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Predicting global ascidian invasions

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Abstract

Aim: Many species of ascidians are invasive and can cause both ecological and economic losses. Here, we describe risk assessment for nineteen ascidian species and predict coastal regions that are more vulnerable to arrival and expansion.

Location: Global.

Methods: We used ensemble niche modelling with three algorithms (Random Forest, Support Vector Machine and MaxEnt) to predict ecologically suitable areas and evaluated our predictions using independent (area under the curve—AUC) and dependent thresholds (true skill statistics—TSS). Environmental variables were maximum and the range of sea surface temperature, mean salinity and maximum chlorophyll. We used our niche modelling results and a modified invasibility index to compare invasion risk among 15 coastal regions.

Results: Currently, the most invaded regions are in temperate latitudes of the Northern Hemisphere and Temperate Australasia, which are regions most prone for new invasions. In the tropics, the West and Central Indo-Pacific are two regions of strong concern, the former with high risk of primary invasion by *Botryllus schlosseri* and *Didemnum perlucidum*. In the Southern Hemisphere, the Southwest and Southeast Atlantic are most at risk, both subject to invasion by *Botrylloides violaceus*, *Didemnum vexillum*, *Molgula manhattensis* and *Styela clava* among others. Regions most at risk of expansion of established invasive species are the Central Indo-Pacific, Northwest Pacific, Mediterranean and West Indo-Pacific.

Main conclusions: All regions studied have areas that are suitable and connected to receive new ascidian introductions or that may permit the spread of already established species. Risk comparison of primary introductions and expansion of established introduced ascidians among regions will allow managers to prioritize species of concern for each region both for monitoring future introductions or to enforce control actions towards established species to decrease the risk of regional expansion.

KEYWORDS
ecological niche modelling, invasibility index, invasion debt, marine trade, risk assessment, species distribution models, Tunicata

1 | INTRODUCTION

Biological invasions are a major threat for biodiversity in marine ecosystems (Molnar, Gamboa, Revenga, & Spalding, 2008). Invasive species can transform ecosystems and cause economic losses (Aguin-Pombo, 2012). Native species may also become invasive by becoming dominant in a region in which one or more barriers that previously limited population growth were removed (Valery, Fritz, Lefeuvre, & Simberloff, 2009). Most invasive species only become invasive when geographic barriers are removed and the species reach new regions outside their native distribution (Parker et al., 2013). The incidence of species causing socioeconomic impact is much greater among non-native species (Hassan & Ricciardi, 2014), and therefore, the magnitude of the impact of invasives is likely to be dependent on their biogeographic origins.

Anthropogenic activities tend to facilitate the invasion of non-native species in coastal, estuarine and marine ecosystems. Globalized maritime trade generates intense movement of species that are transported between biogeographic regions (Hulme, 2009), the result of which is that some regions are invaded by several new species every year (Coles, DeFelice, Eldredge, & Carlton, 1999; Hewitt et al., 2004). Most marine invasions are results of the unintentional transfer of animals and plants in vectors including ballast water, sediment that settles in ballast tanks and ship hull incrustations (Molnar et al., 2008). The increase in propagule pressure also increases the likelihood of establishment of a species, by reducing the effects of demographic and environmental stochasticity (Simberloff, 2009). Multiple origins of propagules further intensify invasions by introducing adaptive genetic variation from different areas and habitats (Ghabooli et al., 2013), and, consequently, the probability of invasion is greater in regions connected to many other regions by commercial maritime routes with heavy traffic, for example many European and Asiatic ports (Kaluza, Kölzsch, Gastner, & Blasius, 2010; Seebens, Gastner, & Blasius, 2013).

Invasion debt is the number of species that will arrive and become invasive, and is very difficult to estimate in any region (Rouget et al., 2016). Current risk assessment models use information that includes propagule number and size, amount of connectivity (ship traffic) between regions and environmental similarity to predict numbers and identity of the next invaders (Crafton, 2015; Herborg, Rudnick, Siliang, Lodge, & Macisaac, 2007; Leidenberger et al., 2015; Seebens, Schwartz, Schupp, & Blasius, 2016).

Species that are transported by ships must overcome a number of ecological and environmental barriers to become established outside of their native distribution (Blackburn et al., 2011). First and foremost, species are more likely to establish in regions environmentally similar to their original environments (Duncan, Blackburn, & Veltman, 1999). Broad physiological tolerances, a suite of traits often in invasive species, can reduce or eliminate the importance of the environmental mismatch between donor and recipient regions, thereby increasing the probability of invasion (Broennimann et al., 2007).

Ecological niche modelling (ENM), usually based on environmental or climatic characteristics, is the most commonly used method in macrogeographic distribution research (Peterson et al., 2011) and has also been used to forecast biological invasions (Broennimann & Guisan, 2008; Carlos-Júnior, Barbosa, Moulton, & Creed, 2014; Jiménez-Valverde et al., 2011; Riul et al., 2013). ENM uses georeferenced records of the presence/absence of individuals and environmental variables in a correlative approach to build a map of habitat suitability that indicates areas where the species is likely to be able to survive (Guisan & Thuiller, 2005; Guisan & Zimmermann, 2000). Introduction of non-native species is mainly associated with navigation routes, and so risk assessments may benefit from the combination of ENM and a measure of connectivity mediated by ship routes as proxies associated with species transport (Crafton, 2015; Herborg et al., 2007; Leidenberger et al., 2015; Seebens et al., 2016).

Ascidians are excellent models for examining introductions and invasion dynamics (Zhan, Briski, Bock, Ghabooli, & MacIsaac, 2015). Ascidians, usually abundant on artificial substrates, often are one of the most species-rich of the reported introduced sessile taxa (Bishop, Wood, Yunnie, & Griffiths, 2015; Marques et al., 2013). Larvae are short-lived and in the water column for only minutes to hours (Lambert, 2005), and thus, it is impossible for them to disperse over great geographic distances. Transoceanic spreading is only possible by human-mediated transport. Recurrent introductions are also common, increasing propagule pressure and the probability of successful establishment (Dupont, Viard, Davis, Nishikawa, & Bishop, 2010). Survival during transport and introduction is enhanced by their ability to colonize degraded and nutrient-rich environments (Bullard & Carman, 2009; Lambert, 2007), to use multiple vectors (Lambert, 2007) and their wide tolerance to some environmental factors (Nagar & Shenkar, 2016). With the continuous development of coastal regions, ports, marinas and sea-farms are important facilitators for ascidian colonization. (Airoldi, Turon, Perkol-Finkel, & Rius, 2015; Connell, 2000).

