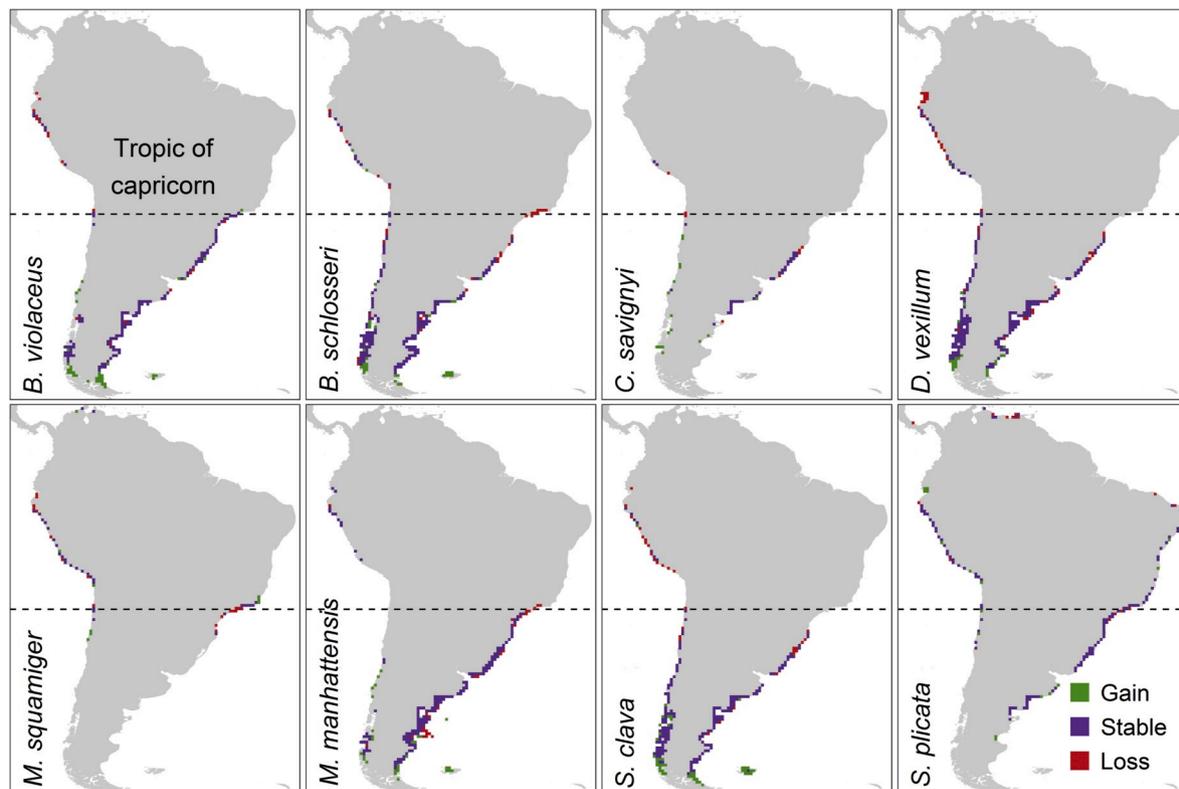
#### 4. Discussion

In this study, we developed ensemble SDMs for eight invasive ascidian species and investigated climate change impacts on their global potential distributions. Ensemble SDMs showed good predictive abilities and indicated that the eight ascidians have not yet colonized the full extent of their present-day suitable habitats worldwide. Our models also predicted that climate change would have different impacts on habitat suitability of these species. Our results hold important implications for developing management strategies for these highly invasive ascidians.

In our analyses, we considered nine predictor variables including water depth and distance to shore, as SDMs without these two geographical variables always resulted in unreasonably wide predictions (Supporting Information Figs. S1c–S8c). This might be owing to common marine environmental variables (such as maximum SST) among regions within the Exclusive Economic Zone (Supporting Information Fig. S13). In addition, we suspect that water depth and distance to shore may represent proxies for other relevant factors such as light. Previous studies have illustrated the important role of light on larval release of ascidians (e.g. Forward et al., 2000). Therefore, SDMs only considering marine environmental variables would produce enlarged predictions. Among the nine predictor variables chosen to construct SDMs, distance to the shore, maximum sea surface temperature, and water depth were the top three influential predictors of ascidian distributions. As these species are mainly restricted to shallow, nearshore habitats (Shenkar and Swalla, 2011; Zhan et al., 2015), it was not surprising that two geographical variables were predicted to play critical roles in regulating



**Fig. 4.** Predicted range shifts of the eight ascidians in North America in 2050s under RCP45 scenario. RCP: representative concentration pathway. 2050s: 2040–2050. Stable areas (in purple) indicate habitats that are predicted to be suitable under both present-day and future climates; loss areas (in red) show areas which are predicted to be no longer suitable in the future; gain areas (in green) represent habitats that are predicted to be suitable in the future. Dashed lines represent the tropic of cancer. To improve readability, we downscaled spatial resolution from 5 arcmin to 30 arcmin. High quality figures are available from Figshare (<https://doi.org/10.6084/m9.figshare.12038619>). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



**Fig. 5.** Predicted range shifts of the eight ascidians in South America in 2050s under RCP45 scenario. RCP: representative concentration pathway. 2050s: 2040–2050. Stable areas (in purple) indicate habitats that are predicted to be suitable under both present-day and future climates; loss areas (in red) show areas which are predicted to be no longer suitable in the future; gain areas (in green) represent habitats that are predicted to be suitable in the future. Dashed lines represent the tropic of capricorn. To improve readability, we downscaled spatial resolution from 5 arcmin to 30 arcmin. High quality figures are available from Figshare (<https://doi.org/10.6084/m9.figshare.12038619>). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

