Title

Impacts of climate change on geographical distributions of invasive ascidians

Running title

Climate change impacts ascidian distributions

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Abstract

Ocean warming derived from global climate change renders marine ecosystems susceptible to biological invasions. Here, we projected habitat suitability of eight highly invasive ascidians under present-day and future climate scenarios. The mean sea surface temperature was predicted as the most important environmental factor affecting distributions. SDM projection results indicated that the tested ascidians might respond differently to future climate change. Alarmingly, the currently colonized areas are much smaller than predicted. So far, a lower number of invasive ascidians have been detected in some areas such as South American coasts. Such findings suggest that these aforementioned areas have a high risk of new invasions. In contrast, African coasts, excluding the Mediterranean side, are not prone to new invasions. Our results highlight the importance of impacts of climate change on future invasions and the need for accurate modelling of invasion risks, which can be used as a guide to develop management strategies.

Keywords

benthos; biological invasion; climate change; habitat; management strategy; species distribution model.

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 changes (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 a number of 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; Raitsos 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 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 an earlier and more intense recruitment, as well as a higher growth rate, of

introduced ascidians, which might lead to changes in benthic community structure. Sorte et al. (2010) also found that introduced species had higher thermal tolerance, survival, and growth than natives in a marine fouling community, and accordingly they 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 as a result of climate change, 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 the 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 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*, *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 increasingly 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 study impacts of climate changes on potential distributions of eight aquatic invasive species in the Canadian Arctic, and found that climate changes could result in poleward gains in habitat suitability.

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 study area can influence the outcome of SDMs (VanDerWal et al., 2009; Barve et al., 2011), thus it is a good practice to consider spatial extent of the study area (Lins et al., 2018). Ascidians are mainly distributed in near-shore waters, 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). 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 cell. After this data cleaning procedure, a total of 3,189 occurrence records (ranging from 77 to 1,367 records per species; Supporting Information Fig. 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, 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); consequently, nine predictor variables (i.e. water depth, distance to shore, annual mean temperature, range values of temperature, annual mean salinity, range values of salinity, annual mean current velocity, maximum values of current velocity, and minimum values of current velocity) were used to develop SDMs (Supporting Information Fig. S9). Water depth and distance to the shore were included in our analyses since SDMs without considering these two variables would fail to distinguish the known distribution patterns of ascidians (Supporting Information Fig. 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 expect 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, three 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 than the application of a single algorithm, owing to its ability to combine results of different models, to account for the 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 species presence-absence (1-0) data. True absence data is always difficult to acquire, thus we adopted 10,000 randomly generated pseudo-absence points within the study area as an alternative (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 ≤ 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

186 random discrimination, and 1 representing perfect discrimination (Swets, 1988; Allouche et al.,
187 2006). Algorithms with TSS > 0.75 and AUC > 0.90 were further considered in this study (Landis and
188 Koch, 1977; Swets, 1988). The relative contribution of each predictor variable on ascidian
189 distribution was assessed by a randomisation approach (Thuiller et al., 2014; Guisan et al., 2017).
190 Committee averaging ensemble models were developed by using all data, which in turn were used to
191 map the habitat suitability of ascidians under present and future climate scenarios. The committee
192 averaging method represents the level of agreement among binary predictions of suitability from the
193 different single algorithms (Thuiller et al., 2014; Guisan et al., 2017). In order to establish a threshold
194 for declaring an area as suitable habitat, the continuous predictions of habitat suitability, which
195 ranged from 0 to 1, were converted into binary maps by selecting probability thresholds maximizing
196 the TSS (Jiménez-Valverde and Lobo, 2007; Thuiller et al., 2014; Guisan et al., 2017). Thus, we did
197 not adopt a fixed threshold value, but rather sought to find an optimal threshold for each species. The
198 coefficient of variation across single SDM predictions was calculated to estimate uncertainty among
199 model outputs (Thuiller et al., 2014; Guisan et al., 2017). Previous studies have demonstrated that
200 species dispersal capability can influence SDM projections (Guisan et al., 2017). In this study, we
201 estimated habitat suitability of ascidians assuming no dispersal limitations (also known as unlimited
202 dispersal ability hypothesis) – a widely used hypothesis: species have unlimited dispersal ability thus
203 can occur in climatic suitable areas. To estimate the range size of suitable habitats, projections in
204 geographic coordinate system were transformed to the Lambert Cylindrical Equal Area projection
205 with a grid cell resolution of 10 km x 10 km. All analyses were carried out in R 3.4.3 (R Core Team,
206 2017).
207
208 **3 RESULTS**
209 **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 excellent predictive performance for all eight ascidian species (Supporting Information Table S1, S2). Therefore, the seven best-performing algorithms, including ANN, CTA, FDA, GBM, GLM, MARS, and RF, were selected to evaluate variable importance and to construct ensemble SDMs. The ensemble SDMs exhibited excellent 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, water depth, distance to the shore, and annual mean sea surface temperature were consistently identified as the three most important variables for all species tested (overall means of importance = 0.267, 0.431, and 0.443, respectively), followed by range of annual mean surface temperature and mean salinity (mean importance across species: 0.093 and 0.078); whereas mean current velocity, minimum current velocity, maximum current velocity, and range of annual sea surface salinity consistently contributed least to the distributions (mean importance = 0.008, 0.014, 0.015, and 0.028, respectively; Fig. 1).

Table 1 Predictive performance of ensemble species distribution models for eight ascidian species and suitable habitat ranges of each species under present-day climate. TSS: true skill statistics; AUC: area under the receiver operating characteristic curve. The predictive abilities are expressed as mean values ± standard error. The range of suitable habitat is represented by the number of raster cells (i.e., 100 km^2) predicted to be suitable for each species.

Species	AUC	TSS	Number of raster cells
Botrylloides violaceus	0.992 (± 0.001)	0.959 (± 0.005)	22,644
Botryllus schlosseri	0.992 (± 0.001)	0.948 (± 0.001)	28,624

Ciona savignyi	0.999 (± 0.000)	0.993 (± 0.004)	4,048
Didemnum vexillum	0.996 (± 0.001)	0.972 (± 0.004)	14,747
Microcosmus squamiger	0.996 (± 0.002)	0.965 (± 0.014)	5,904
Molgula manhattensis	0.994 (± 0.001)	0.956 (± 0.003)	37,744
Styela clava	0.995 (± 0.001)	0.966 (± 0.001)	15,915
Styela plicata	0.993 (± 0.001)	0.960 (± 0.004)	28,100

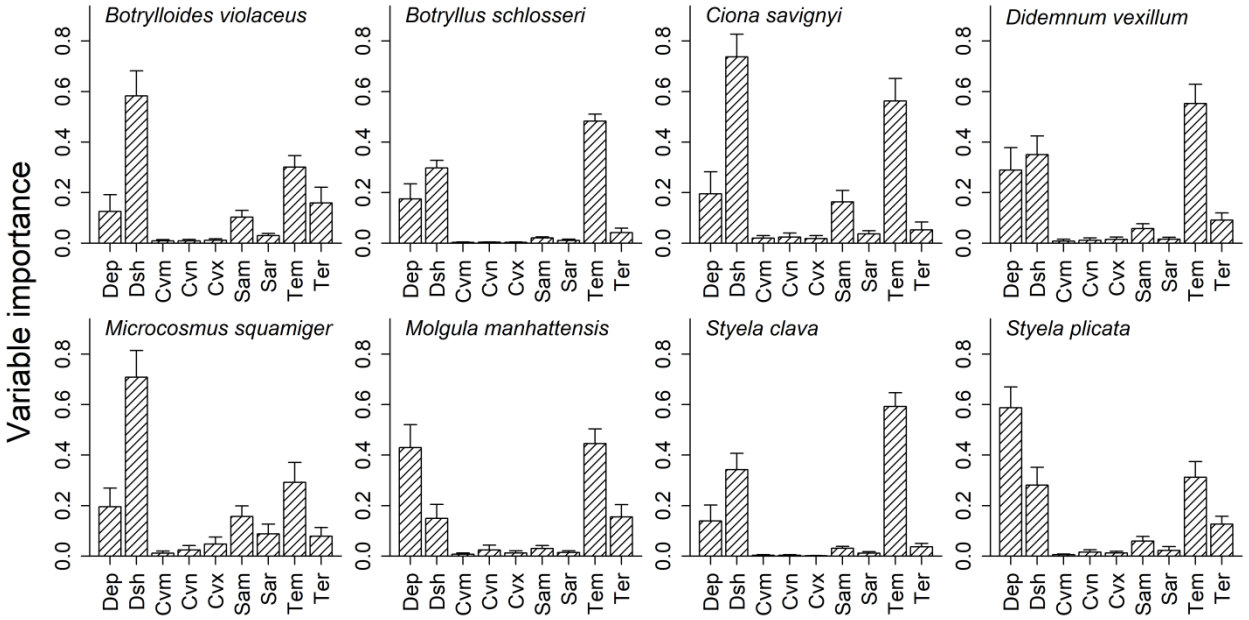

Fig. 1 Relative contributions of the nine predictor variables to distributions of eight ascidians. Dep: water depth, Dsh: distance to the shore, Cvm: mean current velocity, Cvn: minimum current velocity, Cvx: maximum current velocity, Sam: annual mean salinity, Sar: range of annual mean salinity, Tem: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

3.2 Habitat suitability under present-day climates

The coefficient of variation of species habitat suitability predicted by single SDMs showed that

241 variability in species occurrence probability within suitable ranges was relatively small and
242 significantly lower than that within unsuitable ranges (Supporting Information Fig. S1b-S8b). The
243 eight ascidians were predicted to have different ranges of suitable habitat under present-day climates:
244 *M. manhattensis* has the largest suitable habitat followed by *B. schlosseri*, *S. plicata*, and *B. violaceus*,
245 while suitable ranges of *C. savignyi* and *M. squamiger* were predicted to be the smallest (Table 1).
246 Interestingly, the eight ascidians showed important differences in the distribution of suitable areas.
247 For example, in Europe, the suitable habitats of *B. violaceus* and *D. vexillum* were predicted to occur
248 mainly along coastal areas of Atlantic side of the north Iberian Peninsula, Atlantic coast of France, the
249 United Kingdom, Ireland, Belgium, Netherlands Denmark, and Norway, whereas coastal areas of the
250 Mediterranean Sea were most suitable for *M. squamiger* (Supporting Information Fig. S1a-S8a).
251 Despite the different geographical ranges of climatically suitable habitats, the eight ascidians all
252 preferred shallow, nearshore waters. It is important to note that under present-day conditions, these
253 species have not yet fully occupied their predicted suitable habitats (Supporting Information Fig. S1a-
254 S8a). For instance, *B. violaceus*, *D. vexillum*, and *S. clava* have not been reported in the South
255 America, though southern coastal Argentina and Chile present suitable habitats for these species
256 (Supporting Information Fig. S1a, S4a, S7a). According to our predictions, a number of coastal
257 regions have high susceptibility to invasions by the studied ascidians, including the coastal areas of
258 China, Japan, Australia, New Zealand, North America, southern South America, the Mediterranean
259 Sea, and the Atlantic coast of Europe. In contrast, invasion risk of ascidians in Africa was much lower
260 than that in the regions mentioned above (Supporting Information Fig. S1a-S8a, S10).
261

262 **3.3 Impacts of climate changes on ascidian distributions**

263 The eight ascidians responded differently to future climate changes (Fig. 2). The range size of *D.*
264 *vexillum* was predicted to contract in 2050s but expand in 2100s under the four RCP scenarios; the

range sizes were expected to decrease for *B. schlosseri*, *M. squamiger*, and *S. plicata*, but expand for the other four species under future climate conditions (Fig. 2). Regardless of the time periods and RCP scenarios selected, *C. savignyi* was predicted to experience the highest habitat expansion, from 16.5% (RCP26 in 2050s) to 82.0% (RCP85 in 2100s). Our results also showed that climate changes would likely lead to greater habitat contraction in *M. squamiger* (from 17.4% decrease under RCP60 in 2050s to 44.0% decrease under RCP85 in 2100s) (Fig. 2).