For example, ascidian establishment and encrustation on artificial structures for commercial cultivation of shellfish jeopardize that industry (McKindsey, Landry, Beirn, & Davies, 2007) and increase production costs as a consequence of the necessary and often frequent cleaning. Despite the importance of several ascidian species as biological invaders and the environmental and economic impact they cause, very few risk assessments combine predictive models of environmental suitability or estimates of propagule pressure to predict future introductions and invasion (but see Herborg, O'Hara, & Therriault, 2009; Locke, 2009; Januario, Estay, Labra, & Lima, 2015) and none at a global scale. However, similar studies with other taxa show that this approach may be effectively applied (Crafton, 2015; Keller, Drake, Drew, & Lodge, 2011; Seebens et al., 2016).

In this study, we carried out a global risk analysis of invasion and range expansion for 19 ascidian species that were already transported and introduced to one or more locations beyond their native region. We used an ensemble niche modelling approach combined with a modified index of vector connectivity (after Seebens et al., 2013) to quantify invasion risk across a broad group of species and coastal regions.

2 | METHODS

2.1 | Species and occurrences

We evaluated global invasion risk for 19 ascidian species that are invasive (1st criteria) or introduced into at least two regions of the world (2nd criteria). These 19 species, taken from the 64 introduced species listed in Shenkar and Swalla (2011), comprise all three orders in the class Ascidiacea, of which seven are colonial and 12 are solitary (Table 1). Occurrence records were obtained from published taxonomic, ecological and oceanographic studies, searching by the name

TABLE 1 Current presence of ascidian species in 15 coastal regions. XX means that the species occurs in more than three grid cells inside the region, while X means the species occurs in three or less cells (see text for details). In bold probable native range of the species, when known

	WIPac	NWPac	CIPac	Taus	NEPac	TEPac	SEPac	NWAtl	TWAtl	SWAtl	NES	Lusit	Med	TEAtl	SEAtl
Ascidia sydneiensis	XX	XX	XX	XX	X	X			XX	XX				X	XX
Ascidiella aspersa	X	X		XX				X		X	**XX**	**XX**	XX	XX	X
Botrylloides nigrum	XX		XX	X	X	X			**XX**	XX		X	X	X	
Botrylloides violaceus		**XX**	X		XX			XX			XX	X			
Botryllus schlosseri		XX	X	XX	XX		X	XX	X		XX	XX	**XX**	X	X
Ciona intestinalis		X						XX			**XX**				
Ciona robusta		**XX**		XX	XX		XX			XX	X		XX		XX
Ciona savignyi		XX	X		XX					X			X		
Clavelina lepadiformis								X			**XX**	XX	XX		X
Clavelina oblonga								X	**XX**	XX		X	XX	X	
Corella eumyota				XX			XX			**X**	XX	X			XX
Didemnum perlucidum		X	XX	X	X				XX	XX				X	
Didemnum vexillum		**XX**		X	XX	X		XX			XX	XX	X		
Ecteinascidia turbinata	X								**XX**			X	XX	XX	
Microcosmus exasperatus	XX	X	XX	XX				X	XX	XX		X	XX	XX	X
Microcosmus squamiger	X		X	**XX**	XX							XX	XX		XX
Molgula manhattensis		XX		X	XX			**XX**			XX	XX	X		
Styela clava		**XX**		X	XX			XX			XX	X	X		
Styela plicata	X	XX	XX	XX	XX			X	XX	XX		X	XX	X	X
Total # species	7	13	9	13	12	3	3	11	8	10	10	14	14	9	9

WIPac, West Indo-Pacific; NWPac, Northwest Pacific; CIPac, Central Indo-Pacific; Taus, Temperate Australasia; NEPac, Northeast Pacific; TEPac, Tropical East Pacific; SEPac, Southeast Pacific; NWAtl, Northwest Atlantic; TWAtl, Tropical West Atlantic; SWAtl, Southwest Atlantic; NES, Northern European seas; Lusit, Lusitanian Sea; Med, Mediterranean Sea; TEAtl, Tropical East Atlantic; SEAtl, Southeast Atlantic.

of the species in Web of Science and Google Scholar portals. We also accessed Monniot's private database of taxonomic publications (Pers. Commun., Françoise Monniot) and geographic distribution databases (OBIS and GBIF) using accepted names and resolved synonyms. When geographic coordinates were unavailable, we acquired them using Google Maps and information from the reported location, considering the presence of rocky shores and other available hard substrate for attachment or the existence of a port or marina to select the locality with higher probability of the species occurrence. The database including occurrences is available upon request.

2.2 | Environmental variables

We modelled environmental suitability using variables from the Bio-Oracle dataset (Tyberghein et al., 2012), which has 23 global marine environmental layers with spatial resolution associated with a grid of cells of 5 arc-minutes (approximately 9 km^2). This resolution was recently found to be the best for modelling the invasive ascidian *Ciona intestinalis* (Lowen, McKindsey, Therriault, & DiBacco, 2016).

We selected only variables of fundamental environmental dimensions for the survival of ascidians and that may limit their distributions. The most important environmental variables associated with the natural distribution of ascidians are seawater temperature and salinity (Brunetti, Beghi, Bressan, & Marin, 1980; Epelbaum, Herborg, Therriault, & Pearcea, 2009; Sims, 1984), with salinity being more limiting, because few species survive below 25 ppt (Lambert, 2005). Chlorophyll concentration was used as a proxy of the planktonic autotrophic biomass, the main food source for filter feeders, including ascidians, which can thrive in eutrophic conditions (Marins, Novaes, Rocha, & Junqueira, 2010). To control for multicollinearity (strongly correlated environmental layers, with $r > .9$), we systematically selected one of the layers and dropped the other, resulting in a final set of uncorrelated variables that comprised temperature (sea surface range and maximum), maximum chlorophyll (data between 2002 and 2009) and mean salinity (data between 1961 and 2009). Although mean salinity does not reflect physiological limits of the species, low salinity can limit ascidians and we assume that the low and the mean should be strongly correlated, and thus, the mean serves as a proxy. Following recommendations of Bio-Oracle dataset, we limited our analysis to latitudes between 70°N and 70°S.