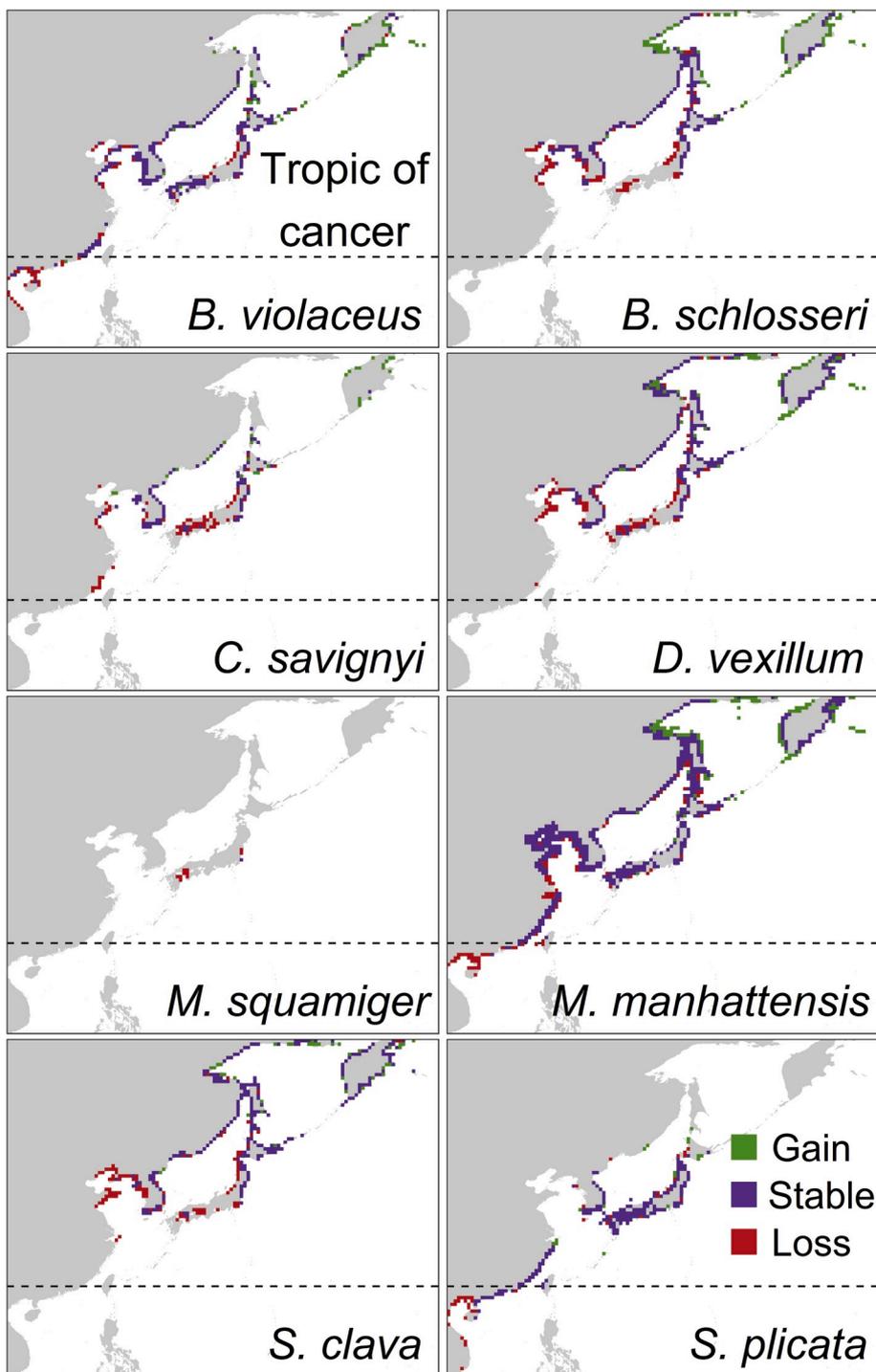
their distributions. Our finding regarding the importance of temperature agrees with previous studies (Belanger et al., 2012; Bosch et al., 2018; Goldsmit et al., 2018). Furthermore, Belanger et al. (2012) demonstrated that mean annual temperature was the most important predictor variable regulating benthic marine biogeographic structure. Similarly, using SDMs, Bosch et al. (2018) provided convincing evidence that the mean sea surface temperature was the most relevant predictor of global distributions for 514 marine species.

Water salinity also strongly influences ascidian development and distributions (Thiyagarajan and Qian, 2003; Epelbaum et al., 2009; Locke and Carman, 2009; Nagar and Shenkar, 2016). In our study, ensemble SDMs highlighted that the effect of salinity was not nearly as strong as that of temperature in any of the eight ascidian species. Such difference was mainly due to the limited variation of salinity in our study areas. We focused only on coastal areas within the Exclusive Economic Zone. Within this area, maximum sea surface temperature was evenly distributed and covered a wide range from  $-1.7$  to  $34.8$  °C, whereas minimum sea surface salinity mainly varied only between 26 and 38‰ (Supporting Information Fig. S14). This relatively minor variation in minimum sea surface salinity might partly account for our model's failure to highlight the importance of salinity in affecting ascidian distributions.

According to our SDM predictions, the eight ascidians displayed different distribution patterns under present-day climates (Supporting Information Figs. S1a–S8a) and were expected to respond differently to future climate changes (Figs. 3–7). Under present-day climates, predicted suitable habitats of the eight ascidians were often larger than their current known distribution ranges. This finding is consistent with several previous SDM studies on ascidians (Herborg et al., 2009; Goldsmit et al., 2018; Lins et al., 2018). Several possible factors including

dispersal limitation and sampling bias have been proposed to explain this phenomenon (see Goldsmit et al., 2018). Owing to intensive human activities such as global shipping, invasion risks of *M. manhattensis*, *B. schlosseri*, *B. violaceus*, *S. plicata*, *D. vexillum*, and *S. clava* induced by such activities were expected to be high due to their large area of suitable habitats, while risks of *M. squamiger* and *C. savignyi* spread were relatively low (Figs. 3–7). These findings are troubling because several biological features of ascidians such as a relative short planktonic larval phase (usually minutes to several days) lead to a high level of dispersal limitation, particularly at regional and continental scales (Zhan et al., 2015). Thus, great care must be taken to ensure that intensive human activities such as shipping and aquaculture do not facilitate further spread of these invasive species to uncolonized areas. We developed SDMs using nine abiotic predictors, however, it is possible that factors not represented by these predictors might also play an important role in determining the distribution of ascidians. It should also be noted that in addition to abiotic factors, biotic interactions could also play a critical role in regulating species distribution. Accordingly, our results of wider potential ranges than current known distribution ranges might also result from the lack of consideration of factors impeding the establishment of the species in these areas.

The future changes in marine environmental conditions, including increments of maximum sea surface temperature (Supporting Information Fig. S15), are likely to result in changes to the habitat suitability of ascidians. Overall, we expect a poleward expansion of these warm-temperate species, with loss of suitable habitats on the warmer trailing edges. This is a feature commonly predicted for marine organisms (Perry et al., 2005; Cheung et al., 2009) including ascidians (Dijkstra et al., 2017; Tracy et al., 2017). Our results support the findings by Goldsmit et al. (2018), who estimated climate change impacts on habitat