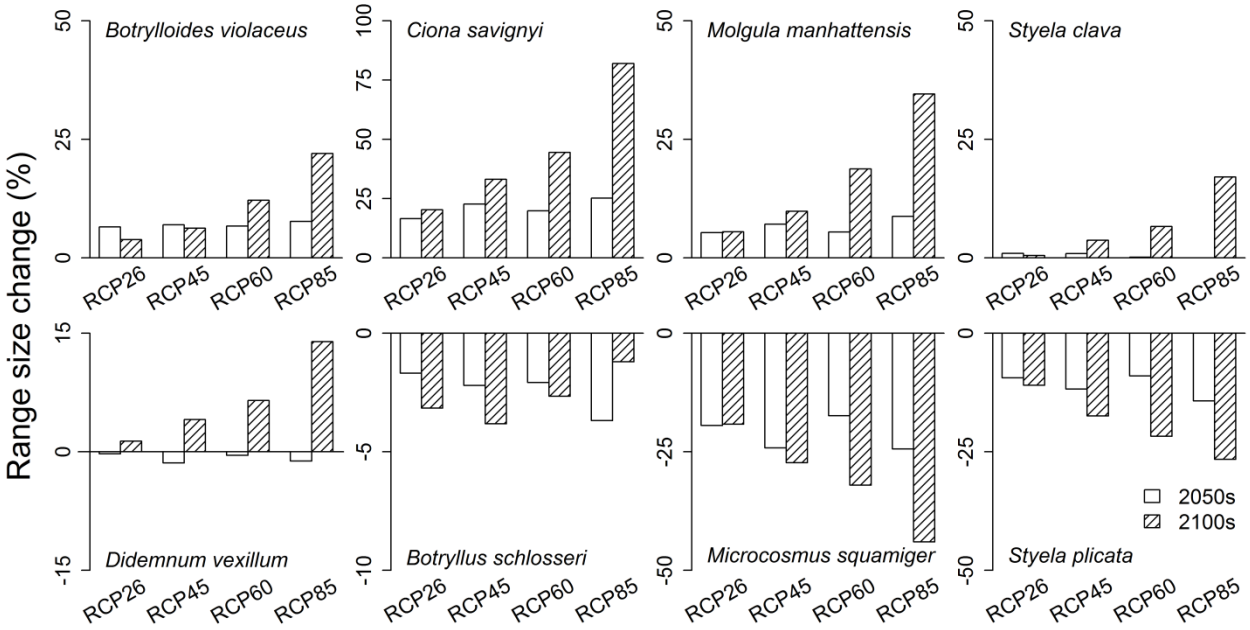

Fig. 2 Range size changes of the eight ascidians under future climates. RCP: representative concentration pathway. 2050s: 2040-2050, 2100s: 2090-2100.

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). These models highlighted that the northern Atlantic coast was more susceptible to invasions, especially by *B. violaceus*, *B. schlosseri*, *D. vexillum*, *M.*

281 *manhattensis*, and *S. clava* (Fig. 3, Table 2). Additional spread of *S. plicata* was forecasted to be
282 limited to the United Kingdom, Ireland and the Netherlands. However, species range increases in
283 Northern Europe may be offset by losses in the southern part of the continent owing to reduced
284 suitability (Table 2). For example, suitable habitat along the Mediterranean Sea was likely to decrease
285 under RCP45 in 2050s for all ascidians except *C. savignyi* and *S. plicata*, whose habitats were
286 expected to remain nearly unchanged (Fig. 3).
287
288 **Table 2** Suitable habitat ranges of each species under present-day climate and range size change
289 (percentage values in parentheses) under RCP45 in 2050s. Four regions (i.e. Americas, Europe,
290 Western Pacific, and Africa) were divided as shown in Figure 3, 4, 5, and S10. Range size change was
291 calculated as: (suitable range under RCP45 in 2050s – present-day suitable range)/present-day
292 suitable range. Suitable habitat range is represented by the number of raster cells (i.e., 100 km^2)
293 predicted to be suitable for each species.

Species	Present-day suitable range and range change under RCP45 in 2050s			
	Americas	Europe	Western Pacific	Africa
B. violaceus	8,966 (9.6%)	5,441 (7.2%)	7,349 (5.6%)	694 (–12.2%)
B. schlosseri	8,591 (12.3%)	11,767 (–9.5%)	7,170 (–6.0%)	774 (–12.5%)
C. savignyi	1,725 (45.4%)	825 (55.3%)	1,504 (–16.6%)	24 (–33.3%)
D. vexillum	5,327 (18.1%)	5,484 (–6.6%)	3,471 (–22.4%)	372 (–22.8%)
M. squamiger	1,333 (–20.4%)	1,780 (–49.7%)	1,806 (–1.9%)	769 (–27.4%)
M. manhattensis	14,378 (12.3%)	12,237 (6.0%)	10,402 (1.6%)	630 (–20.5%)
S. clava	5,111 (26.9%)	5,774 (–3.6%)	4,543 (–20.1%)	355 (–26.5%)
S. plicata	9,135 (–17.3%)	5,557 (9.8%)	9,679 (–9.2%)	2,961 (–32.3%)

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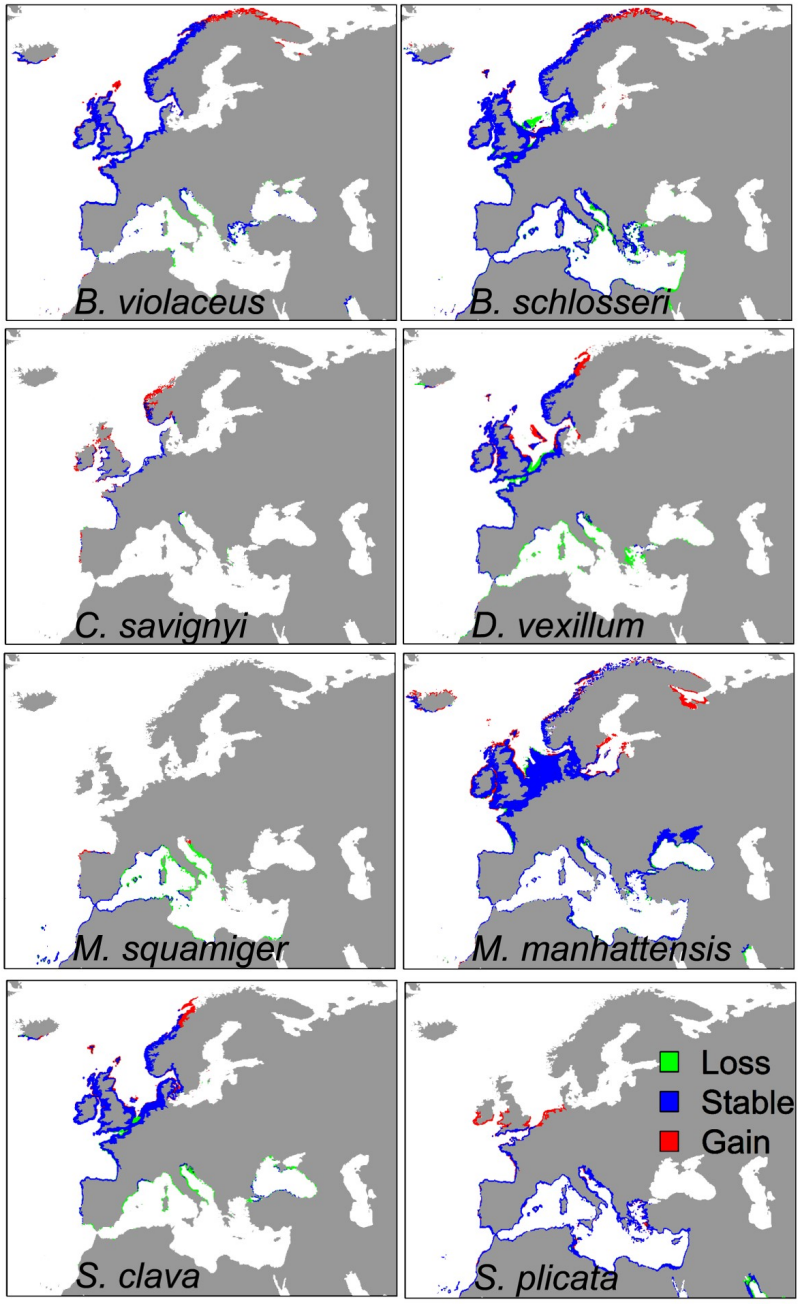
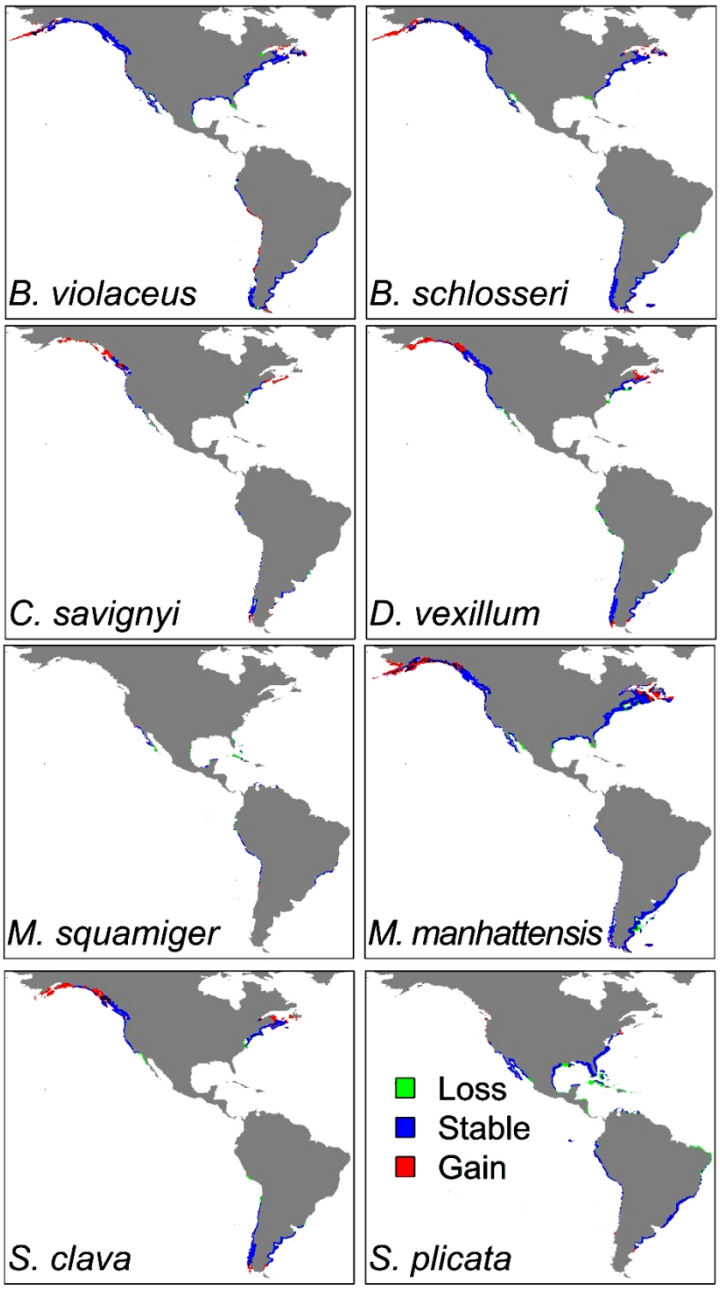