We only considered map cells that were within the average width of the exclusive economic zone (EEZ) agreed upon by the United Nations (200 nautical miles or 370 km from the coast) and, when necessary, we also included a radius of 12 km around islands if outside of that limit. It is important to limit the study to the areas accessible to species (all of the species used in this study live in shallow waters) because of the influence of total area on the parameterization of the algorithms, validation of models and comparison between algorithms (Barve et al., 2011). It has a critical effect on prevalence (the proportion of locations where the species is recorded), which affects the metrics of evaluation and accuracy of presence/background models such as MaxEnt (Phillips, 2008; Veloz, 2009).

2.3 | Ecological niche modelling

The approach used in this study is based on the hypothesis that a robust association of environmental variables predicting the survival of a species can be established from the identification of the environmental variables associated with a set of points where the species occur (Phillips & Dudík, 2008). We used occurrence records without distinction between native and non-native status. This is because the native regions of many species are not well known and because without distinction, the inclusion of all records encompasses the actual tolerance ranges and therefore better represents the niche of the species. Following this practice, the models obtained are considerably better than when using only occurrences from the native distributions, suggesting a greater consensus among the modelling techniques (Broennimann & Guisan, 2008).

After gathering information on occurrence locations (presence) and environmental parameters associated with each 9 km^2 cell of the grid, we disregarded duplicate records in any cell. Using R vers. 3.1.2 (R Core Team 2014), we parameterized three algorithms to create niche models: (1) MaxEnt (Phillips, Anderson, & Schapire, 2006); (2) support vector machine (SVM; Guo, Kelly, & Graham, 2005); and (3) random forest (RF; Prasad, Iverson, & Liaw, 2006). We also used the MaxEnt environment to investigate the percentage contribution of each variable to the final model (Phillips, Dudík, & Schapire, 2004).

These models have different conceptions and different characteristics of the real world (Diniz-Filho et al., 2009). We evaluated the results from the three algorithms in five replicates for each species per algorithm, resulting in a total of 475 response outputs. We randomly restricted 70% of the occurrence records for model training and 30% for testing the results, with which we evaluated the distributional models using independent (area under the curve—AUC) and dependent measures (true skill statistics—TSS; Liu, Guo, Ke, Wang, & Li, 2011). The closer the AUC value is to 1.0 the better the fit (0.5 or lower indicates that the model is no better than random). True skill statistics (TSS) is a threshold-dependent measure, suggested for studies based on presence–absence/background predictions, but is not affected by the number of points used for validation (it is less sensitive to prevalence than AUC; Lobo, Jiménez-Valverde, & Real, 2008; Liu, White, & Newell, 2009). Both metrics produce correlated results (Allouche, Tsoar, & Kadmon, 2006) and were calculated using 10,000 pseudo-absences (Liu et al., 2009). In the TSS index, the average rate of prediction success ranges from −1 to 1, where 1 indicates perfect fit and values <0 indicate results no better than random.

The algorithms were then parameterized using all records (100% of occurrences), and results were combined by calculating a mean suitability for each 9 km^2 cell, weighting each algorithm by its TSS value (Diniz-Filho et al., 2009), to generate a single map that highlights the similarities between the algorithms. The use of this procedure is because common areas predicted by all algorithms are unlikely to be an artefact of their particularities (Araújo & New, 2007). Environmentally suitable areas for each species were categorized using a gradient from deep blue to red to indicate low to high suitability. Coastal regions that only have cells with shades of blue were considered poorly suitable, light-blue to yellow were intermediate, and red cells were highly suitable, regardless of the size of the area of interest.

2.4 | Connectivity index

Evaluating invasion risk using environmental suitability alone can be incomplete because of the lack of information about vector activity or propagule pressure in a region. Joint assessment of connectivity between donor and recipient regions, estimation of the likelihood of species transport and evaluation of the propagule pressure reaching the recipient region are also required. Transport of juvenile or adult organisms by merchant ships is the main vector of marine introductions (Coutts & Dodgshun, 2007; Hewitt, Gollasch, & Minchin, 2009), and "invasion probability indices" were calculated by Seebens et al. (2013) for ports taking into consideration 15 coastal regions (modified from Spalding et al., 2007). That is, for each recipient region, 14 indices were calculated, one for each potential donor coastal region. Those indices used information including distance between ports for all legs of the journey, travel time, ballast water volume and treatment, and environment similarity (based on temperature and salinity). Here, we modified Seebens' index to calculate a connectivity index for each combination of species and recipient region, taking into account the presence of the 19 target ascidian species in all possible donor regions connected to any recipient region. To calculate this modified index, we summed Seebens' invasion probability indices of the recipient region with all possible donor regions in which a target species was present. Some donor regions had very few records of species of interest, and given that propagule pressure (sensu Lockwood, Cassey, & Blackburn, 2009) is a function of species abundance in the donor regions, we simply divided the Seebens' index by two for those connections including donor regions with ≤ three grid cells having the target ascidian species.

To calculate a general risk index of primary invasion for each region (suitability + connectivity for all 19 species), we calculated the weighted average of the individual connectivity indices for each species not yet established in that region, with weighting as a function of environment suitability of the region for each species (high suitability = 3, intermediate = 2, low = 1). As most cells in any region were still unoccupied by the target species, there is a possibility of regional expansion after establishment in and near ports. We used the same rule to calculate an average risk of regional expansion, considering only the species already established in each region.

3 | RESULTS

Most of the 19 target species are found worldwide, with records from more than six regions. *Botryllus schlosseri* and *Styela plicata* are the most widely distributed species, occurring in 12 regions and very common in seven. Other widely distributed species were *Ascidiella aspersa*, *Ascidia sydneiensis*, *Botrylloides nigrum* and *Microcosmus exasperatus*, all in 10 or more regions. Most species, though, occur in an intermediate number of regions (6–8) while *Ciona intestinalis*, *Ciona savignyi*, *Clavelina lepadiformis* and *Ecteinascidia turbinata* are currently restricted to three or five regions (Table 1). The Mediterranean and Lusitanian Seas had the greatest species richness among the regions with 14 of 19 species (Figure 1, Table 1). Next, the Pacific Northwest and Temperate Australasia had 13 species, the Northeast Pacific with 12 and Northwest Atlantic with 11, and the Southwest Atlantic and Northern European Seas with 10 species. The lowest species richness was found in the Tropical East Pacific and Southeast Pacific.