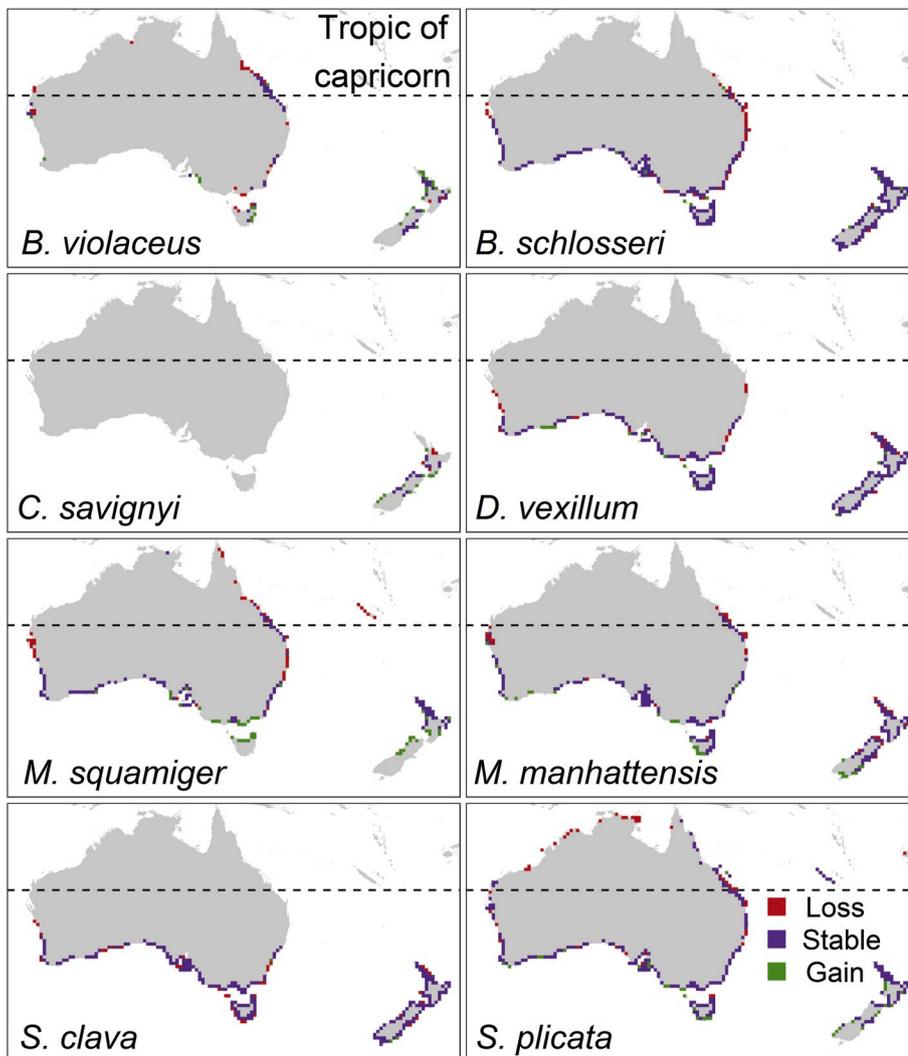


**Fig. 6.** Predicted range shifts of the eight ascidians along coastal areas of East Asia in 2050s under RCP45 scenario. RCP: representative concentration pathway. 2050s: 2040–2050. Stable areas (in purple) indicate habitats that are predicted to be suitable under both present-day and future climates; loss areas (in red) show areas which are predicted to be no longer suitable in the future; gain areas (in green) represent habitats that are predicted to be suitable in the future. Dashed lines represent the tropic of cancer. To improve readability, we downscaled spatial resolution from 5 arcmin to 30 arcmin. High quality figures are available from Figshare (<https://doi.org/10.6084/m9.figshare.12038619>). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

suitability of eight invaders including *B. violaceus* in the Canadian Arctic. Their results predicted suitable habitat of *B. violaceus* to increase by 17.1% under RCP45 emission scenario by mid-century, with a poleward shift. Shifts in species ranges related to climate changes have been documented or projected for many marine species (Perry et al., 2005; Vermeij and Roopnarine, 2008; Cheung et al., 2009; Assis et al., 2018a; Chan et al., 2019). Such distribution shifts can pose great threats to marine ecosystems by altering species interactions, and to humans dependent on living marine resources. For instance, a coastal fish species distributed along the west coast of southern Africa experienced a southward distributional shift during ocean warming, resulting in hybridization with its local congeners (Potts et al., 2014). Moreover, a

ten-year study in eastern Australia demonstrated that ocean warming increased the proportion of herbivorous fishes in kelp forests, which in turn led to the loss of kelp (Vergés et al., 2016). Species loss as a result of direct and indirect effects of the new invaders, as well as hybridization with native species on the newly colonized areas, allow biological changes to persist even if the initiating driver (climate change) has waned. Further studies are required to investigate the impacts of distribution shifts of invasive ascidians on native ecosystems.

According to our SDM predictions under future climate scenarios, five ascidians were expected to expand their geographic ranges while three species were likely to experience contractions. These different responses to climate change might reflect different environmental



**Fig. 7.** Predicted range shifts of the eight ascidians along coastal areas of Australia and New Zealand in 2050s under RCP45 scenario. RCP: representative concentration pathway. 2050s: 2040–2050. Stable areas (in purple) indicate habitats that are predicted to be suitable under both present-day and future climates; loss areas (in red) show areas which are predicted to be no longer suitable in the future; gain areas (in green) represent habitats that are predicted to be suitable in the future. Dashed lines represent the tropic of capricorn. To improve readability, we downscaled spatial resolution from 5 arcmin to 30 arcmin. High quality figures are available from Figshare (<https://doi.org/10.6084/m9.figshare.12038619>). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

tolerance among these ascidians (e.g. [Thiyagarajan and Qian, 2003](#); [Dijkstra et al., 2008](#); [Jiang et al., 2008](#); [Westerman et al., 2009](#); [Pineda et al., 2012](#); [Madariaga et al., 2014](#); [Rius et al., 2014](#)). For instance, our SDM predictions suggest that under future climate conditions, *B. violaceus* will likely expand its range while the one of *B. schlosseri* will possibly contract. The different responses might be due to differences in their environmental tolerances, especially temperature (e.g. [Dijkstra et al., 2008](#); [Epelbaum et al., 2009](#); [Sorte et al., 2011](#)). *B. violaceus* was able to tolerate a wider range of temperature than *B. schlosseri* ([Epelbaum et al., 2009](#); [Sorte et al., 2011](#)), suggesting that the former species might be more resistant than the latter to environmental changes (especially elevated SST) and more likely to expand its range in future. However, it is important to consider the possibility of rapid microevolution of these ascidians during invasions (e.g., [Huang et al., 2017](#); [Chen et al., 2018](#); [Ni et al., 2019](#)), which may lead to larger distribution ranges than predicted here. A well-known example is the rapid adaptation to extreme temperature and salinity in *Ciona robusta* during invasions of the Red Sea ([Chen et al., 2018](#)). It is noteworthy that the eight species investigated have a warm-temperate distribution range (Supporting Information Fig. S16), yet diverse responses to climate change were predicted. This may indicate the high sensitivity of our modelling approach to nuances in tolerance limits of the species that can be detected only after careful analysis of their distribution patterns. Similar results were also detected in other aquatic organisms. For example, [Van Zuiden et al. \(2016\)](#) used SDMs to identify species-specific responses to

climate change by fishes from three thermal guilds in Ontario, Canada. Further studies are required to examine environmental preferences of ascidians and confirm whether these ascidians display different thresholds of environmental tolerance.