Fig. 3 Predicted range shifts of the eight ascidians in Europe in 2050s under RCP45 scenario. RCP: representative concentration pathway. 2050s: 2040-2050. Stable areas (in blue) indicate habitats that are predicted to be suitable under both present-day and future climates; loss areas (in green) show areas which are predicted to be no longer suitable in the future; gain areas (in red) represent habitats that are predicted to become suitable in the future.

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, 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 (Fig. 4). Most ascidians were projected to encounter suitable habitat only north of the Tropic of Cancer in the northern hemisphere and south of the Tropic of Capricorn in the southern hemisphere; north of the Tropic of Capricorn, all species except *S. plicata* were expected to experience suitable habitats only on the west coast, if at all (Fig. 4).



311

312 **Fig. 4** Predicted range shifts of the eight ascidians in the Americas in 2050s under RCP45 scenario.
313 RCP: representative concentration pathway. 2050s: 2040-2050. Stable areas (in blue) indicate
314 habitats that are predicted to be suitable under both present-day and future climates; loss areas (in
315 green) show areas which are predicted to be no longer suitable in the future; gain areas (in red)
316 represent habitats that are predicted to be suitable in the future.

317

The coasts of China, Korea, and Japan were predicted under future climate change scenarios to be suitable habitats for all eight ascidians. Seven species, including *B. violaceus*, *B. schlosseri*, *C. savignyi*, *D. vexillum*, *M. manhattensis*, *S. clava*, and *S. plicata*, will generally lose habitat suitability in East Asia and, owing to climate changes, all these species except *S. plicata* would extend their habitats further north in Hokkaido in Northern Japan (Fig. 5). The coasts of Australia and New Zealand were expected to remain susceptible to invasions by all ascidians in 2050s, with little expected changes in patterns (Fig. 5). *M. squamiger* and *S. plicata* habitat might expand to include Tasmania and adjacent coastal mainland Australia, as well as the South Island of New Zealand. In addition, *S. plicata* would experience loss of suitable habitats in some regions of Northern Australia.

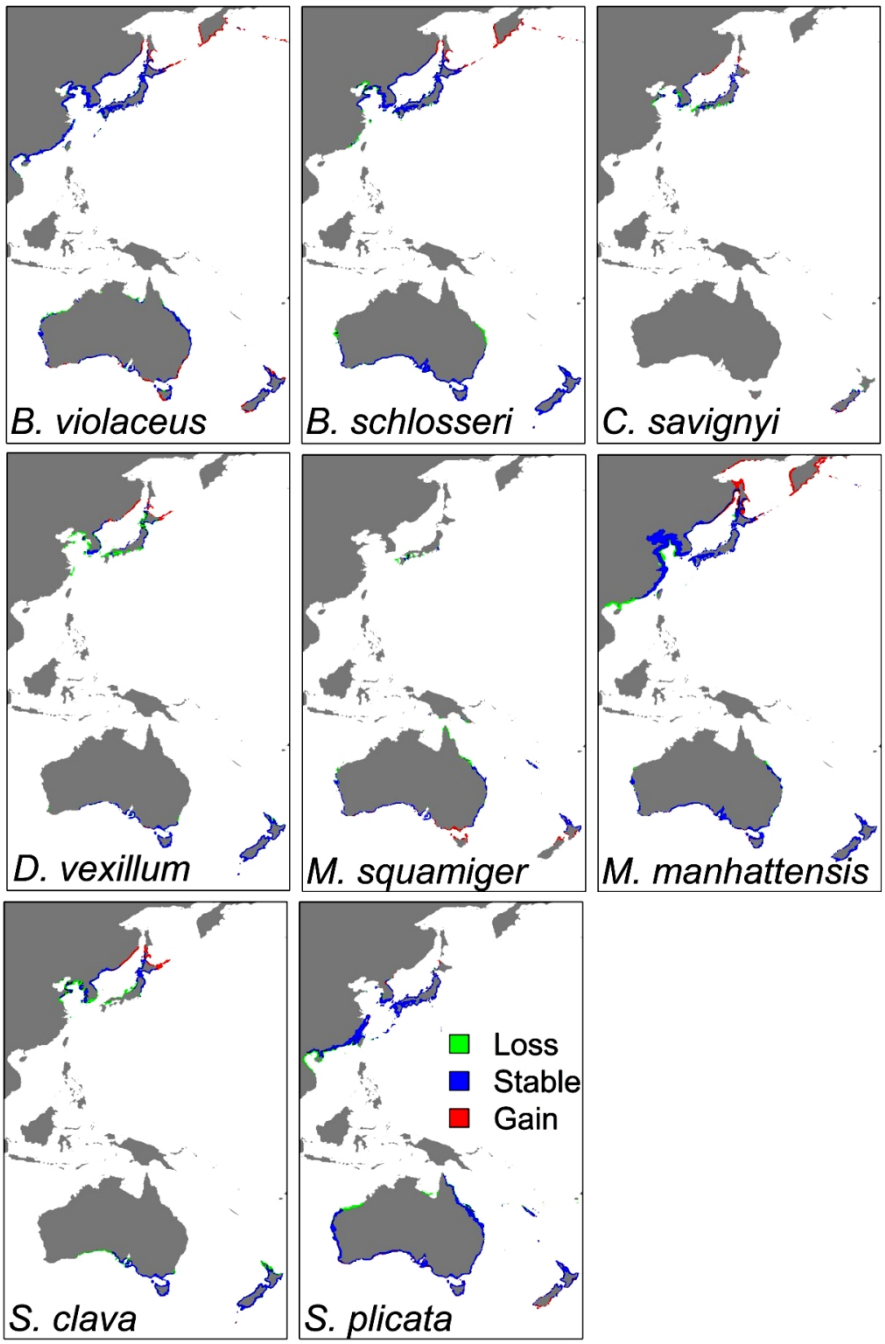


Fig. 5 Predicted range shifts of the eight ascidians along coastal areas of the Western Pacific in 2050s under RCP45 scenario. RCP: representative concentration pathway. 2050s: 2040-2050. Stable areas (in blue) indicate habitats that are predicted to be suitable under both present-day and future climates; loss areas (in green) show areas which are predicted to be no longer suitable in the future; gain areas (in red) represent habitats that are predicted to be suitable in the future.

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 these species would behave differently under future climate scenarios. Our results hold important implications for developing management strategies for these highly invasive ascidians.

Among the nine predictor variables chosen to construct SDMs, distance to the shore, water depth, and annual mean sea surface temperature were the top three influential predictors of ascidian distributions. As these species are mainly restricted to shallow, nearshore habitats, it was not surprising that two geographical variables were predicted to play critical roles in regulating their distributions. Our finding regarding the importance of annual mean sea surface temperature is in agreement 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, mean sea surface temperature was evenly distributed and covered a wide range from -1.7 to 30.2 °C, whereas mean sea surface salinity mainly varied only between 30 and 38‰ (Supporting

Information Fig. S11). This relatively minor variation in mean 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 Fig. S1a-S8a) and were expected to respond differently to future climate changes (Fig. 3-5). 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 (Fig. 3-5). 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.

Future climate changes are likely to result in changes in habitat suitability. Overall, we predicted 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) and for ascidians as well (Tracy et al., 2017). Our results support the findings by Goldsmit et al. (2018), who estimated climate change impacts on habitat suitability of eight invaders including *B. violaceus* in the Canadian Arctic. Their results predicted suitable habitat of *B. violaceus*

382 to increase by 17.1% under RCP45 emission scenario by mid-century, with a poleward shift. Shifts in
383 species ranges related to climate changes have been documented or projected for many marine
384 species (Perry et al., 2005; Vermeijj and Roopnarine, 2008; Cheung et al., 2009; Assis et al., 2018a;
385 Chan et al., 2019). Such distribution shifts can pose great threats to marine ecosystems by altering
386 species interactions, and to humans dependent on living marine resources. For instance, a coastal fish
387 species distributed along the west coast of southern Africa experienced a southward distributional
388 shift during ocean warming, resulting in hybridization with its local congeners (Potts et al., 2014).
389 Moreover, a ten-year study in eastern Australia demonstrated that ocean warming increased the
390 proportion of herbivorous fishes in kelp forests, which in turn led to the loss of kelp (Vergés et al.,
391 2016). Species loss as a result of direct and indirect effects of the new invaders, as well as
392 hybridization with native species on the newly colonized areas, allow biological changes to persist
393 even if the initiating driver (climate change) has waned. Further studies are required to investigate the
394 impacts of distribution shifts of invasive ascidians on native ecosystems.