The number of unique records per species ranged from 37 to 194, and most occupied cells were in regions with wide temperature variation coupled with little variation in chlorophyll *a* and salinity, while

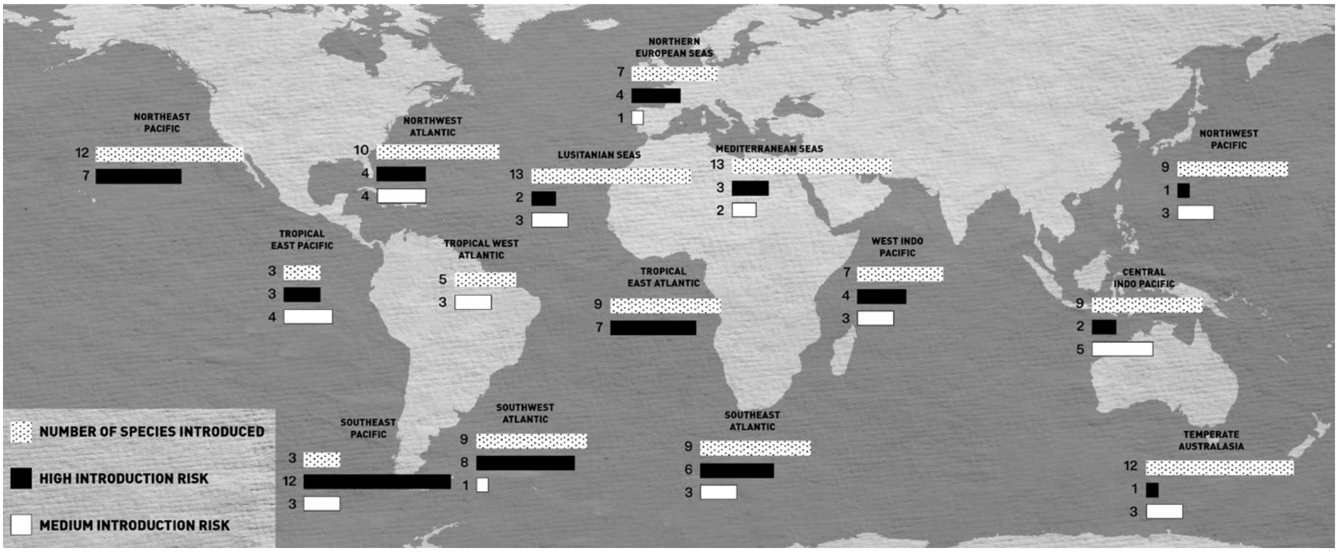


FIGURE 1 Coastal regions used in this article, following Seebens et al. (2013), including the number of introduced ascidians already established and the number of species with medium and high risk of introduction

maximum chlorophyll *a* and maximum sea surface temperature were the main drivers for most species in the MaxEnt models (Table 2).

The SVM, RF and MaxEnt models predicted adequate areas well (TSS > 0.4) with high AUC values (AUC > 0.7) and little variation. Both evaluation indices indicated that the RF and SVM models performed similarly and produced better predictions than MaxEnt (Table S1). Although some regions are more diverse than others, the ensemble model showed that all 15 coastal regions included in the study have large areas with suitable environment for primary introduction or range expansion of established populations, with greater suitability in coastal shallow waters and decreasing towards the oceanic domain (Figures S1–S7).

Currently, regions most at risk of primary introductions include the Mediterranean Sea, Northwest Pacific, the Northwest Atlantic, Central Indo-Pacific and West Indo-Pacific (Figure 2). Some of those regions are also suitable for the more aggressive invaders,

TABLE 2 Summary of the environmental variables used in the ecological niche models of ascidians and contribution of the variables used for the predictive performance of the MaxEnt model. The environmental information was obtained from Bio-Oracle database and is presented as values extracted from the raster grid cells of the species. *N* = number of grid cells with the species

		Environmental variables						Percentage contribution (%)			
		SST (°C)		SAL (PSS)		CHL (mg/m^3)		CHL	SAL	SST	
Species	*N*	Min	Max	Mean	*SD*	Mean	*SD*	Max	Mean	Max	Range
Ascidia sydneiensis (Stimpson, 1855)	194	1.0	34.7	34.6	1.23	2.4	3.40	50	8	37	5
Ascidiella aspersa (Müller, 1776)	164	−0.3	30.6	33.2	5.37	4.6	5.02	43	12	21	24
Botrylloides nigrum (Herdman, 1886)	103	13.7	34.0	36.1	1.23	2.1	2.99	34	20	40	7
Botrylloides violaceus (Oka, 1927)	135	−1.3	31.0	33.0	1.53	4.9	5.36	42	13	21	25
Botryllus schlosseri (Pallas, 1774)	185	−0.3	31.3	33.8	3.78	4.0	4.10	47	10	20	23
Ciona intestinalis (Linnaeus, 1767)	87	−2.0	26.1	29.1	6.92	8.0	8.50	68	4	16	12
Ciona robusta (Hoshino e Tokioka, 1967)	81	3.8	30.4	35.2	2.18	4.4	5.90	50	19	29	2
Ciona savignyi (Herdman, 1882)	47	0.3	31.1	32.8	1.74	6.2	7.89	61	10	20	10
Clavelina lepadiformis (Müller, 1776)	52	1.1	29.1	34.7	3.11	3.8	4.37	41	20	21	18
Clavelina oblonga (Herdman, 1880)	57	11.2	31.4	35.8	0.78	3.8	5.47	42	19	35	4
Corella eumyota (Traustedt, 1882)	128	2.6	23.3	34.8	0.72	3.7	2.87	38	22	37	4
Didemnum perlucidum (Monniot F, 1983)	52	15.6	31.8	35.4	0.66	2.2	3.17	38	8	45	9
Didemnum vexillum (Kott, 2002)	101	−0.2	29.1	32.4	2.21	7.1	5.94	59	5	29	7
Ecteinascidia turbinata (Herdman, 1880)	37	11.6	31.7	36.0	1.49	3.4	4.05	37	23	37	4
Microcosmus exasperatus (Heller, 1878)	184	10.9	34.8	36.2	1.75	2.0	2.79	40	23	33	4
Microcosmus squamiger (Hartmeyer e Michaelsen, 1928)	105	10.3	33.7	36.1	1.36	2.2	2.07	36	25	22	17
Molgula manhattensis (De Kay, 1843)	87	−1.5	32.1	30.6	5.61	9.8	8.09	74	4	12	10
Styela clava (Herdman, 1881)	107	−2.0	29.7	32.4	2.73	5.6	5.44	53	6	22	19
Styela plicata (Lesueur, 1823)	154	2.5	32.5	35.0	2.04	4.5	5.13	55	8	28	9

SST, sea surface temperature; SAL, salinity; PSS, practical salinity scale; CHL, chlorophyll *a*; *SD*, standard deviation.