A crucial point in all modelling approaches is the correctness of taxonomic assignments. For broadly distributed taxa, there is always the possibility that unrecognized cryptic speciation can confound analyses, and this is particularly true for ascidians (e.g., [Teske et al., 2011](#); [Zhan et al., 2012](#); [Pérez-Portela et al., 2013](#)). In our target species, genetic evidence provided confidence that we dealt with single species entities in most cases (*Botrylloides violaceus*, [Bock et al., 2011](#); *Ciona savignyi*, [Griggio et al., 2014](#), [Nydham and Harrison, 2007](#); *Didemnum vexillum*, [Stefaniak et al., 2009](#); *Microcosmus squamiger*, [Rius et al., 2012](#); *Molgula manhattensis*, [Haydar et al., 2011](#); *Styela clava*, [Goldstien et al., 2011](#); *Styela plicata*: [Pineda et al., 2011](#)). For *Botryllus schlosseri*, however, concern exists about its taxonomic status and the accuracy of existing reports, as the species has been shown to comprise several genetic clades ([Bock et al., 2012](#); [Nydham et al., 2017](#)) and speciation processes may be ongoing in some clades ([Griggio et al., 2014](#)). Even though reference databases may confound different clades of this species complex, we are confident that most records correspond to the widespread and invasive clade (i.e., Clade A in [Bock et al., 2012](#)). Thus, our results should be still valid in this regard, though caution should be applied in this case. In addition, it is important to note that SDMs only capture correlations between species distribution data and environmental variables but do

not account for different life-history characteristics (Guisan and Thuiller, 2005; Guisan et al., 2017; Briscoe et al., 2019). For instance, ascidians have diverse reproductive modes (from asexual to sexual reproduction) (Zhan et al., 2015) and SDMs cannot incorporate these differences. Process-explicit models may represent an alternative to overcome these barriers (Briscoe et al., 2019).

Another important conclusion of our analyses is the contrasting distribution forecasts for South America and Africa. The former presents a large fraction of already suitable habitats that have not been colonized by the species studied, and was forecasted to experience poleward gains of suitable habitats in the future, particularly in the Atlantic and Pacific coasts of the Patagonian region. This region emerges, therefore, as a high-risk area and one suitable for enhanced surveillance and pathway control. On the contrary, African coasts (excluding the Mediterranean side) have a low present-day risk of invasions by the studied species and the situation is unlikely to change appreciably in the future, so this continent is, for the time being, of least concern in this respect. We analysed maximum SST data within different continental coasts and found that maximum SST along the African coast was significantly higher than in other regions (Supporting Information Fig. S17). The extremely high values of maximum SST along African coasts might partially account for the relatively low habitat suitability of ascidians in this region. However, important shipping ports, such as those in South Africa, can change this picture rapidly as warming increases (Rius et al., 2014). Consequently, those hot spots should be closely monitored.

Our results highlight the importance of climate change impacts on invasive ascidian distributions and can be used as a guide to develop management strategies given that these organisms are among the most troublesome invaders in the sea. SDM predictions indicated that invasion risks of the eight ascidians were mainly concentrated along coastal areas of the Americas, Europe, East Asia, and Australasia. In areas where ascidians have already become established, physical and chemical eradication methods are required to protect marine ecosystems (Zhan et al., 2015). In areas less likely to be suitable for ascidian colonization under future climates - such as coasts of the Mediterranean Sea for *B. schlosseri* and *M. squamiger* and East Asia for *C. savignyi* and *M. squamiger* - prevention measures may be most effective. Eradication of established invasive species is very difficult and always requires long-term economic and social supports, and this is also the case for ascidians (e.g., Forrest and Hopkins, 2013; Sambrook et al., 2014). Therefore, effective prevention approaches should focus on curtailing initial spread to uncolonized regions (Olenin et al., 2011; Zhan et al., 2015). It should be noted that invasive ascidians tend to colonize artificial habitats; however, we could not incorporate artificial habitats into SDMs owing to the lack of data availability. Urbanized coasts may have higher risks to receive invasions in habitats predicted by SDMs to be suitable (Airoldi et al., 2015). Consequently, coasts in urbanized areas should be prioritized for surveillance and prevention programs. Environmental DNA (eDNA) has proven useful for early detection of invasive species (Dejean et al., 2012; Larson et al., 2017), and Zhan et al. (2015) proposed the method be used for invasive ascidians. However, additional work is required to develop highly sensitive, species-specific eDNA markers for the suite of ascidians now spreading globally (Simpson et al., 2017). Further global progress on limiting dispersal opportunities by ballast water and hull fouling is needed to curtail spread of ascidian species.

## 5. Conclusions

Modelling approaches hold a great potential to optimize prevention and management decisions. In this study, we found that the scope for expansion of invasive ascidian species was different and could be assessed by using the ensemble SDM approach. Our study predicted where ascidian species would and would not survive if introduced, and also identified high risk areas where monitoring and control efforts should be concentrated. We encourage the application of modelling

procedures to forecast marine invasion dynamics and accordingly to develop management strategies such as early detection in high risk areas.

## Declaration of competing interest

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

## CRediT authorship contribution statement

**Zhixin Zhang:** Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Investigation, Visualization, Writing - original draft, Writing - review & editing. **César Capinha:** Methodology, Software, Validation, Formal analysis, Visualization, Writing - original draft, Funding acquisition. **Dirk N. Karger:** Methodology, Software, Validation, Formal analysis, Visualization, Writing - original draft, Funding acquisition. **Xavier Turon:** Methodology, Validation, Visualization, Writing - original draft, Funding acquisition. **Hugh J. MacIsaac:** Methodology, Validation, Writing - original draft, Funding acquisition. **Aibin Zhan:** Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Resources, Investigation, Writing - original draft, Project administration, Funding acquisition, Data curation, Writing - original draft, Visualization, Investigation, Supervision, Software, Validation.

## Acknowledgements

We would like to thank all members in Zhan Laboratory for their assistance in literature review for data collection. This work was supported by the National Natural Science Foundation of China (Nos. 31622011, 31772449) to AZ, the project CTM 2017-88080 (MCIU/AEI/FEDER/UE) of the Spanish Government to XT, an NSERC Discovery grant and Canada Research Chair in Aquatic Invasive Species to HJM. CC was funded by National Funds through FCT, I.P., under the programme of 'Stimulus of Scientific Employment - Individual Support' within the contract 'CEECIND/02037/2017'. DNK received funding from the ERA-Net BiodivERsA - Belmont Forum, with the national funder Swiss National Foundation (20BD21\_184131), part of the 2018 Joint call BiodivERsA-Belmont Forum call (project 'FutureWeb').