395 According to our SDM predictions under future climate scenarios, four ascidians were expected
396 to expand their geographic ranges while geographical distributions of three species were likely to
397 contract. These different responses to climate changes might reflect different environmental tolerance
398 among these ascidians. It is noteworthy that the eight species investigated have a warm-temperate
399 distribution range, yet diverse responses to climate change were predicted. This may indicate the high
400 sensitivity of our modelling approach to nuances in tolerance limits of the species that can be detected
401 only after careful analysis of their distribution patterns. Similar results were also detected in other
402 aquatic organisms. For example, Van Zuiden et al. (2016) used SDMs to identify species-specific
403 responses to climate change by fishes from three thermal guilds in Ontario, Canada. Species-specific
404 environmental tolerance to temperature and salinity has been previously investigated in several
405 ascidian species (see Pineda et al., 2012; Madariaga et al., 2014; Rius et al., 2014). Further studies are

406 required to examine environmental preferences of ascidians and confirm whether these ascidians
407 display different thresholds of environmental tolerance.
408 A crucial point in all modelling approaches is the correctness of taxonomic assignments. For
409 broadly distributed taxa, there is always the possibility that unrecognized cryptic speciation can
410 confound analyses, and this is particularly true for ascidians (e.g., Teske et al., 2011; Zhan et al.,
411 2012; Pérez-Portela et al., 2013). In our target species, genetic evidence provided confidence that we
412 dealt with single species entities in most cases (*Botrylloides violaceus*, Bock et al., 2011; *Ciona*
413 *savignyi*, Griggio et al., 2014, Nydam and Harrison, 2007; *Didemnum vexillum*, Stefaniak et al., 2009;
414 *Microcosmus squamiger*, Rius et al., 2012; *Molgula manhattensis*, Haydar et al., 2011; *Styela clava*,
415 Goldstien et al., 2011; *Styela plicata*: Pineda et al., 2011). For *Botryllus schlosseri*, however, concern
416 exists about its taxonomic status and the accuracy of existing reports, as the species has been shown
417 to comprise several genetic clades (Bock et al., 2012; Nydam et al., 2017) and speciation processes
418 may be ongoing in some clades (Griggio et al., 2014). Even though reference databases may
419 confound different clades of this species complex, we are confident that most records correspond to
420 the widespread and invasive clade (i.e., Clade A in Bock et al., 2012). Thus, our results should be still
421 valid in this regard, though caution should be applied in this case. In addition, it is important to note
422 that SDMs only capture correlations between species distribution data and environmental variables
423 but do not account for different life-history characteristics (Guisan and Thuiller, 2005; Guisan et al.,
424 2017; Briscoe et al., 2019). For instance, ascidians have diverse reproductive modes (from asexual to
425 sexual reproduction) (Zhan et al., 2015) and SDMs cannot incorporate these differences. Process-
426 explicit models may represent an alternative to overcome these barriers (Briscoe et al., 2019).
427 Another important conclusion of our analyses is the contrasting distribution forecasts for South
428 America and Africa. The former presents a large fraction of already suitable habitats that have not
429 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. 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 *D. vexillum* and *M. manhattensis* - 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 predicted suitable habitats by SDMs (Airoldi et al., 2015). Consequently coasts in urbanized areas should be prioritized to conduct surveillance and implement 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.

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 CTM2017-88080 (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’).

Conflict of Interest: The authors declare that they have no conflict of interest.

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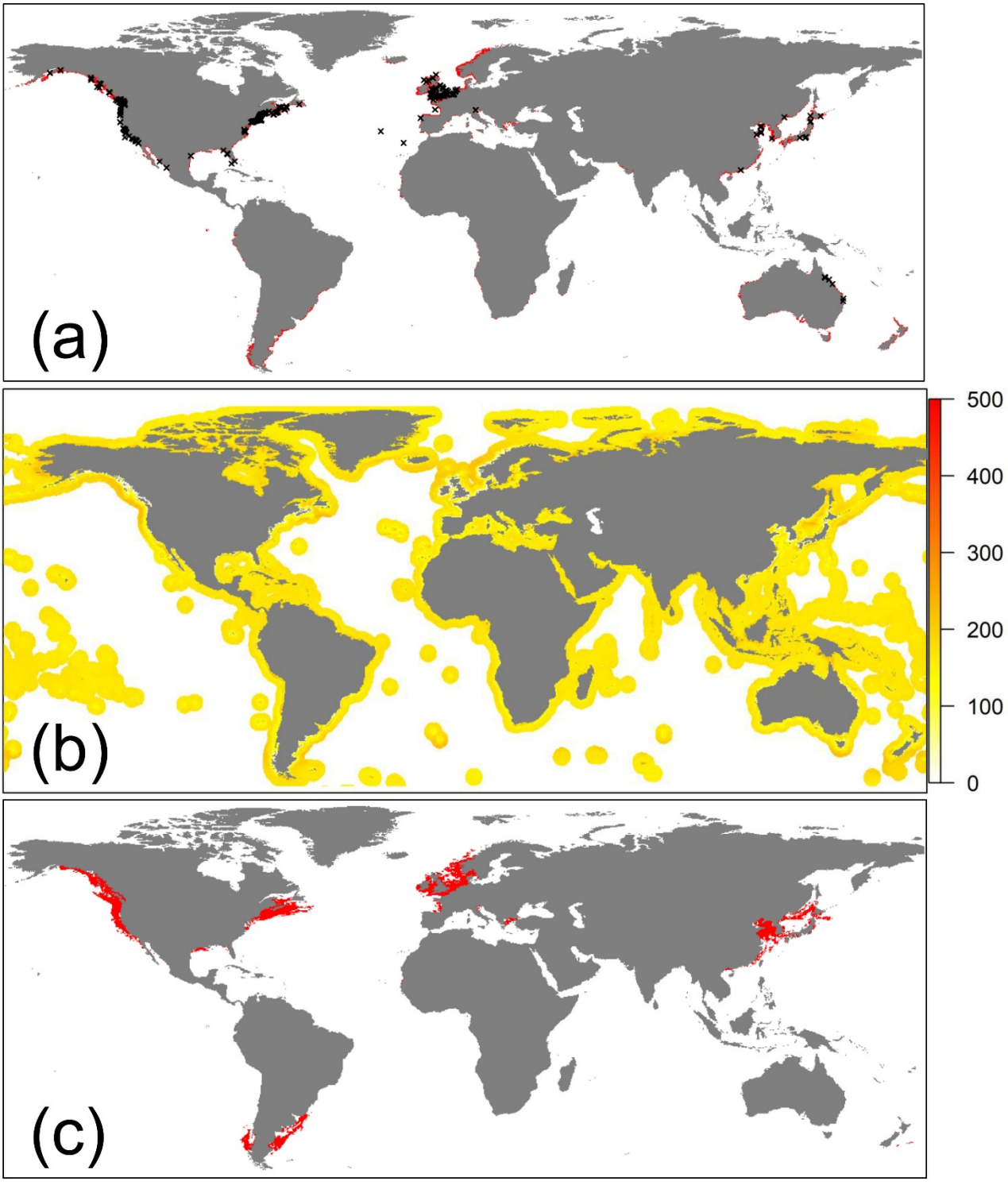
Declaration of interests

 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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Supporting Information



~~**Figure S1.** Habitat suitability of *Botrylloides violaceus* under present-day climate conditions. Habitat suitability ranges from 0 to 1000. Black crosses indicate occurrence records of *B. violaceus* used to develop species distribution models. 341 occurrence records of *B. violaceus* were used.~~

Figure S1. (a) Suitable range of *Botrylloides violaceus* under present-day climate conditions projected by ensemble SDM. Red area represents suitable range. Black crosses indicate occurrence records of *B. violaceus* used to develop SDMs. 333 occurrence records of *B. violaceus* were used. (b) Coefficient of variation of present-day species occurrence probability predicted by seven single SDMs. Coefficient of variation in suitable range (i.e. red area in panel (a)) (45.863 ± 0.148) was significantly lower than that in unsuitable range (163.505 ± 0.012) (Mann–Whitney *U* Test; $p < 2.2\times10^{-16}$). Results were expressed as mean ± standard error. Coefficient of variation was calculated as follows: coefficient of variation = standard deviation/mean*100%. (c) Suitable range of *B. violaceus* under present-day climate conditions projected by ensemble SDM without considering water depth and distance to shore.

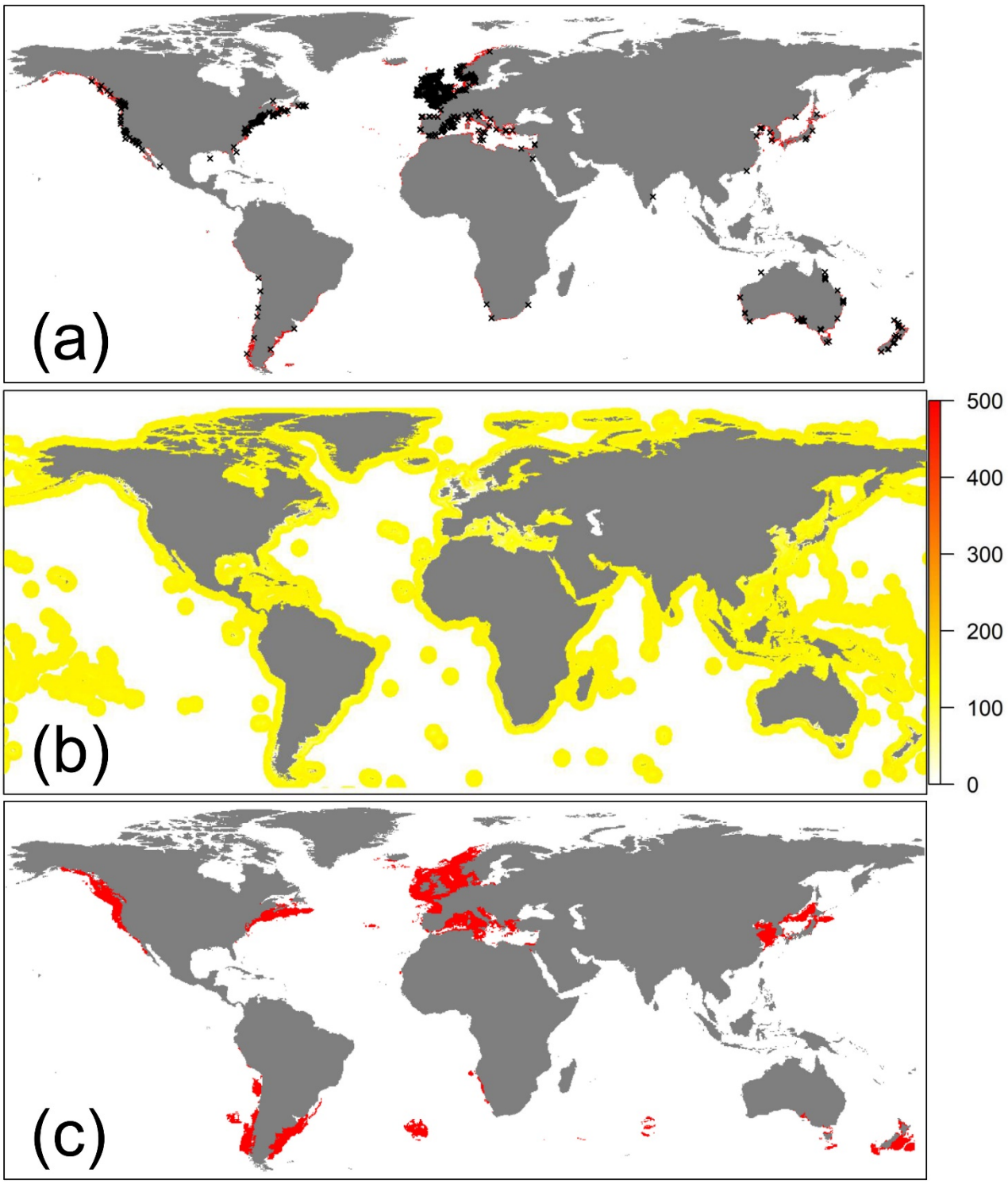


Figure S2. (**a**) Suitable range of *Botryllus schlosseri* under present-day climate conditions projected by ensemble SDM. Red area represents suitable range. Black crosses indicate occurrence records of *B. schlosseri* used to develop SDMs. 1367 occurrence records of *B. schlosseri* were used. (**b**) Coefficient of variation of present-day species occurrence probability predicted by seven single

SDMs. Coefficient of variation in suitable range (i.e. red area in panel (a)) (35.885 ± 0.113) was significantly lower than that in unsuitable range (136.869 ± 0.010) (Mann–Whitney *U* Test; $p < 2.2\times10^{-16}$). Results were expressed as mean ± standard error. Coefficient of variation was calculated as follows: coefficient of variation = standard deviation/mean*100%. (c) Suitable range of *B. schlosseri* under present-day climate conditions projected by ensemble SDM without considering water depth and distance to shore.