A. sydneiensis, *Botrylloides violaceus*, *B. schlosseri*, *C. robusta* and *Didemnum perlucidum*. The Tropical West, Southwest and Southeast Atlantic regions, Temperate Australasia, Northeast Pacific and Northern European Seas were at intermediate risk. The Southwest Atlantic is suitable for eight species (seven of those extremely invasive), the Northeast Pacific for seven (three invasive), the Southeast Atlantic for six (five invasive) and the Northern European Seas for four (three invasive). The remaining regions were less at risk, among which the Tropical East Pacific was the least environmentally suitable; nonetheless, it is still at risk by the aggressive invaders *M. exasperatus* and *D. perlucidum*.

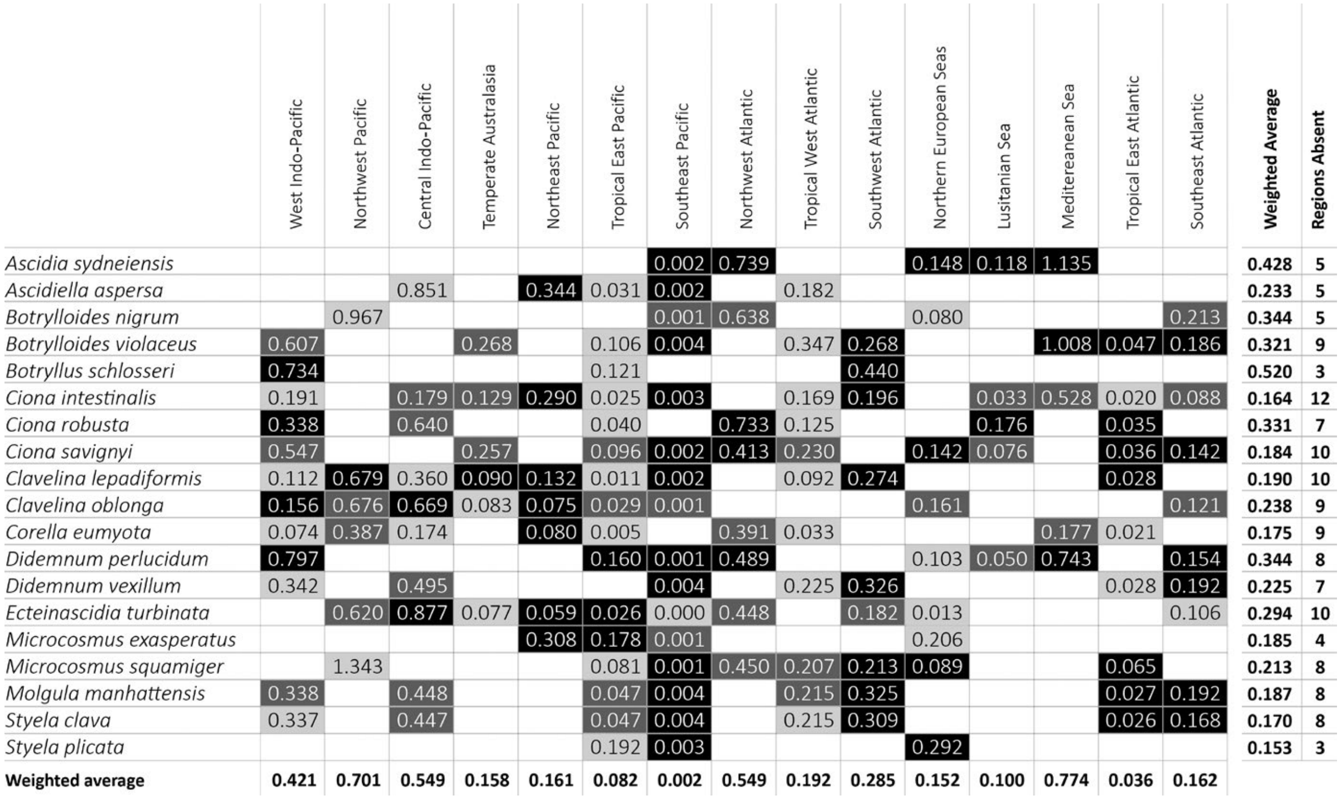
Regions with established species are at risk that those species will progressively expand their distribution (Figure 3). Range expansion of highly invasive species is expected, including *A. aspersa*, *S. plicata* and *M. exasperatus* in the Northwest Atlantic; *S. clava* and *M. manhattensis* in the Mediterranean Sea; *A. aspersa* and *M. exasperatus* in the Northwest Pacific; *S. plicata* and *M. squamiger* in the West Indo-Pacific; *C. robusta* in the Northern European Seas; *D. perlucidum* in the Northeast Pacific and *D. vexillum* in Temperate Australasia.

From the perspective of predicting future introductions, the species which posed the greatest risk were *B. schlosseri* (mainly in West Indo-Pacific), *A. sydneiensis* (Mediterranean and Northwest Atlantic), *D. perlucidum* (Mediterranean and West Indo-Pacific), *C. robusta* (Northwest Atlantic) and *B. violaceus* (Mediterranean, Figure 2, Appendix S1).