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2020.104993>.

## References

- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Method. Ecol. Evol.* 3, 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>.
- Airoldi, L., Turon, X., Perkol-Finkel, S., Rius, M., 2015. Corridors for aliens but not for natives: effects of marine urban sprawl at a regional scale. *Divers. Distrib.* 21, 755–768. <https://doi.org/10.1111/ddi.12301>.
- Aldred, N., Clare, A.S., 2014. Impact and dynamics of surface fouling by solitary and compound ascidians. *Biofouling* 30, 259–270. <https://doi.org/10.1080/08927014.2013.866653>.
- Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* 43, 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>.
- Anacleto, P., Maulvault, A.L., Lopes, V.M., Repolho, T., Diniz, M., Nunes, M.L., Marques, A., Rosa, R., 2014. Ecophysiology of native and alien-invasive clams in an ocean warming context. *Comp. Biochem. Physiol. Mol. Integr. Physiol.* 175, 28–37. <https://doi.org/10.1016/j.cbpa.2014.05.003>.
- Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* 22, 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>.
- Assis, J., Araújo, M.B., Serrão, E.A., 2018a. Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. *Global Change Biol.* 24, e55–e66. <https://doi.org/10.1111/gcb.13818>.

- Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2018b. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. *Global Ecol. Biogeogr.* 27, 277–284. <https://doi.org/10.1111/geb.12693>.
- Atlas, N.B.N., 2019. NBN Atlas website at. <http://www.nbnatlas.org>. (Accessed 20 November 2019).
- Atlas of Living Australia, 2019. Atlas of living Australia website at. <http://www.ala.org.au>. (Accessed 20 November 2019).
- Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., Villalobos, F., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* 222, 1810–1819. <https://doi.org/10.1016/j.ecolmodel.2011.02.011>.
- Basher, Z., Bowden, D.A., Costello, M.J., 2014. Global marine environment dataset (GMED). Version 1.0 (Rev.01.2014). Available from. <http://gmed.auckland.ac.nz>.
- Belanger, C.L., Jablonski, D., Roy, K., Berke, S.K., Krug, A.Z., Valentine, J.W., 2012. Global environmental predictors of benthic marine biogeographic structure. *Proc. Natl. Acad. Sci. Unit. States Am.* 109, 14046–14051. <https://doi.org/10.1073/pnas.1212381109>.
- Blum, J.C., Chang, A.L., Liljeström, M., Schenk, M.E., Steinberg, M.K., Ruiz, G.M., 2007. The non-native solitary ascidian *Ciona intestinalis* (L.) depresses species richness. *J. Exp. Mar. Biol. Ecol.* 342, 5–14. <https://doi.org/10.1016/j.jembe.2006.10.010>.
- Bock, D.G., Zhan, A., Lejeune, C., Maclsaac, H.J., Cristescu, M.E., 2011. Looking at both sides of the invasion: patterns of colonization in the violet tunicate *Botrylloides violaceus*. *Mol. Ecol.* 20, 503–516. <https://doi.org/10.1111/j.1365-294X.2010.04971.x>.
- Bock, D.G., Maclsaac, H.J., Cristescu, M.E., 2012. Multilocus genetic analyses differentiate between widespread and spatially restricted cryptic species in a model ascidian. *Proc. Biol. Sci.* 279, 2377–2385. <https://doi.org/10.1098/rspb.2011.2610>.
- Boria, R.A., Olson, L.E., Goodman, S.M., Anderson, R.P., 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol. Model.* 275, 73–77. <https://doi.org/10.1016/j.ecolmodel.2013.12.012>.
- 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. <https://doi.org/10.1111/ddi.12668>.
- Braby, C.E., Somero, G.N., 2006. Following the heart: temperature and salinity effects on heart rate in native and invasive species of blue mussels (genus *Mytilus*). *J. Exp. Biol.* 209, 2554–2566. <https://doi.org/10.1242/jeb.02259>.
- Briscoe, N.J., Elith, J., Salguero-Gomez, R., Lahoz-Monfort, J.J., Camac, J.S., Giljohann, K.M., Holden, M.H., Hradsky, B.A., Kearney, M.R., McMahon, S.M., Phillips, B.L., Regan, T.J., Rhodes, J.R., Vesik, P.A., Wintle, B.A., Yen, J.D.L., Guillera-Arroita, G., 2019. Forecasting species range dynamics with process-explicit models: matching methods to applications. *Ecol. Lett.* 22, 1940–1956. <https://doi.org/10.1111/ele.13348>.
- Buonomo, R., Chefaoui, R.M., Lacida, R.B., Engelen, A.H., Serrão, E.A., Airolidi, L., 2018. Predicted extinction of unique genetic diversity in marine forests of *Cystoseira* spp. *Mar. Environ. Res.* 138, 119–128. <https://doi.org/10.1016/j.marenres.2018.04.013>.
- Chan, F.T., Stanislawczyk, K., Sneekes, A.C., Dvoretzky, A., Gollasch, S., Minchin, D., David, M., Jelmer, A., Albrechtsen, J., Bailey, S.A., 2019. Climate change opens new frontiers for marine species in the Arctic: current trends and future invasion risks. *Global Change Biol.* 25, 25–38. <https://doi.org/10.1111/gcb.14469>.
- Chen, Y., Shenkar, N., Ni, P., Lin, Y., Li, S., Zhan, A., 2018. Rapid microevolution during recent range expansion to harsh environments. *BMC Evol. Biol.* 18, 187. <https://doi.org/10.1186/s12862-018-1311-1>.
- Cheung, W.W., Lam, V.W., Sarmiento, J.L., Kearney, K., Watson, R., Pauly, D., 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish. Fish.* 10, 235–251. <https://doi.org/10.1111/j.1467-2979.2008.00315.x>.
- de la Hoz, C.F., Ramos, E., Puente, A., Juanes, J.A., 2019. Climate change induced range shifts in seaweeds distributions in Europe. *Mar. Environ. Res.* 148, 1–11. <https://doi.org/10.1016/j.marenres.2019.04.012>.
- Dejean, T., Valentini, A., Miquel, C., Taberlet, P., Bellemain, E., Miaud, C., 2012. Improved detection of an alien invasive species through environmental DNA barcoding: the example of the American bullfrog *Lithobates catesbeianus*. *J. Appl. Ecol.* 49, 953–959. <https://doi.org/10.1111/j.1365-2664.2012.02171.x>.
- Dijkstra, J., Dutton, A., Westerman, E., Harris, L., 2008. Heart rate reflects osmotic stress levels in two introduced colonial ascidians *Botryllus schlosseri* and *Botrylloides violaceus*. *Mar. Biol.* 154, 805–811. <https://doi.org/10.1007/s00227-008-0973-4>.
- Dijkstra, J.A., Westerman, E.L., Harris, L.G., 2011. The effects of climate change on species composition, succession and phenology: a case study. *Global Change Biol.* 17, 2360–2369. <https://doi.org/10.1111/j.1365-2486.2010.02371.x>.
- Dijkstra, J.A., Westerman, E.L., Harris, L.G., 2017. Elevated seasonal temperatures eliminate thermal barriers of reproduction of a dominant invasive species: a community state change for northern communities? *Divers. Distrib.* 23, 1182–1192. <https://doi.org/10.1111/ddi.12604>.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- Ehrenfeld, J.G., 2010. Ecosystem consequences of biological invasions. *Annu. Rev. Ecol. Syst.* 41, 59–80. <https://doi.org/10.1146/annurev-ecolsys-102209-144650>.