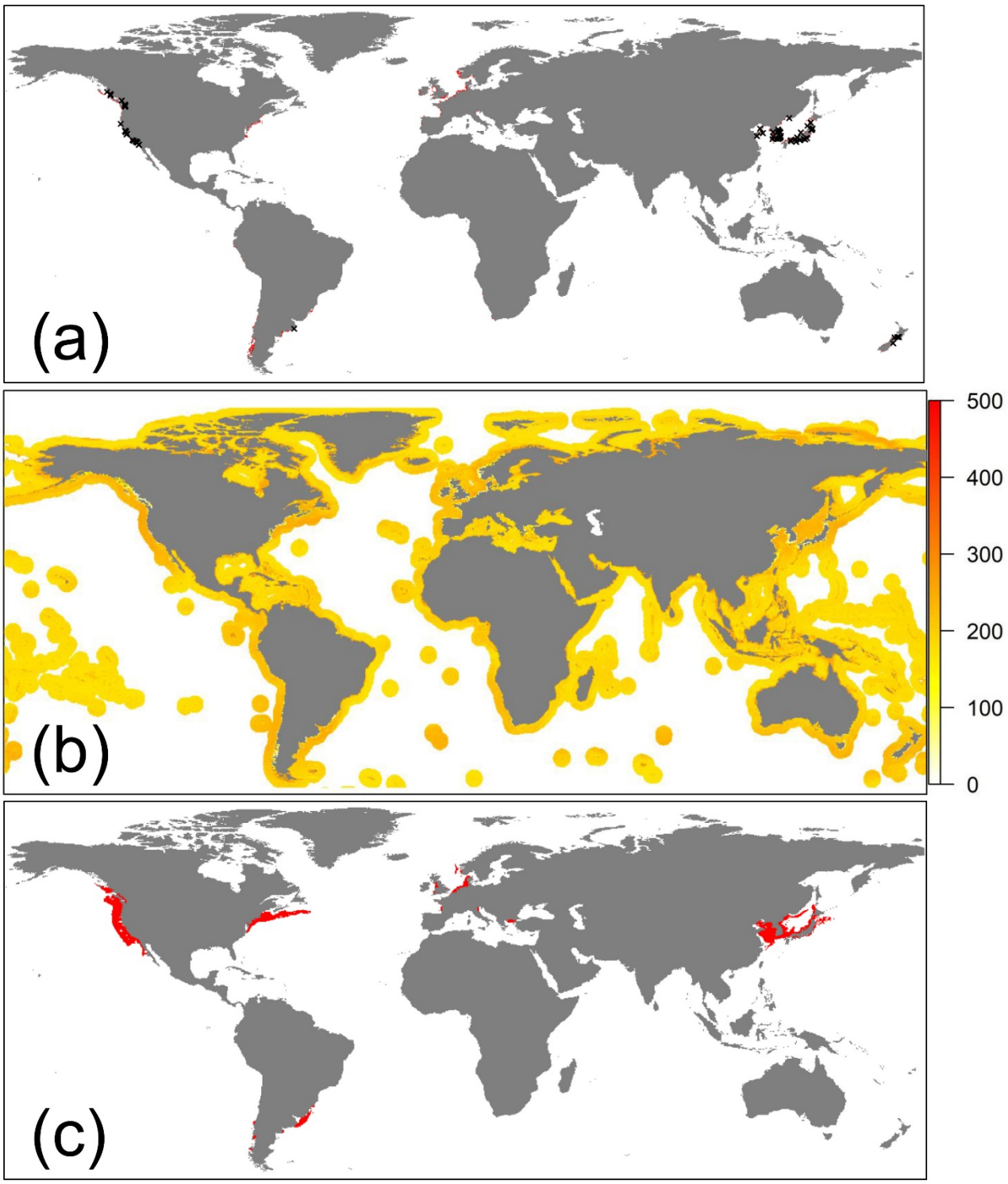


Figure S3. (a) Suitable range of *Ciona savignyi* under present-day climate conditions projected by ensemble SDM. Red area represents suitable range. Black crosses indicate occurrence records of *C. savignyi* used to develop SDMs. 93 occurrence records of *C. savignyi* were used. (b) Coefficient of variation of present-day species occurrence probability predicted by seven single SDMs. Coefficient

of variation in suitable range (i.e. red area in panel (a)) (33.827 ± 0.223) was significantly lower than that in unsuitable range (194.589 ± 0.019) (Mann–Whitney *U* Test; $p < 2.2\times10^{-16}$). Results were expressed as mean ± standard error. Coefficient of variation was calculated as follows: coefficient of variation = standard deviation/mean*100%. (c) Suitable range of *C. savignyi* under present-day climate conditions projected by ensemble SDM without considering water depth and distance to shore.

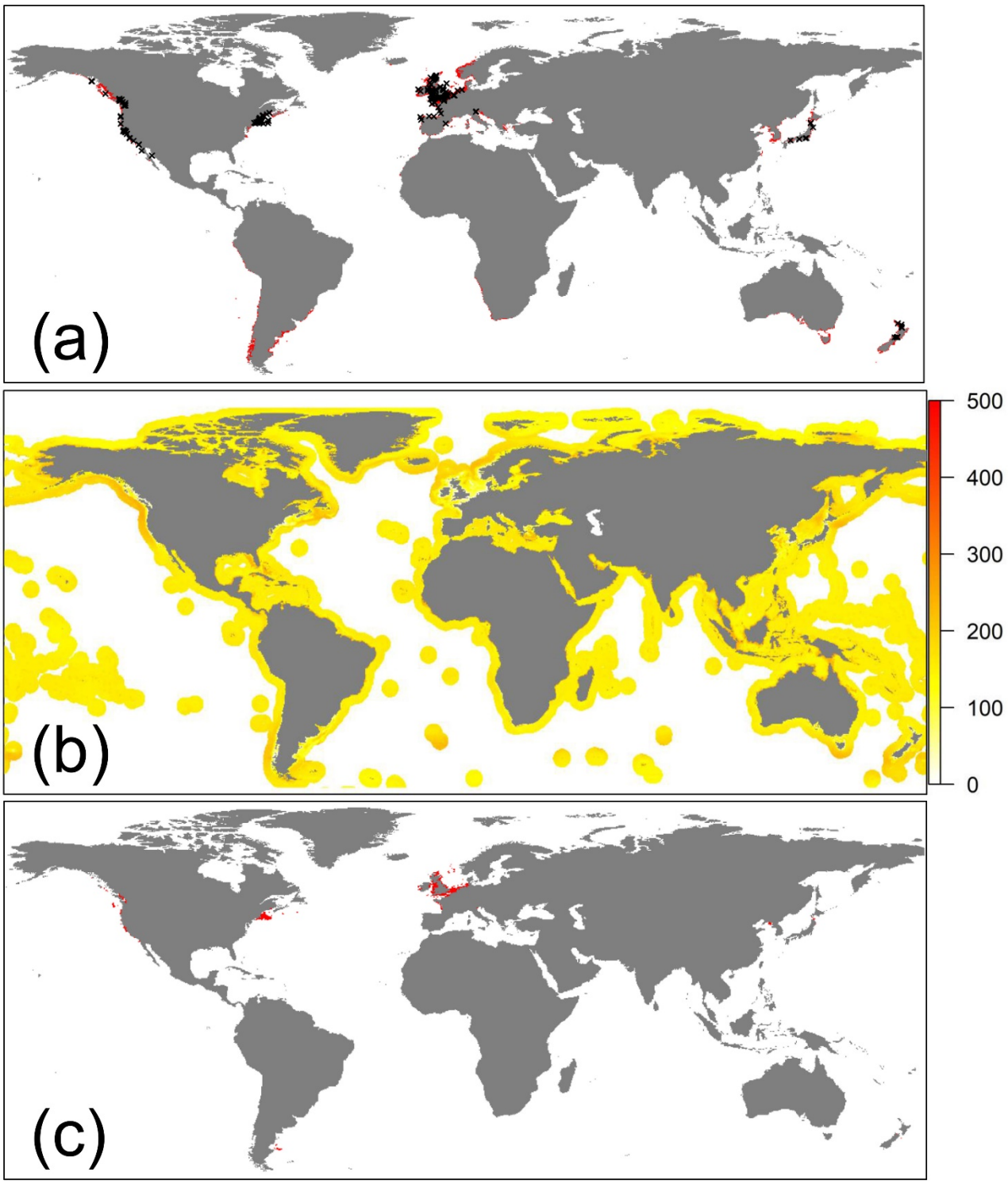


Figure S4. (a) Suitable range of *Didemnum vexillum* under present-day climate conditions projected by ensemble SDM. Red area represents suitable range. Black crosses indicate occurrence records of *D. vexillum* used to develop SDMs. 252 occurrence records of *D. vexillum* were used. (b) Coefficient of variation of present-day species occurrence probability predicted by seven single

SDMs. Coefficient of variation in suitable range (i.e. red area in panel (a)) (46.178 ± 0.157) was significantly lower than that in unsuitable range (156.493 ± 0.016) (Mann–Whitney *U* Test; $p < 2.2\times10^{-16}$). Results were expressed as mean ± standard error. Coefficient of variation was calculated as follows: coefficient of variation = standard deviation/mean*100%. (c) Suitable range of *D. vexillum* under present-day climate conditions projected by ensemble SDM without considering water depth and distance to shore.