4 | DISCUSSION

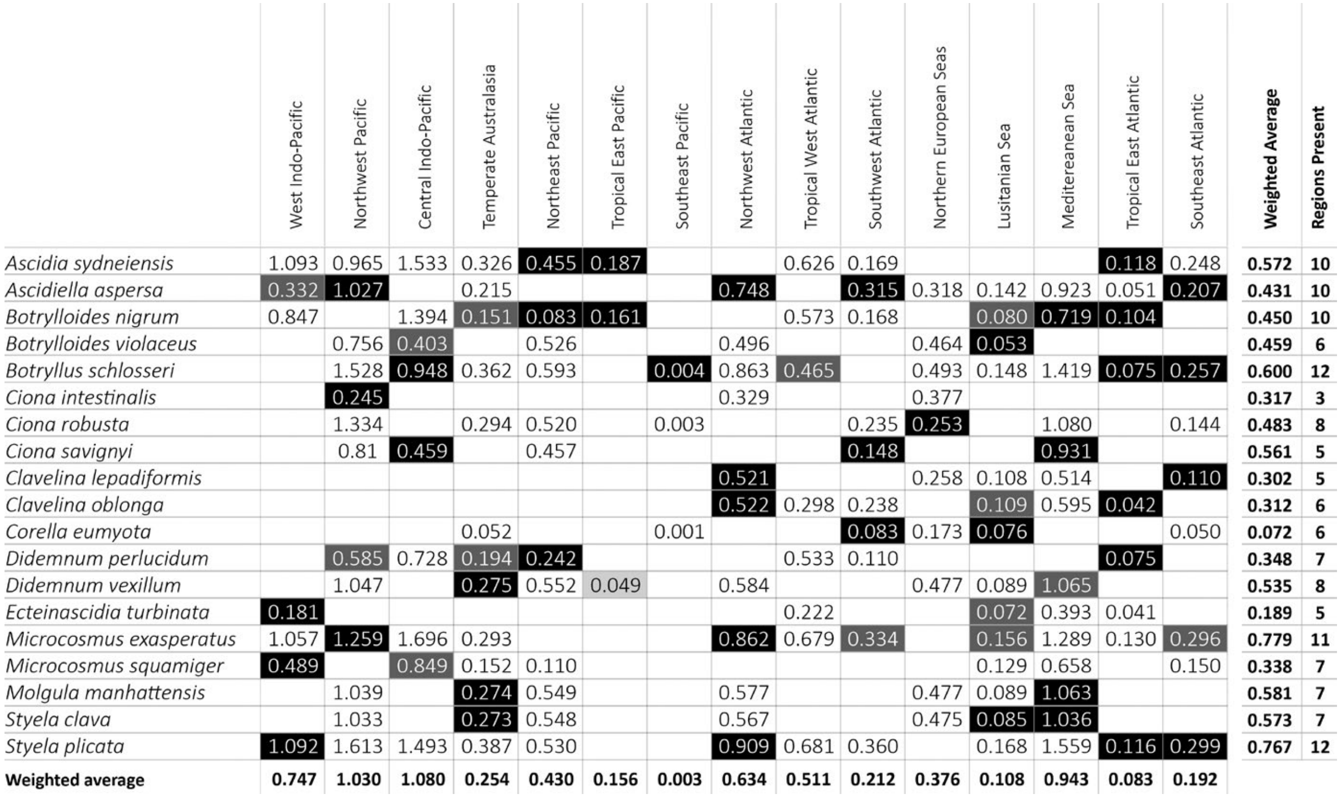
The current distribution of ascidian species is consistent with the likelihood that historical trends of introductions were mediated by navigation and transoceanic shipping. Regions most vulnerable to propagule pressure (Northwest Pacific, Mediterranean and Northwest Atlantic—Seebens et al., 2013) are those in which records of introduced ascidians are concentrated, where they occur in greater diversity and abundance. Most marine trade routes are within temperate latitudes of the Northern Hemisphere (Kaluza et al., 2010), and thus, most introduced ascidians in this study are also native to temperate regions (Table 1). But surprisingly, all tropical regions have already been invaded and are at high risk of new invasions and of range expansion of established species (except for Tropical East Pacific).

In addition to more transport opportunities, temperate species are also more tolerant of environmental variability because of seasonality in their natural environments (Macpherson, 2002). Apparently, this tolerance is essentially a pre-adaptation that allows



	West Indo-Pacific	Northwest Pacific	Central Indo-Pacific	Temperate Australasia	Northeast Pacific	Tropical East Pacific	Southeast Pacific	Northwest Atlantic	Tropical West Atlantic	Southwest Atlantic	Northern European Seas	Lusitanian Sea	Mediterranean Sea	Tropical East Atlantic	Southeast Atlantic	**Weighted Average**	**Regions Absent**
Ascidia sydneiensis							0.002	0.739			0.148	0.118	1.135			**0.428**	**5**
Ascidiella aspersa			0.851		0.344	0.031	0.002		0.182							**0.233**	**5**
Botrylloides nigrum		0.967					0.001	0.638			0.080				0.213	**0.344**	**5**
Botrylloides violaceus	0.607			0.268		0.106	0.004		0.347	0.268			1.008	0.047	0.186	**0.321**	**9**
Botryllus schlosseri	0.734					0.121				0.440						**0.520**	**3**
Ciona intestinalis	0.191		0.179	0.129	0.290	0.025	0.003		0.169	0.196		0.033	0.528	0.020	0.088	**0.164**	**12**
Ciona robusta	0.338		0.640			0.040		0.733	0.125			0.176		0.035		**0.331**	**7**
Ciona savignyi	0.547			0.257		0.096	0.002	0.413	0.230		0.142	0.076		0.036	0.142	**0.184**	**10**
Clavelina lepadiformis	0.112	0.679	0.360	0.090	0.132	0.011	0.002		0.092	0.274				0.028		**0.190**	**10**
Clavelina oblonga	0.156	0.676	0.669	0.083	0.075	0.029	0.001				0.161				0.121	**0.238**	**9**
Corella eumyota	0.074	0.387	0.174		0.080	0.005		0.391	0.033				0.177	0.021		**0.175**	**9**
Didemnum perlucidum	0.797					0.160	0.001	0.489			0.103	0.050	0.743		0.154	**0.344**	**8**
Didemnum vexillum	0.342		0.495				0.004		0.225	0.326				0.028	0.192	**0.225**	**7**
Ecteinascidia turbinata		0.620	0.877	0.077	0.059	0.026	0.000	0.448		0.182	0.013				0.106	**0.294**	**10**
Microcosmus exasperatus					0.308	0.178	0.001				0.206					**0.185**	**4**
Microcosmus squamiger		1.343				0.081	0.001	0.450	0.207	0.213	0.089			0.065		**0.213**	**8**
Molgula manhattensis	0.338		0.448			0.047	0.004		0.215	0.325				0.027	0.192	**0.187**	**8**
Styela clava	0.337		0.447			0.047	0.004		0.215	0.309				0.026	0.168	**0.170**	**8**
Styela plicata						0.192	0.003				0.292					**0.153**	**3**
Weighted average	**0.421**	**0.701**	**0.549**	**0.158**	**0.161**	**0.082**	**0.002**	**0.549**	**0.192**	**0.285**	**0.152**	**0.100**	**0.774**	**0.036**	**0.162**		

FIGURE 2 Matrix of risk assessment for ascidian introduction and establishment in coastal regions. White cells indicate where species are already present, and coloured cells indicate environmentally suitable regions by the ensemble of three ecological niche models: MaxEnt, support vector machine and random f. Black cells = high, dark grey = intermediate and light grey = low environmental suitability. Numbers are the connectivity index calculated as the sum of invasion probabilities, computed by Seebens et al. (2013), considering all possible donor regions of a given species (invasion probabilities including donor regions with low presence of the species were divided by two). The weighted average of indices in a given region (or for a given species) used the following weights: 3 for values in black cells, 2 for dark grey and 1 for light grey cells