- Epelbaum, A., Herborg, L.M., Therriault, T.W., Pearce, C.M., 2009. Temperature and salinity effects on growth, survival, reproduction, and potential distribution of two non-indigenous botryllid ascidians in British Columbia. *J. Exp. Mar. Biol. Ecol.* 369, 43–52. <https://doi.org/10.1016/j.jembe.2008.10.028>.
- Fields, P.A., Rudomin, E.L., Somero, G.N., 2006. Temperature sensitivities of cytosolic malate dehydrogenases from native and invasive species of marine mussels (genus *Mytilus*): sequence-function linkages and correlations with biogeographic distribution. *J. Exp. Biol.* 209, 656–667. <https://doi.org/10.1242/jeb.02036>.
- Forrest, B.M., Hopkins, G.A., 2013. Population control to mitigate the spread of marine pests: insights from management of the Asian kelp *Undaria pinnatifida* and colonial ascidian *Didemnum vexillum*. *Management of Biological Invasions* 4, 317–326. <https://doi.org/10.3391/mbi.2013.4.4.06>.
- Forward, R.B., Welch, J.M., Young, C.M., 2000. Light induced larval release of a colonial ascidian. *J. Exp. Mar. Biol. Ecol.* 248, 225–238. [https://doi.org/10.1016/S0022-0981\(00\)00168-4](https://doi.org/10.1016/S0022-0981(00)00168-4).
- GBIF.org, 2019. GBIF occurrence download. Accessed from R via dismo. [www.gbif.org](http://www.gbif.org). <https://CRAN.R-project.org/package=dismo> on 2019-11-20.
- Goldsmith, J., Archambault, P., Chust, G., Villarino, E., Liu, G., Lukovich, J.V., Barber, D. G., Howland, K.L., 2018. Projecting present and future habitat suitability of ship-mediated aquatic invasive species in the Canadian Arctic. *Biol. Invasions* 20, 501–517. <https://doi.org/10.1007/s10530-017-1553-7>.
- Goldstien, S.J., Dupont, L., Viard, F., Hallas, P.J., Nishikawa, T., Schiel, D.R., et al., 2011. Global phylogeography of the widely introduced North West Pacific ascidian *Styela clava*. *PLoS One* 6, e16755. <https://doi.org/10.1371/journal.pone.0016755>.
- Griggio, F., Voskoboinik, A., Iannelli, F., Justy, F., Tilak, M.K., Xavier, T., et al., 2014. Ascidian mitogenomics: comparison of evolutionary rates in closely related taxa provides evidence of ongoing speciation events. *Genome Biology and Evolution* 6, 591–605. <https://doi.org/10.1093/gbe/evu041>.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>.
- Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. *Habitat Suitability and Distribution Models: with Applications in R*. Cambridge University Press, Cambridge.
- Haydar, D., Hoarau, G., Olsen, J.L., Stam, W.T., Wolff, W.J., 2011. Introduced or glacial relict? Phylogeography of the cryptogenic tunicate *Molgula manhattensis* (Ascidacea, Pleurogona). *Divers. Distrib.* 17, 68–80. <https://doi.org/10.1111/j.1472-4642.2010.00718.x>.
- Herborg, L.M., O'Hara, P., Therriault, T.W., 2009. Forecasting the potential distribution of the invasive tunicate *Didemnum vexillum*. *J. Appl. Ecol.* 46, 64–72. <https://doi.org/10.1111/j.1365-2664.2008.01568.x>.
- Huang, X., Ni, P., Gao, Y., Jiang, B., Zhou, Z., Zhan, A., 2017. Rapid response to changing environments during biological invasions: DNA methylation perspectives. *Mol. Ecol.* 26, 6621–6633. <https://doi.org/10.1111/mec.14382>.
- Jiang, A.L., Lin, J., Wang, C.H., 2008. Physiological energetics of the ascidian *Styela clava* in relation to body size and temperature. *Comp. Biochem. Physiol. Mol. Integr. Physiol.* 149, 129–136. <https://doi.org/10.1016/j.cbpa.2006.08.047>.
- Jiménez-Valverde, A., Lobo, J.M., 2007. Threshold criteria for conversion of probability of species presence to either-or presence-absence. *Acta Oecol.* 31 (3), 361–369. <https://doi.org/10.1016/j.actao.2007.02.001>.
- Kaluza, P., Kölzsch, A., Gastner, M.T., Blasius, B., 2010. The complex network of global cargo ship movements. *J. R. Soc. Interface* 7, 1093–1103. <https://doi.org/10.1098/rsif.2009.0495>.
- Kozubíková, E., Filipová, L., Kozák, P., Ďuriš, Z., Martín, M.P., Diéguez-Urbeondo, J., Oidtmann, B., Petrušek, A., 2009. Prevalence of the crayfish plague pathogen *Aphanomyces astaci* in invasive American crayfishes in the Czech republic. *Conserv. Biol.* 23, 1204–1213. <https://doi.org/10.1111/j.1523-1739.2009.01240.x>.
- Lambert, G., 2001. A global overview of ascidian introductions and their possible impact on the endemic fauna. In: Sawada, H., Yokosawa, H., Lambert, C.C. (Eds.), *The Biology of Ascidians*. Springer-Verlag, Tokyo, pp. 249–257.
- Lambert, G., 2007. Invasive sea squirts: a growing global problem. *J. Exp. Mar. Biol. Ecol.* 342, 3–4. <https://doi.org/10.1016/j.jembe.2006.10.009>.
- Landis, J.R., Koch, G.G., 1977. The measurement of observer agreement for categorical data. *Biometrics* 33, 159–174. <https://doi.org/10.2307/2529310>.
- Larson, E.R., Renshaw, M.A., Gantz, C.A., Umeck, J., Chandra, S., Lodge, D.M., Egan, S.P., 2017. Environmental DNA (eDNA) detects the invasive crayfishes *Orconectes rusticus* and *Pacifastacus leniusculus* in large lakes of North America. *Hydrobiologia* 800, 173–185. <https://doi.org/10.1007/s10750-017-3210-7>.
- Lins, D.M., de Marco Jr., P., Andrade, A.F., Rocha, R.M., 2018. Predicting global ascidian invasions. *Divers. Distrib.* 24, 692–704. <https://doi.org/10.1111/ddi.12711>.
- Locke, A., 2009. A screening procedure for potential tunicate invaders of Atlantic Canada. *Aquat. Invasions* 4, 71–79. <https://doi.org/10.3391/ai.2009.4.1.7>.
- Locke, A., Carman, M., 2009. In situ growth of the colonial ascidian *Didemnum vexillum* under different environmental conditions. *Aquat. Invasions* 4, 275–278. <https://doi.org/10.3391/ai.2009.4.1.27>.
- Lyman, J.M., Good, S.A., Gouretski, V.V., Ishii, M., Johnson, G.C., Palmer, M.D., Smith, D.M., Willis, J.K., 2010. Robust warming of the global upper ocean. *Nature* 465, 334–337. <https://doi.org/10.1038/nature09043>.
- Madariaga, D.J., Rivadeneira, M.M., Tala, F., Thiel, M., 2014. Environmental tolerance of the two invasive species *Ciona intestinalis* and *Codium fragile*: their invasion potential along a temperate coast. *Biol. Invasions* 16, 2507–2527. <https://doi.org/10.1007/s10530-014-0680-7>.
- Marins, F.O., Novaes, R.L., Rocha, R.M., Junqueira, A.O., 2010. Non indigenous ascidians in port and natural environments in a tropical Brazilian bay. *Zool.* 27, 213–221. <https://doi.org/10.1590/S1984-46702010000200009>.
- Molnar, J.L., Gamboa, R.L., Revenga, C., Spalding, M.D., 2008. Assessing the global threat of invasive species to marine biodiversity. *Front. Ecol. Environ.* 6, 485–492. <https://doi.org/10.1890/070064>.
- Moraitis, M.L., Tsikopoulou, I., Geropoulos, A., Dimitriou, P.D., Papageorgiou, N., Giannoulaki, M., Valavanis, V.D., Karakassis, I., 2018. Molluscan indicator species and their potential use in ecological status assessment using species distribution