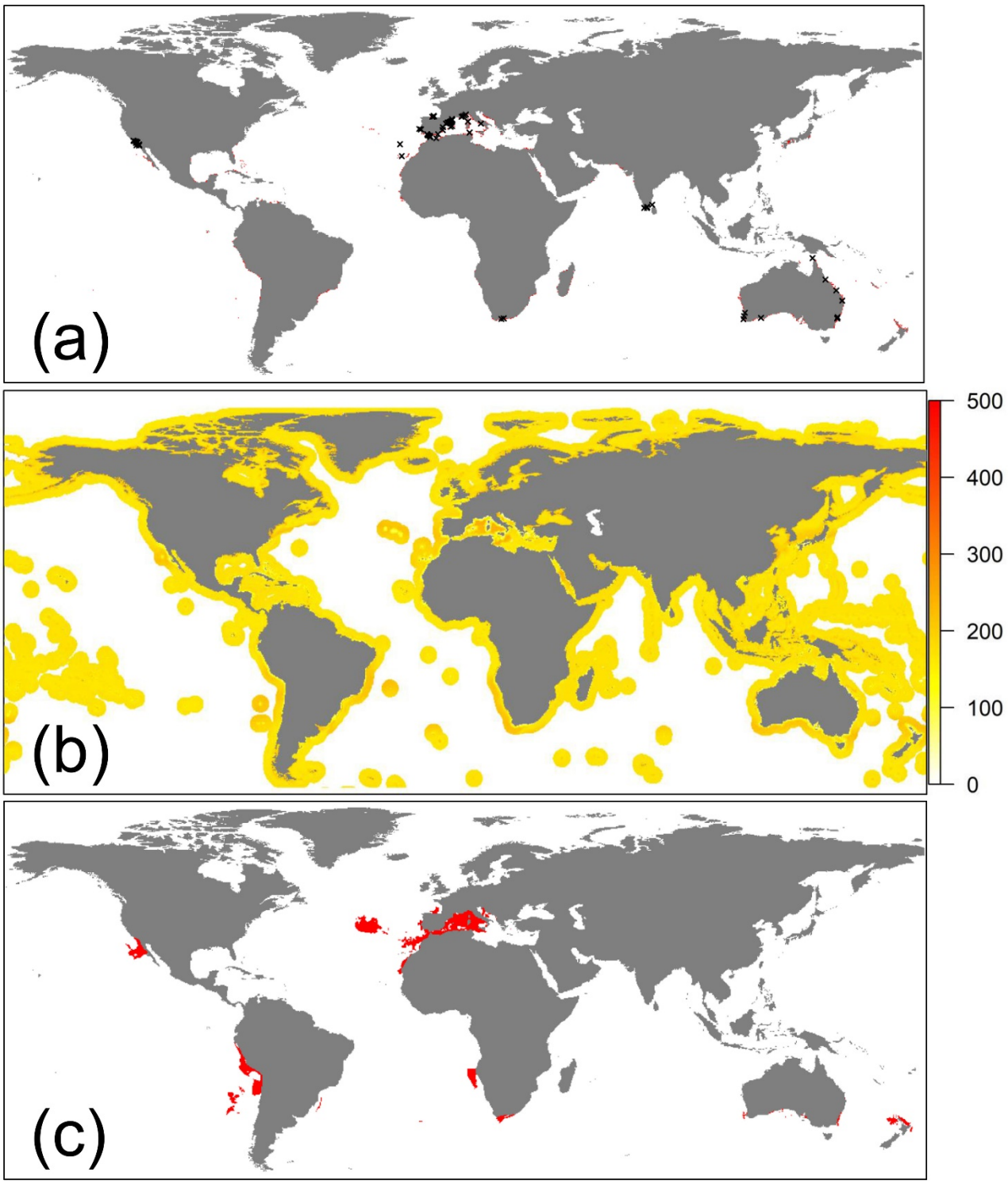


Figure S5. (a) Suitable range of *Microcosmus squamiger* under present-day climate conditions projected by ensemble SDM. Red area represents suitable range. Black crosses indicate occurrence records of *M. squamiger* used to develop SDMs. 77 occurrence records of *M. squamiger* were used. (b) Coefficient of variation of present-day species occurrence probability predicted by seven single

SDMs. Coefficient of variation in suitable range (i.e. red area in panel (a)) (31.695 ± 0.220) was significantly lower than that in unsuitable range (171.412 ± 0.013) (Mann–Whitney *U* Test; $p < 2.2\times10^{-16}$). Results were expressed as mean ± standard error. Coefficient of variation was calculated as follows: coefficient of variation = standard deviation/mean*100%. (c) Suitable range of *M. squamiger* under present-day climate conditions projected by ensemble SDM without considering water depth and distance to shore.

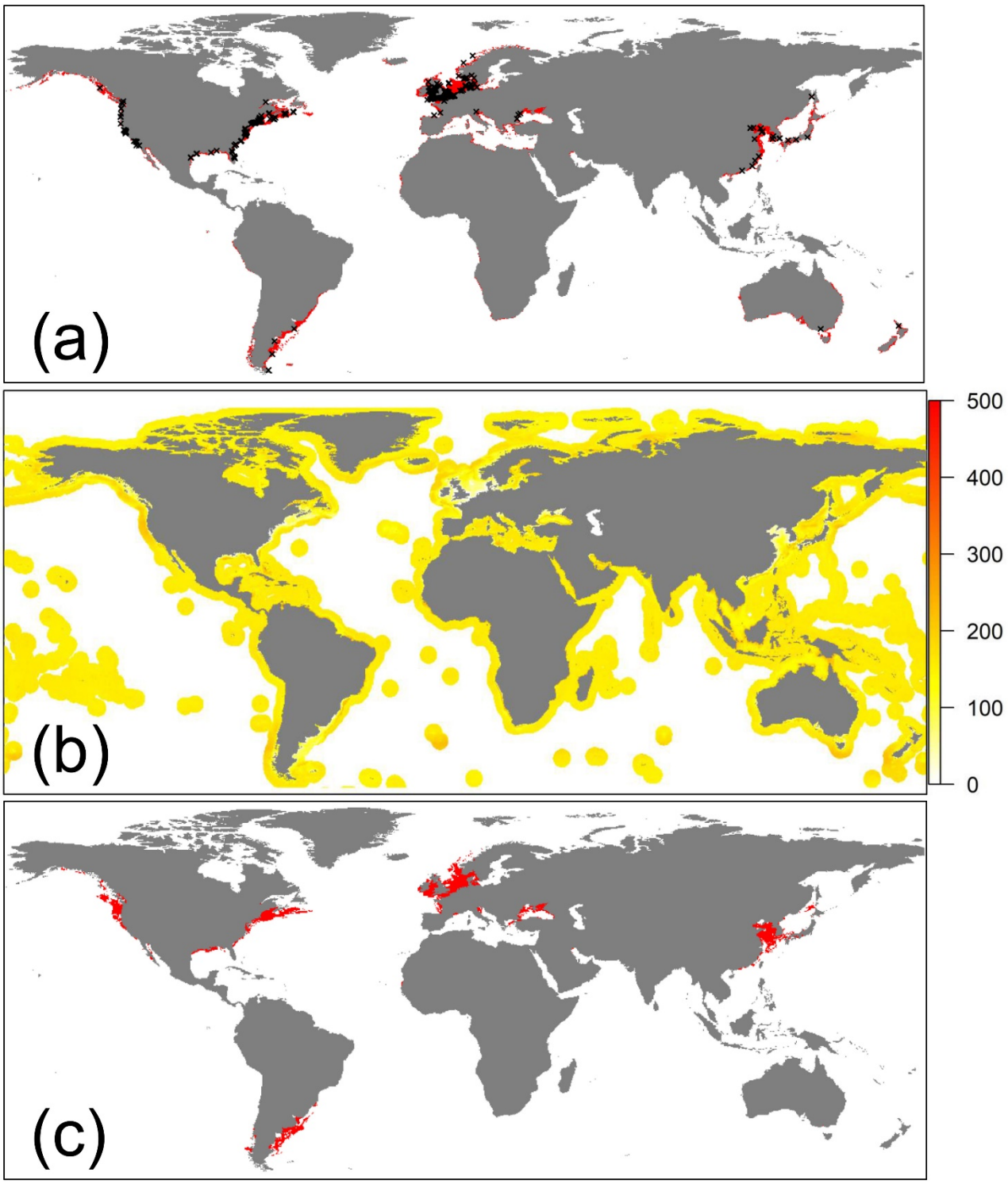


Figure S6. (a) Suitable range of *Molgula manhattensis* under present-day climate conditions projected by ensemble SDM. Red area represents suitable range. Black crosses indicate occurrence records of *M. manhattensis* used to develop SDMs. 368 occurrence records of *M. manhattensis* were used. (b) Coefficient of variation of present-day species occurrence probability predicted by

seven single SDMs. Coefficient of variation in suitable range (i.e. red area in panel (a)) (51.039 ± 0.108) was significantly lower than that in unsuitable range (154.883 ± 0.012) (Mann–Whitney *U* Test; $p < 2.2\times10^{-16}$). Results were expressed as mean ± standard error. Coefficient of variation was calculated as follows: coefficient of variation = standard deviation/mean*100%. (c) Suitable range of *M. manhattensis* under present-day climate conditions projected by ensemble SDM without considering water depth and distance to shore.