	West Indo-Pacific	Northwest Pacific	Central Indo-Pacific	Temperate Australasia	Northeast Pacific	Tropical East Pacific	Southeast Pacific	Northwest Atlantic	Tropical West Atlantic	Southwest Atlantic	Northern European Seas	Lusitanian Sea	Mediterranean Sea	Tropical East Atlantic	Southeast Atlantic	**Weighted Average**	**Regions Present**
Ascidia sydneiensis	1.093	0.965	1.533	0.326	0.455	0.187			0.626	0.169				0.118	0.248	**0.572**	**10**
Ascidiella aspersa	0.332	1.027		0.215				0.748		0.315	0.318	0.142	0.923	0.051	0.207	**0.431**	**10**
Botrylloides nigrum	0.847		1.394	0.151	0.083	0.161			0.573	0.168		0.080	0.719	0.104		**0.450**	**10**
Botrylloides violaceus		0.756	0.403		0.526			0.496			0.464	0.053				**0.459**	**6**
Botryllus schlosseri		1.528	0.948	0.362	0.593		0.004	0.863	0.465		0.493	0.148	1.419	0.075	0.257	**0.600**	**12**
Ciona intestinalis		0.245						0.329			0.377					**0.317**	**3**
Ciona robusta		1.334		0.294	0.520		0.003			0.235	0.253		1.080		0.144	**0.483**	**8**
Ciona savignyi		0.81	0.459		0.457					0.148			0.931			**0.561**	**5**
Clavelina lepadiformis								0.521			0.258	0.108	0.514		0.110	**0.302**	**5**
Clavelina oblonga								0.522	0.298	0.238		0.109	0.595	0.042		**0.312**	**6**
Corella eumyota				0.052			0.001			0.083	0.173	0.076			0.050	**0.072**	**6**
Didemnum perlucidum		0.585	0.728	0.194	0.242				0.533	0.110				0.075		**0.348**	**7**
Didemnum vexillum		1.047		0.275	0.552	0.049		0.584			0.477	0.089	1.065			**0.535**	**8**
Ecteinascidia turbinata	0.181								0.222			0.072	0.393	0.041		**0.189**	**5**
Microcosmus exasperatus	1.057	1.259	1.696	0.293				0.862	0.679	0.334		0.156	1.289	0.130	0.296	**0.779**	**11**
Microcosmus squamiger	0.489		0.849	0.152	0.110							0.129	0.658		0.150	**0.338**	**7**
Molgula manhattensis		1.039		0.274	0.549			0.577			0.477	0.089	1.063			**0.581**	**7**
Styela clava		1.033		0.273	0.548			0.567			0.475	0.085	1.036			**0.573**	**7**
Styela plicata	1.092	1.613	1.493	0.387	0.530			0.909	0.681	0.360		0.168	1.559	0.116	0.299	**0.767**	**12**
Weighted average	**0.747**	**1.030**	**1.080**	**0.254**	**0.430**	**0.156**	**0.003**	**0.634**	**0.511**	**0.212**	**0.376**	**0.108**	**0.943**	**0.083**	**0.192**		

FIGURE 3 Matrix of risk assessment for the expansion of established species. Species are absent from empty cells and widespread in white cells with a numerical value. Coloured cells indicate environmentally suitable regions based on the ensemble of three ecological niche models: MaxEnt, support vector machine and random forest. Black cells = high, dark grey = intermediate and light grey = low environmental suitability. The numbers indicate the connectivity index calculated as in Figure 2

their establishment in less variable regions once the transport barrier is overcome. For example, the cold-water species *C. intestinalis* can survive in subtropical regions even though recruitment only occurs during winter (Astudillo, Leung, & Bonebrake, 2016), and recently, *D. vexillum* was found for the first time outside the temperate region, in warm waters of Ecuador (F. Brown, personal communication).

Our results highlight that even the most invaded regions remain suitable for new invasions (Table 1, Figure 2). The regions with greater invasion risk are the Mediterranean Sea, the Northwest Pacific, Central Indo-Pacific, Northwest Atlantic, Lusitanian Sea and West Indo-Pacific. For instance, the Mediterranean is at high risk of new invasions by *A. sydneiensis*, *B. violaceus* and *D. perlucidum* and at smaller risk for *C. intestinalis* and *C. eumyota*. The donor regions with the greatest connectivity with the east Mediterranean are the Northwest Pacific, while those with the greatest connectivity with the west Mediterranean are the Northwest Atlantic and Southwest Atlantic (Figures S1–S7), and so pre-border management should focus on vectors from those regions. Large-scale monitoring to detect non-native species can be expensive but predictive modelling, like we present here, can help to target locations and species with the greatest invasion risk, which allows the development of DNA-based detection protocols (Stewart-Clark, Davidson, & Greenwood, 2013), and facilitates field monitoring (Minchin, 2007).

At lower risk of new invasions are the regions Southeast Pacific (due to low connectivity) and Tropical East Pacific (due to low suitability, Table 1), but *B. schlosseri* and *C. robusta* have already invaded the former (Turon, Cañete, Sellanes, Rocha, & López-Legentil, 2016) and *A. sydneiensis* the latter (Carman et al., 2011), which remains at risk of being reached by aggressive invaders such as *M. exasperatus* and *D. perlucidum* (Appendix S1).

The major impacts currently reported for introduced ascidians are associated with the bivalve industry because aquaculture facilities create an ideal environment for ascidians, with abundant suspended food and unlimited locations for attachment (bivalve shells, ropes and buoys). All five species with high introduction risk identified in this study are already present in aquaculture facilities worldwide (Rocha, Kremer, Baptista, & Metri, 2009) and may potentially cause serious impacts (McKindsey et al., 2007; Sievers, Fitridge, Dempster, & Keough, 2013). *Botrylloides violaceus* and *B. schlosseri* have already invaded natural substrates in British Columbia (Simkanin, Davidson, Dower, Jamieson, & Therriault, 2012), and *D. perlucidum* has been recently reported to be spreading fast along the west coast of Australia both in aquaculture and in natural habitats (Bridgwood, Muñoz, & McDonald, 2014).