- modeling. *Mar. Environ. Res.* 140, 10–17. <https://doi.org/10.1016/j.marenvres.2018.05.020>.
- Nagar, L.R., Shenkar, N., 2016. Temperature and salinity sensitivity of the invasive ascidian *Microcosmus exasperatus* Heller, 1878. *Aquat. Invasions* 11, 33–43. <https://doi.org/10.3391/ai.2016.11.1.04>.
- Ni, P., Murphy, K.J., Wyeth, R.C., Bishop, C.D., Li, S., Zhan, A., 2019. Significant population methylation divergence and local environmental influence in an invasive ascidian *Ciona intestinalis* at fine geographical scales. *Mar. Biol.* 166, 143. <https://doi.org/10.1007/s00227-019-3592-3>.
- Nydam, M.L., Harrison, R.G., 2007. Genealogical relationships within and among shallow-water *Ciona* species (Asciacea). *Mar. Biol.* 151, 1839–1847. <https://doi.org/10.1007/s00227-007-0617-0>.
- Nydam, M.L., Giesbrecht, K.B., Stephenson, E.E., 2017. Origin and dispersal history of two colonial ascidian clades in the *Botryllus schlosseri* species complex. *PLoS One* 12, e0169944. <https://doi.org/10.1371/journal.pone.0169944>.
- OBIS, 2019. Ocean Biogeographic Information System. Intergovernmental Oceanographic Commission of UNESCO. Accessed from R via robis. [www.iobis.org](http://www.iobis.org). <https://CRAN.R-project.org/package=robis> on 2019-11-20.
- Olenin, S., Elliott, M., Bysveen, I., Culverhouse, P.F., Daunys, D., Dubelaar, G.B.J., Gollasch, S., Gouletquer, P., Jelmert, A., Kantor, Y., Mézeth, K.B., Minchin, D., Occhipinti-Ambrogi, A., Olenina, I., Vandekerckhove, J., 2011. Recommendations on methods for the detection and control of biological pollution in marine coastal waters. *Mar. Pollut. Bull.* 62, 2598–2604. <https://doi.org/10.1016/j.marpolbul.2011.08.011>.
- Pérez-Portela, R., Arranz, V., Rius, M., Turon, X., 2013. Cryptic speciation or global spread? The case of a cosmopolitan marine invertebrate with limited dispersal capabilities. *Sci. Rep.* 3, 3197. <https://doi.org/10.1038/srep03197>.
- Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. *Science* 308, 1912–1915. <https://doi.org/10.1126/science.1111322>.
- Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol. Econ.* 52, 273–288. <https://doi.org/10.1016/j.ecolecon.2004.10.002>.
- Pineda, M.C., López-Legentil, S., Turon, X., 2011. The whereabouts of an ancient wanderer: global phylogeography of the solitary ascidian *Styela plicata*. *PLoS One* 6, e25495. <https://doi.org/10.1371/journal.pone.0025495>.
- Pineda, M.C., McQuaid, C.D., Turon, X., López-Legentil, S., Ordóñez, V., Rius, M., 2012. Tough adults, frail babies: an analysis of stress sensitivity across early life-history stages of widely introduced marine invertebrates. *PLoS One* 7, e46672. <https://doi.org/10.1371/journal.pone.0046672>.
- Potts, W.M., Henriques, R., Santos, C.V., Munnik, K., Anson, I., Dufois, F., Booth, A.J., Kirchner, C., Sauer, W.H., Shaw, P.W., 2014. Ocean warming, a rapid distributional shift, and the hybridization of a coastal fish species. *Global Change Biol.* 20, 2765–2777. <https://doi.org/10.1111/gcb.12612>.
- R Core Team, 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raitsos, D.E., Beaugrand, G., Georgopoulos, D., Zenetos, A., Pancucci-Papadopoulos, A.M., Theocharis, A., Papatthanassiou, E., 2010. Global climate change amplifies the entry of tropical species into the Eastern Mediterranean Sea. *Limnol. Oceanogr.* 55, 1478–1484. <https://doi.org/10.4319/lo.2010.55.4.1478>.
- Rhein, M., Rintoul, S.R., Aoki, S., Campos, E., Chambers, D., Feely, R.A., Gulev, S., Johnson, G.C., Josey, S.A., Kostianoy, A., Mauritzen, C., Roemmich, D., Talley, L.D., Wang, F., 2014. Observations: ocean. In: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Rius, M., Turon, X., Ordóñez, V., Pascual, M., 2012. Tracking invasion histories in the sea: facing complex scenarios using multilocus data. *PLoS One* 7, e35815. <https://doi.org/10.1371/journal.pone.0035815>.
- Rius, M., Clusella-Trullas, S., McQuaid, C.D., Navarro, R.A., Griffiths, C.L., Matthee, C.A., Heyden, S., Turon, X., 2014. Range expansions across ecoregions: interactions of climate change, physiology and genetic diversity. *Global Ecol. Biogeogr.* 23, 76–88. <https://doi.org/10.1111/geb.12105>.
- Sambrook, K., Holt, R.H., Sharp, R., Griffith, K., Roche, R.C., Newstead, R.G., et al., 2014. Capacity, capability and cross-border challenges associated with marine eradication programmes in Europe: the attempted eradication of an invasive non-native ascidian, *Didemnum vexillum* in Wales, United Kingdom. *Mar. Pol.* 48, 51–58. <https://doi.org/10.1016/j.marpol.2014.03.018>.
- Scheele, B.C., Pasmans, F., Skerratt, L.F., Berger, L., Martel, A., Beukema, W., et al., 2019. Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. *Science* 363, 1459–1463. <https://doi.org/10.1126/science.aav0379>.