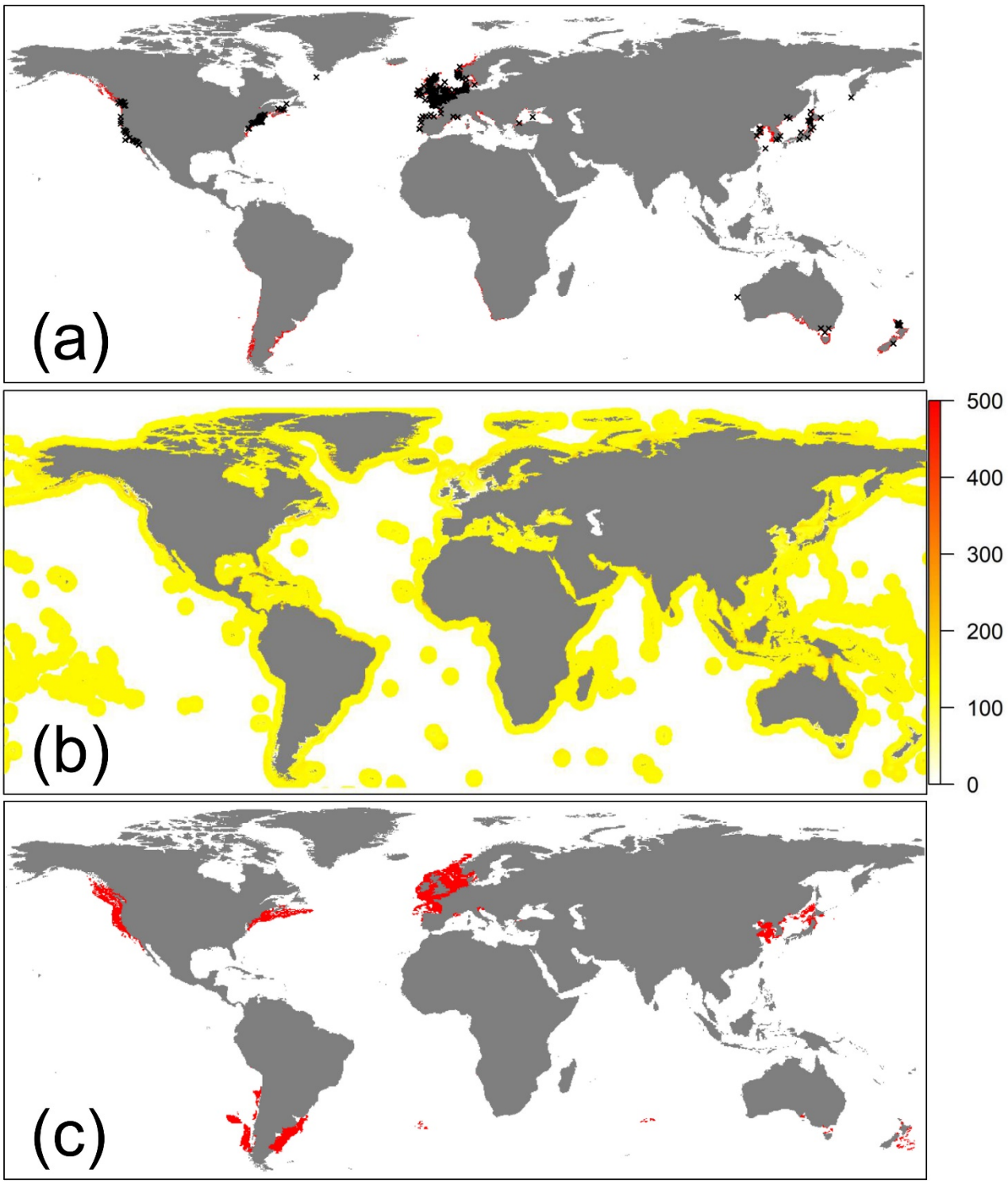


Figure S7. (a) Suitable range of *Styela clava* under present-day climate conditions projected by ensemble SDM. Red area represents suitable range. Black crosses indicate occurrence records of *S. clava* used to develop SDMs. 521 occurrence records of *S. clava* were used. (b) Coefficient of variation of present-day species occurrence probability predicted by seven single SDMs. Coefficient

of variation in suitable range (i.e. red area in panel (a)) (37.301 ± 0.169) was significantly lower than that in unsuitable range (137.427 ± 0.010) (Mann–Whitney *U* Test; $p < 2.2\times10^{-16}$). Results were expressed as mean ± standard error. Coefficient of variation was calculated as follows: coefficient of variation = standard deviation/mean*100%. (c) Suitable range of *S. clava* under present-day climate conditions projected by ensemble SDM without considering water depth and distance to shore.

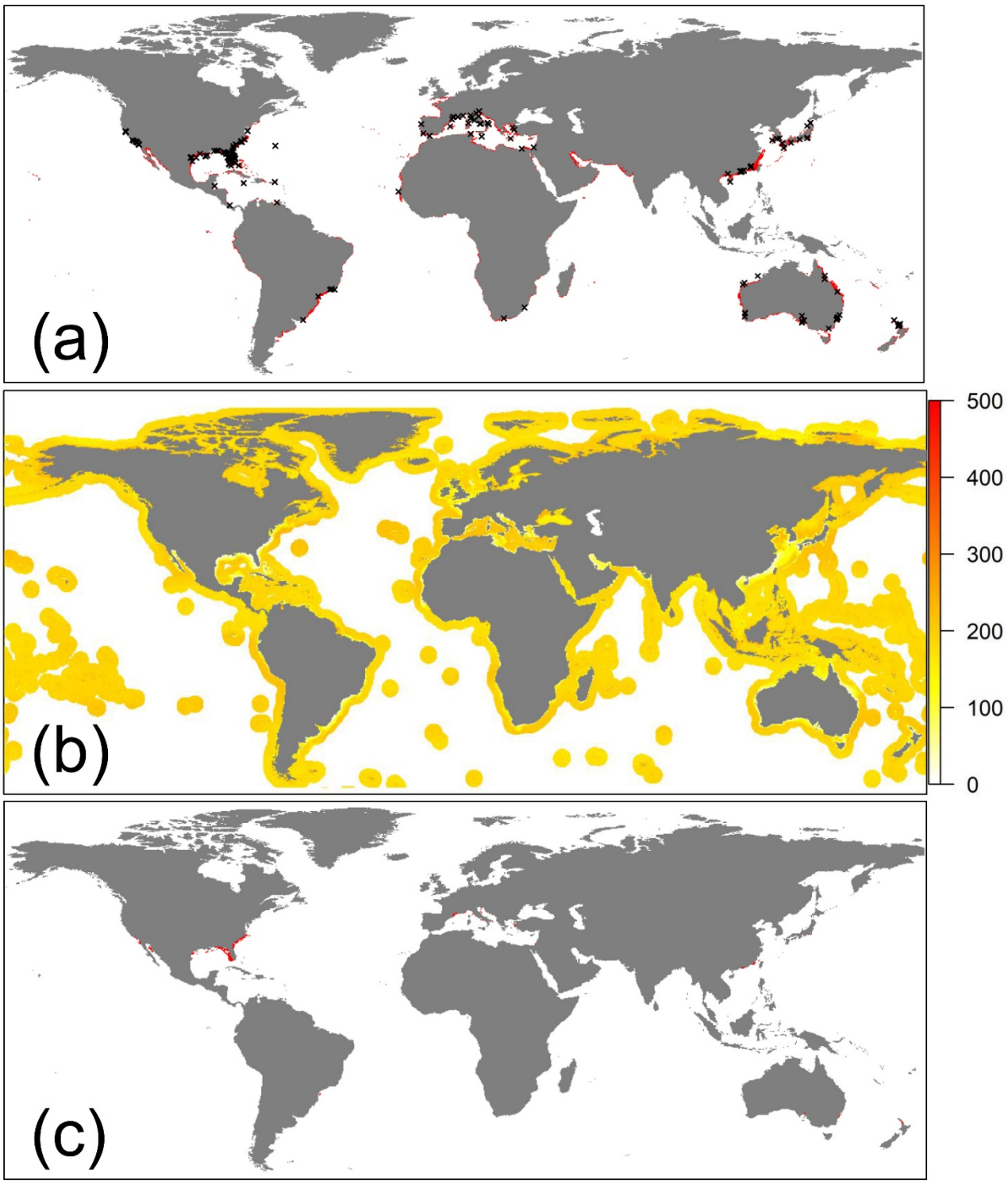


Figure S8. (a) Suitable range of *Styela plicata* under present-day climate conditions projected by ensemble SDM. Red area represents suitable range. Black crosses indicate occurrence records of *S. plicata* used to develop SDMs. 178 occurrence records of *S. plicata* were used. (b) Coefficient of variation of present-day species occurrence probability predicted by seven single SDMs. Coefficient

of variation in suitable range (i.e. red area in panel (a)) (39.872 ± 0.101) was significantly lower than that in unsuitable range (184.213 ± 0.016) (Mann–Whitney *U* Test; $p < 2.2\times10^{-16}$). Results were expressed as mean ± standard error. Coefficient of variation was calculated as follows: coefficient of variation = standard deviation/mean*100%. (c) Suitable range of *S. plicata* under present-day climate conditions projected by ensemble SDM without considering water depth and distance to shore.

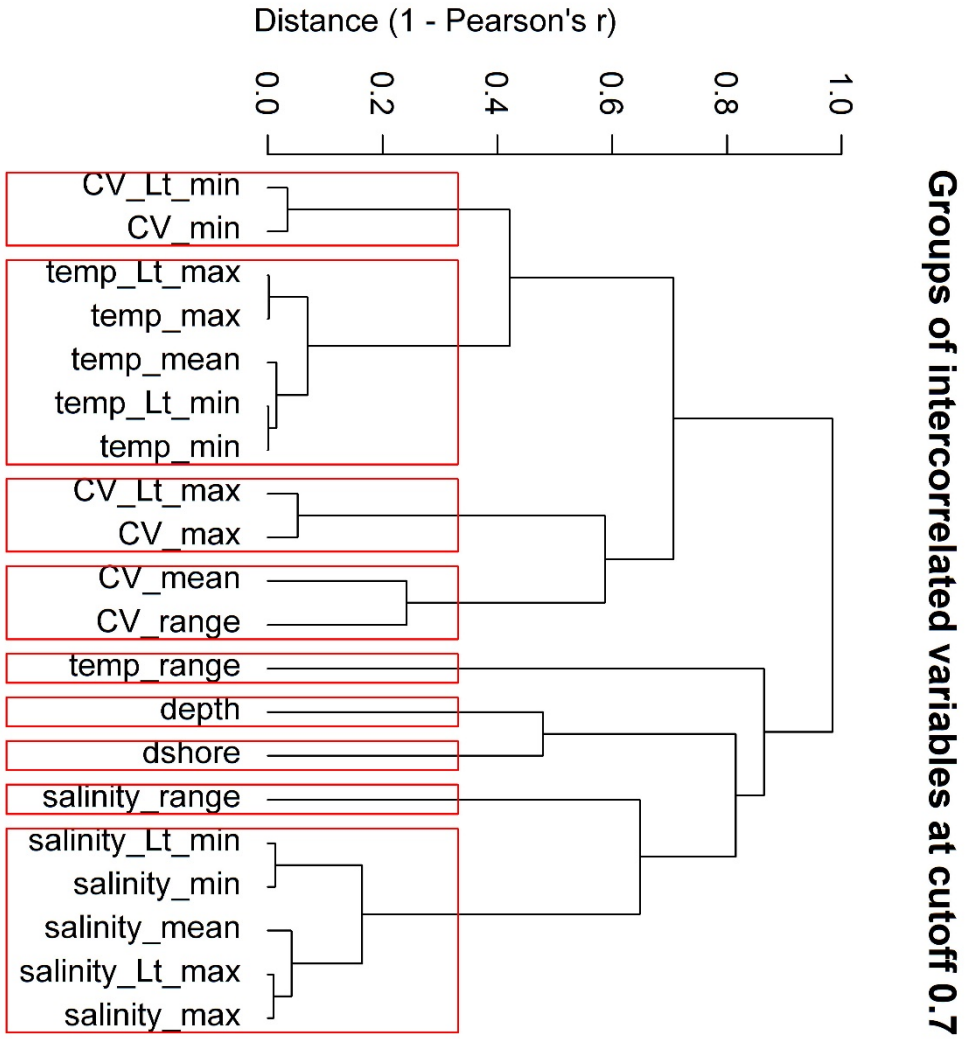


Figure S9. Collinearity analysis results of the twenty~~eight~~ marine predictor variables. temp: ~~annual~~ sea surface temperature; Lt: mean values of the minimum and maximum records per year; CV: current velocity. depth: water depth; dshore: distance to the shore. Detailed descriptions about predictors can be found in Bio-ORACLE v2.0 (http://www.bio-oracle.org). Only one predictor was selected among highly correlated predictors (i.e., Pearson's correlation coefficients $|r| > 0.7$).