Future invasion prediction in the only previous risk analysis of ascidians on a larger scale used environmental match and vessel ballast water tracks in Atlantic Canada (Locke, 2009). That study listed

17 species, six of which were in common with this study (*A. aspersa*, *C. lepadiformis*, *D. vexilum*, *S. plicata*, *A. sydneiensis* and *C. eumyota*). The first four already arrived in the north-eastern United States and have a high probability of spreading towards Canada in the near future, while *A. sydneiensis* has a high risk of primary introduction and *C. eumyota* has a low risk. Both *C. robusta* and *M. exasperatus*, species not considered by Locke (2009), have a high probability of arriving in Atlantic Canada (however, with low probability of establishment). Although our risk probabilities were calculated for a larger region, they can be informative for local scales, for example which species arriving close to the Atlantic Canada have the potential to spread given a suitable environment (see Figures S1–S7).

ENMs are often criticized for the lack of causality between variables and output distribution (Hortal, Lobo, & Jiménez-Valverde, 2012), and so, to include causality, we used variables that are essential to ascidian distributions. Possibly, the lack of data for low salinity in Bio-Oracle may be a limitation in our study if the correlation between average and low salinity is not as strong as we assume. Ascidians are limited by low salinity, which may vary widely each day in some areas, depending upon the tidal regime. Thus, we may have overestimated environmental suitability in some places with widely variable freshwater input. Also, using species with a history of introduction tends to concentrate records in harbours, where eutrophication is common due to proximity to major urban centres. As expected, therefore, chlorophyll concentration was a major predictor of ascidian distribution (Table 2). Chlorophyll concentration decreases with distance from shore to the open ocean, and so including depth or distance from the coast in the analysis was unnecessary.

The large spatial scale of our analysis may overestimate the risk of establishment because local microenvironmental conditions of bays, channels and estuaries where harbours are usually located cannot be precisely measured and those conditions may be adverse for ascidians (because of wide variation in salinity, for instance). Also, we cannot include conditions such as hard substrates for attachment and biological interactions such as predation and space competition (Kremer & Rocha, 2016; Lambert, 2005) which can also limit establishment, even under favourable environmental conditions. The risk of establishment might also be overestimated by applying a status of high suitability to an entire region, if only a few locations of high suitability are found within it (Figures S1–S7). For instance, the Mediterranean Sea was considered highly suitable to *A. sydneiensis*, yet only a few regions provided best suitable conditions (Figure S1).

However, here, we may have underestimated some processes, such as transport by other vectors and secondary regional spread, both of which can increase local propagule pressure and, as a consequence, increase the probability of primary introduction and establishment by regional dispersal. Aquaculture importation and recreational boating are other important vectors for ascidian recruitment, also not specifically included in our models. Yet, aquaculture was responsible for the establishment of *S. clava*, *B. violaceus* and *B. schlosseri* in Canada (Locke, Hanson, Ellis, Thompson, & Rochette, 2007). Additionally, *B. violaceus* and *D. vexillum* may have arrived in New England with the importation of oysters (*Crassostrea gigas*) from the Pacific (Dijkstra, Harris, & Westerman, 2007). The importance of the connectivity of coastal zones was shown in the Gulf of Saint Lawrence (Darbyson, Locke, Hanson, & Martin, 2009) and in California (Zabin et al., 2014) where recreational boats are some of the most important vectors for local ascidian dispersal.

ENMs for invasive species commonly do not meet a central assumption of equilibrium with the environment, because those species are in the process of expanding their occurrence region, which is especially true for recent invasions (Václavík & Meentemeyer, 2012). On the other hand, ENM predictions that use occurrences from native distributions only assume that species retain their niche (Peterson, Soberón, & Sánchez-Cordero, 1999; Wiens & Graham, 2005), even though species have the potential to undergo niche shift after introduction (Broennimann et al., 2007). Using occurrence records from both the native and invaded areas, we took into account these possible niche shifts that a species may undergo during the invasion process. This is currently the best procedure to predict the potential of future spread of invasive species (Broennimann & Guisan, 2008; Jiménez-Valverde et al., 2011). To add to the complexity, some species now classified as native may actually be ancient introductions that were undocumented (Haydar, 2012). Thus, even if some predictions are overestimated across large regions, the maps continue to provide a way for local managers and researchers to evaluate more restricted regions, similar to the way Leidenberger et al. (2015) analysed the northern European sea. Managers should be aware that, with our results in hand, there are still specific conditions that should be evaluated because they influence introduction risk. Ship history (time spent in previous ports-of-call, number of regions visited by the ship and time since last application of antifouling paint), for instance, is a predictor of propagule and colonization pressures (Sylvester et al., 2011).

The predictions of this study depend strongly on the current global distribution of the target species. Occurrence records were used not only to calibrate and test ENMs, but also to customize the index of invasibility of coastal regions for each species. This index took into account the abundance of the species at donor regions because propagule size is probably larger for abundant species, resulting in a species-specific customized proxy for propagule pressure. More than 100 independent records were available for 11 of the species analysed in this study (only five species with 50 or less), and future models may be further refined by more surveys that aim specifically at early detection of non-native species around the globe. Although correct species identification is imperative for a reliable dataset, recent taxonomic research shows how easy is to confuse similar species (e.g., Brunetti et al., 2015; Vandepas et al., 2015).

By combining our predictions of environmental suitability with connectivity and invasibility estimates, we were able to predict a combined estimate of the debt of introduction, establishment and spread (Rouget et al., 2016) in order to indicate areas that should be prioritized for monitoring for future introductions and areas where immediate measures should target the expansion of the distributions of already established species. We also identified which species have a higher risk of spreading and becoming invasive, making them a priority for impact determination (Figures S1–S7). Genetic studies of bioinvasions can also use our results, because we predict the most important directions of gene flow and possible origins of multiple invasions, indicating where researchers should direct their collecting efforts. Our study demonstrates that ENM can be an important tool in risk assessment when trying to predict new areas of invasion based on dispersal probability between areas and propagule pressure. A periodic review of models that continuously includes new records is required, especially for easily dispersed species.

Most marine invasions have resulted of conditions for species transport and establishment, and we know that those conditions are changing fast in response to both climate change (IPCC, 2014) and increasing global commerce. The increase in water temperature already favours the spread of tropical species towards the poles (e.g., see Canning-Clode & Carlton, 2017), and the increase in ship numbers and in new routes will increase propagule pressure and probability of establishment. Thus, a necessary approach for the future is to update the models every 10 years at least. With our modelling approach, we identified possible locations of future marine species invasions, in the hope that by predicting invasion risk, we can find innovative new ways to reduce this problem in the future.

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BIOSKETCH

The authors of this article are interested in the fields of species distribution modelling, biodiversity, biological invasions and ecosystem conservation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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