- Shenkar, N., Swalla, B.J., 2011. Global diversity of ascidiacea. *PLoS One* 6, e20657. <https://doi.org/10.1371/journal.pone.0020657>.
- Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., Garcia-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M., 2013. Impacts of biological invasions: what's what and the way forward. *Trends Ecol. Evol.* 28, 58–66. <https://doi.org/10.1016/j.tree.2012.07.013>.
- Simpson, T.J., Dias, P.J., Snow, M., Muñoz, J., Berry, T., 2017. Real-time PCR detection of *Didemnum perlucidum* (Monniot, 1983) and *Didemnum vexillum* (Kott, 2002) in an applied routine marine biosecurity context. *Molecular Ecology Resources* 17, 443–453. <https://doi.org/10.1111/1755-0998.12581>.
- Sorte, C.J., Williams, S.L., Zerebecki, R.A., 2010. Ocean warming increases threat of invasive species in a marine fouling community. *Ecology* 91, 2198–2204. <https://doi.org/10.1890/10-0238.1>.
- Sorte, C.J., Jones, S.J., Miller, L.P., 2011. Geographic variation in temperature tolerance as an indicator of potential population responses to climate change. *J. Exp. Mar. Biol. Ecol.* 400, 209–217. <https://doi.org/10.1016/j.jembe.2011.02.009>.
- Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B., Osman, R.W., 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. *Proc. Natl. Acad. Sci. Unit. States Am.* 99, 15497–15500. <https://doi.org/10.1073/pnas.242437499>.
- Stefaniak, L., Lambert, G., Gittenberger, A., Zhang, H., Lin, S., Whitlatch, R.B., 2009. Genetic conspecificity of the worldwide populations of *Didemnum vexillum* Kott, 2002. *Aquat. Invasions* 4, 29–44. <https://doi.org/10.3391/ai.2009.4.1.3>.
- Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. *Science* 240, 1285–1293. <https://doi.org/10.1126/science.3287615>.
- Syfert, M.M., Smith, M.J., Coomes, D.A., 2013. The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS One* 8, e55158. <https://doi.org/10.1371/journal.pone.0055158>.
- Teske, P.R., Rius, M., McQuaid, C.D., Styan, C.A., Piggott, M.P., Benhissoune, S., et al., 2011. “Nested” cryptic diversity in a widespread marine ecosystem engineer: a challenge for detecting biological invasions. *BMC Evol. Biol.* 11, 176. <https://doi.org/10.1186/1471-2148-11-176>.
- Thiyagarajan, V., Qian, P.Y., 2003. Effect of temperature, salinity and delayed attachment on development of the solitary ascidian *Styela plicata* (Lesueur). *J. Exp. Mar. Biol. Ecol.* 290, 133–146. [https://doi.org/10.1016/S0022-0981\(03\)00071-6](https://doi.org/10.1016/S0022-0981(03)00071-6).
- Thuiller, W., Georges, D., Engler, R., 2014. *biomod2: Ensemble Platform for Species Distribution Modeling*. R package version 3.3.7.
- Thuiller, W., Guéguen, M., Renaud, J., Karger, D.N., Zimmermann, N.E., 2019. Uncertainty in ensembles of global biodiversity scenarios. *Nat. Commun.* 10, 1446. <https://doi.org/10.1038/s41467-019-09519-w>.
- Tracy, B.M., Larson, K.J., Ashton, G.V., Lambert, G., Chang, A.L., Ruiz, G.M., 2017. Northward range expansion of three non-native ascidians on the west coast of North America. *Biol. Invasions Record* 6, 203–209. <https://doi.org/10.3391/bir.2017.6.3.04>.
- U.S. Geological Survey, 2019. Biodiversity information serving our nation (BISON). Available at: <https://bison.usgs.gov>. (Accessed 20 November 2019).
- Van Zuiden, T.M., Chen, M.M., Stefanoff, S., Lopez, L., Sharma, S., 2016. Projected impacts of climate change on three freshwater fishes and potential novel competitive interactions. *Divers. Distrib.* 22, 603–614. <https://doi.org/10.1111/ddi.12422>.
- VanDerWal, J., Shoo, L.P., Graham, C., Williams, S.E., 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? *Ecol. Model.* 220, 589–594. <https://doi.org/10.1016/j.ecolmodel.2008.11.010>.
- Vergés, A., Doropoulos, C., Malcolm, H.A., Skye, M., Garcia-Pizá, M., Marzinelli, E.M., Campbell, A.H., Ballesteros, E., Hoey, A.S., Vila-Concejo, A., Bozec, Y., Steinberg, P.D., 2016. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proc. Natl. Acad. Sci. Unit. States Am.* 113, 13791–13796. <https://doi.org/10.1073/pnas.1610725113>.
- Vermeij, G.J., Roopnarine, P.D., 2008. The coming arctic invasion. *Science* 321, 780–781. <https://doi.org/10.1126/science.1160852>.
- Westernman, E.L., Whitlatch, R., Dijkstra, J.A., Harris, L.G., 2009. Variation in brooding period masks similarities in response to changing temperatures. *Mar. Ecol. Prog. Ser.* 391, 13–19. <https://doi.org/10.3354/meps08107>.
- Zhan, A., Darling, J.A., Bock, D.G., Lacoursiere-Roussel, A., MacIsaac, H.J., Cristescu, M.E., 2012. Complex genetic patterns in closely related colonizing invasive species. *Ecology and Evolution* 2, 1331–1346. <https://doi.org/10.1002/ece3.258>.
- Zhan, A., Briski, E., Bock, D.G., Ghabooli, S., MacIsaac, H.J., 2015. Ascidiaceans as models for studying invasion success. *Mar. Biol.* 162, 2449–2470. <https://doi.org/10.1007/s00227-015-2734-5>.