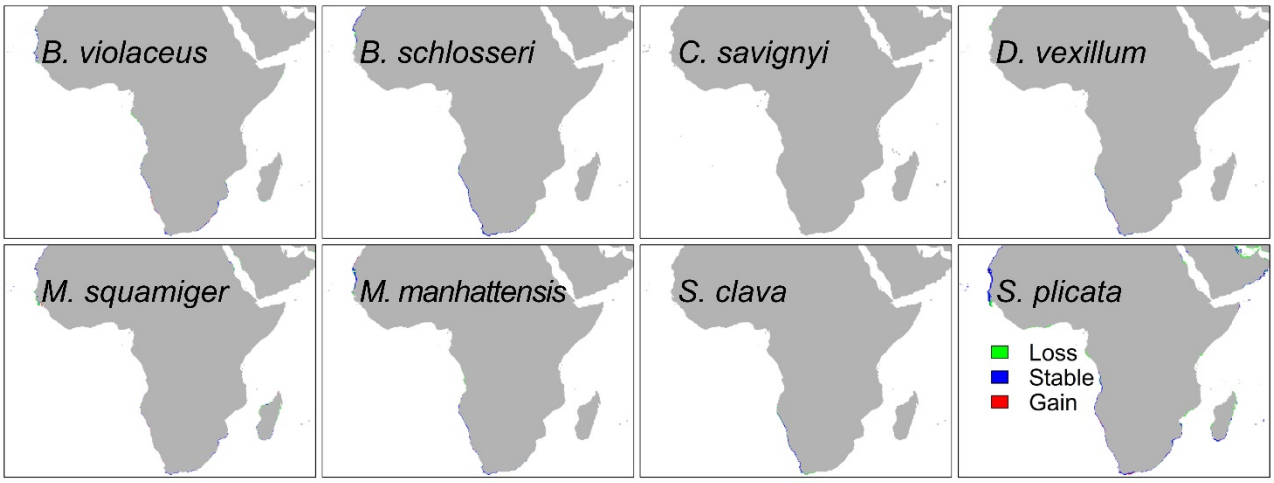


Figure S10. Predicted range shifts of the eight ascidians along African coastal areas in 2050s under RCP45 scenario. RCP: representative concentration pathway. 2050s: 2040-2050. Stable areas (in blue) indicate habitats that are predicted to be suitable under both present-day and future climates; loss areas (in green) show areas which are predicted no longer to be suitable in future; gain areas (in red) represent habitats that are predicted to be suitable in future.

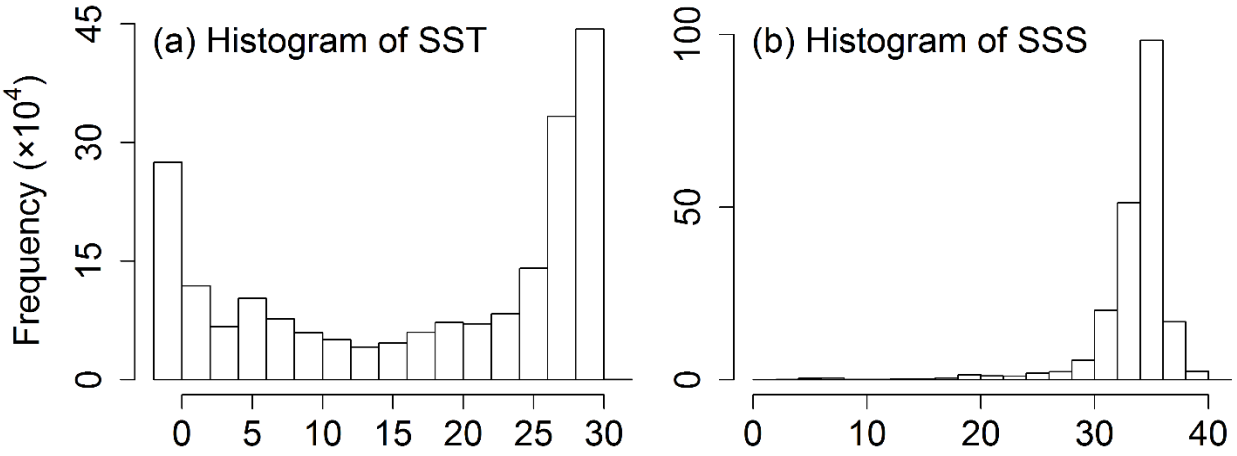


Figure S11. Frequency histograms of (a) mean sea surface temperature (SST) (in ℃) and (b) mean sea surface salinity (SST) (in ‰) within the Exclusive Economic Zone (i.e., within 370 km of the coast). SST is evenly distributed while SSS mainly concentrates between 30 to 38‰.

120 **Table S1** Mean (± standard error) AUC values of the ten algorithms used to predict habitat suitability of eight ascidians. AUC: area under the receiver
121 operating characteristic curve. AUC values were calculated by a five-fold cross-validation with 10 repetitions. The numbers in red represent algorithms
122 with AUC < 0.90. ANN: artificial neural network, CTA: classification tree analysis, FDA: flexible discriminant analysis, GAM: generalized additive
123 model, GBM: generalized boosting model, GLM: generalized linear model, MARS: multiple adaptive regression splines, Maxent: maximum entropy,
124 RF: random forest, SRE: surface range envelop.

Species	ANN	CTA	FDA	GAM	GBM	GLM	MARS	Maxent	RF	SRE
Botrylloides violaceus	0.979	0.951	0.979	0.975	0.991	0.991	0.990	0.916	0.989	0.845
	(± 0.003)	(± 0.008)	(± 0.003)	(± 0.003)	(± 0.001)	(± 0.001)	(± 0.002)	(± 0.006)	(± 0.002)	(± 0.010)
Botryllus schlosseri	0.984	0.970	0.982	0.988	0.991	0.988	0.990	0.945	0.993	0.868
	(± 0.002)	(± 0.002)	(± 0.002)	(± 0.002)	(± 0.001)	(± 0.001)	(± 0.001)	(± 0.005)	(± 0.001)	(± 0.006)
Ciona savignyi	0.989	0.951	0.991	0.925	0.996	0.980	0.984	0.893	0.998	0.786
	(± 0.005)	(± 0.011)	(± 0.001)	(± 0.018)	(± 0.003)	(± 0.006)	(± 0.008)	(± 0.015)	(± 0.000)	(± 0.013)
Didemnum vexillum	0.983	0.964	0.984	0.971	0.994	0.991	0.991	0.922	0.990	0.843
	(± 0.002)	(± 0.007)	(± 0.002)	(± 0.005)	(± 0.001)	(± 0.002)	(± 0.002)	(± 0.008)	(± 0.002)	(± 0.011)
Microcosmus squamiger	0.952	0.919	0.983	0.899	0.991	0.977	0.970	0.931	0.968	0.778
	(± 0.010)	(± 0.018)	(± 0.001)	(± 0.015)	(± 0.001)	(± 0.006)	(± 0.008)	(± 0.014)	(± 0.008)	(± 0.024)
Molgula manhattensis	0.982	0.955	0.981	0.983	0.994	0.987	0.992	0.925	0.994	0.832

	(± 0.002)	(± 0.006)	(± 0.002)	(± 0.002)	(± 0.001)	(± 0.002)	(± 0.001)	(± 0.008)	(± 0.001)	(± 0.012)
Styela clava	0.982	0.966	0.988	0.986	0.993	0.993	0.994	0.950	0.992	0.866
	(± 0.004)	(± 0.005)	(± 0.001)	(± 0.002)	(± 0.001)	(± 0.001)	(± 0.001)	(± 0.004)	(± 0.001)	(± 0.005)
Styela plicata	0.977	0.931	0.977	0.959	0.991	0.985	0.984	0.952	0.992	0.810
	(± 0.005)	(± 0.013)	(± 0.003)	(± 0.008)	(± 0.001)	(± 0.002)	(± 0.003)	(± 0.012)	(± 0.001)	(± 0.009)

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Table S2 Mean (± standard error) TSS values of the ten algorithms used to predict habitat suitability of eight ascidians. TSS: true skill statistics. TSS values were calculated by a five-fold cross-validation with 10 repetitions. The numbers in red represent algorithms with TSS < 0.75. ANN: artificial neural network, CTA: classification tree analysis, FDA: flexible discriminant analysis, GAM: generalized additive model, GBM: generalized boosting model, GLM: generalized linear model, MARS: multiple adaptive regression splines, Maxent: maximum entropy, RF: random forest, SRE: surface range envelop.

Species	ANN	CTA	FDA	GAM	GBM	GLM	MARS	Maxent	RF	SRE
Botrylloides violaceus	0.926	0.914	0.880	0.928	0.947	0.932	0.936	0.829	0.939	0.690
	(± 0.009)	(± 0.013)	(± 0.010)	(± 0.005)	(± 0.005)	(± 0.003)	(± 0.007)	(± 0.012)	(± 0.006)	(± 0.019)
Botryllus schlosseri	0.935	0.922	0.910	0.932	0.941	0.928	0.938	0.880	0.943	0.736
	(± 0.003)	(± 0.004)	(± 0.005)	(± 0.004)	(± 0.003)	(± 0.004)	(± 0.003)	(± 0.010)	(± 0.002)	(± 0.012)
Ciona savignyi	0.963	0.927	0.968	0.850	0.985	0.957	0.959	0.786	0.990	0.572
	(± 0.010)	(± 0.017)	(± 0.005)	(± 0.036)	(± 0.006)	(± 0.011)	(± 0.016)	(± 0.030)	(± 0.001)	(± 0.025)
Didemnum vexillum	0.924	0.934	0.897	0.924	0.948	0.956	0.958	0.843	0.944	0.685
	(± 0.009)	(± 0.011)	(± 0.009)	(± 0.009)	(± 0.008)	(± 0.005)	(± 0.004)	(± 0.017)	(± 0.009)	(± 0.022)
Microcosmus squamiger	0.872	0.843	0.912	0.792	0.920	0.920	0.902	0.844	0.879	0.555
	(± 0.027)	(± 0.032)	(± 0.008)	(± 0.028)	(± 0.017)	(± 0.018)	(± 0.016)	(± 0.024)	(± 0.017)	(± 0.048)
Molgula manhattensis	0.929	0.910	0.891	0.928	0.939	0.927	0.934	0.843	0.942	0.664

	(± 0.008)	(± 0.008)	(± 0.006)	(± 0.006)	(± 0.004)	(± 0.004)	(± 0.005)	(± 0.015)	(± 0.007)	(± 0.025)
Styela clava	0.934	0.938	0.908	0.943	0.956	0.949	0.955	0.896	0.951	0.733
	(± 0.009)	(± 0.005)	(± 0.007)	(± 0.005)	(± 0.004)	(± 0.004)	(± 0.003)	(± 0.008)	(± 0.004)	(± 0.010)
Styela plicata	0.898	0.875	0.894	0.891	0.940	0.926	0.938	0.881	0.928	0.621
	(± 0.009)	(± 0.014)	(± 0.010)	(± 0.013)	(± 0.009)	(± 0.006)	(± 0.010)	(± 0.022)	(± 0.010)	(± 0.017)

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