



Extrapolation in species distribution modelling. Application to Southern Ocean marine species

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ABSTRACT

Species distribution modelling (SDM) has been increasingly applied to Southern Ocean case studies over the past decades, to map the distribution of species and highlight environmental settings driving species distribution. Predictive models have been commonly used for conservation purposes and supporting the delineation of marine protected areas, but model predictions are rarely associated with extrapolation uncertainty maps.

In this study, we used the Multivariate Environmental Similarity Surface (MESS) index to quantify model uncertainty associated to extrapolation. Considering the reference dataset of environmental conditions for which species presence-only records are modelled, extrapolation corresponds to the part of the projection area for which one environmental value at least falls outside of the reference dataset.

Six abundant and common sea star species of marine benthic communities of the Southern Ocean were used as case studies. Results show that up to 78% of the projection area is extrapolation, i.e. beyond conditions used for model calibration. Restricting the projection space by the known species ecological requirements (e.g. maximal depth, upper temperature tolerance) and increasing the size of presence datasets were proved efficient to reduce the proportion of extrapolation areas. We estimate that multiplying sampling effort by 2 or 3-fold should help reduce the proportion of extrapolation areas down to 10% in the six studied species.

Considering the unexpectedly high levels of extrapolation uncertainty measured in SDM predictions, we strongly recommend that studies report information related to the level of extrapolation. Waiting for improved datasets, adapting modelling methods and providing such uncertainty information in distribution modelling studies are a necessity to accurately interpret model outputs and their reliability.

1. Introduction

Among the broad array of analytical tools developed for marine ecology studies over the last two decades, Species Distribution Modelling (SDM) has been increasingly used (Peterson 2001, Elith et al. 2006, Austin 2007, Gobeyn et al. 2019) and applied to Southern Ocean pelagic (Pinkerton et al. 2010, Freer et al. 2019), benthic organisms (Loots et al. 2007, Pierrat et al. 2012, Basher and Costello 2016, Xavier et al. 2016, Gallego et al. 2017, Guillaumot et al. 2018a, 2018b, Fabri-Ruiz et al. 2019, Jerosch et al. 2019) and even marine mammals (Nachtsheim et al. 2017). SDM represents a complementary approach to individual-based modelling and eco-physiological experiments, quickly and synthetically identifying environmental correlates of species distribution (Brotons et al. 2012, Feng and Papeş 2017, Feng et al. 2020). SDM is also used to define species distribution spatial range (Nori et al. 2011, Walsh

and Hudiburg 2018) and can be used as decision criteria for conservation purposes (Guisan et al. 2013, Marshall et al. 2014). For instance, it is currently used in proposals developed by national committees of the CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) to support the definition and delineation of marine protected areas (Ballard et al. 2012, CCAMLR report WG-FSA-15/64, Arthur et al. 2018).

Applying SDM to Southern Ocean case studies is particularly challenging due to major constraints and biases that may reduce modelling performance. As for many oceanographic studies, access to environmental data with high temporal and spatial resolutions is difficult (Davies et al. 2008, Robinson et al. 2011). Antarctic coastal areas, in particular, are rarely accessed and documented due to logistical constraints, access being for example impossible during the austral winter due to sea ice cover (De Broyer et al. 2014). The availability of species

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absence records is also a limiting factor to modelling performances and model calibrations (Brotons et al. 2004, Wisz and Guisan 2009). Models are usually based on a limited number of presence-only records and limited number of sampling sites, which are both spatially aggregated in the vicinity of scientific stations, where access is frequent and datasets from different seasons, have been compiled over decades and even beyond (De Broyer et al. 2014, Guillaumot et al. 2018a, Fabri-Ruiz et al. 2019, Guillaumot et al. 2019).

When generating a SDM, the model is fit to data with a given range of value for each environmental descriptor (i.e. the calibration range). When transferring model predictions, a portion of the environment may cover additional conditions that are outside this calibration range: these are non-analog conditions and the model extrapolates (Randin et al. 2006, Williams and Jackson 2007, Williams et al. 2007, Fitzpatrick and Hargrove 2009, Owens et al. 2013, Yates et al. 2018). Considering the limited number of species presence-only records occupied by each marine benthic species, and the poor quality and precision of environmental descriptors available for modelling Southern Ocean species distributions (Guillaumot et al. 2018a, Fabri-Ruiz et al. 2019), a large proportion of cells might be expected to be extrapolations beyond the calibration range of the model.

The Multivariate Environmental Similarity Surface (MESS) approach analyses spatial extrapolation by extracting environmental values covered by presence-only records and estimates areas where environmental conditions are outside the range of conditions contained in the calibration area (Elith et al. 2010). The method considers that extrapolation occurs when at least one environmental descriptor value is outside the range of the environment envelop for model calibration (more details given in Appendix 4).

The MESS approach was initially used to determine the environmental barriers to the invasion of the cane toad in Australia, when facing new environments and under future conditions (Elith et al. 2010). Implemented in MaxEnt (Elith et al. 2011), MESS was subsequently used by several authors for defining the climatic limits to the colonisation of new environments by non-native species, such as the American bullfrog in Argentina (Nori et al. 2011), for studying contrasts between native and potential ecological niches like in the study of the spotted knapweed (*Centaurea stoebe*) (Broennimann et al. 2014), or for defining the limits to model transferability and predicting the distribution of trees under future environmental conditions (Walsh and Hudiburg 2018).

More recently, the MESS approach was used to define model uncertainties related to extrapolation (Escobar et al. 2015, Li et al. 2015, Cardador et al. 2016, Luizza et al. 2016, Iannella et al. 2017, Milanese et al. 2017, Silva et al. 2019) and extrapolation areas where environmental conditions are non-analog to conditions of model calibration (Fitzpatrick and Hargrove 2009, Anderson 2013). Associating uncertainty information to model predictions has been acknowledged as a necessity for reliable interpretations of model predictions (Grimm and Berger 2016, Yates et al. 2018). It is also a requirement for specifying the level of risk associated with predictions and evaluating whether uncertainty can be mitigated to improve model outcomes (Guisan et al. 2013).

This study addresses the importance of extrapolation and associated uncertainties in SDMs generated at broad spatial scale for Southern Ocean species: an analysis that is seldom performed although important to characterise model reliability. Using the case study of six abundant and common sea star species in marine benthic communities, objectives of this work are to evaluate the importance of extrapolation proportions in wide projection areas, and to provide some methodological clues to mitigate the effects of extrapolation and improve model accuracy.

2. Methods

2.1. Studied species and environmental descriptors







The distribution of six sea star species (Asteroidea: Echinodermata) was studied (Table 1). The six species, *Acodontaster hodgsoni* (Bell, 1908), *Bathybiaster loripes* (Sladen, 1889), *Glabraster antarctica* (Smith, 1876), *Labidiaster annulatus* Sladen, 1889, *Odontaster validus* Koehler, 1906 and *Psilaster charcoti* (Koehler, 1906) are abundant and common in benthic communities in the Southern Ocean. The biology, ecology and distribution of these species have been extensively studied and are relatively well documented (McClintock et al. 2008, Mah and Blake 2012, Lawrence 2013). Presence-only records were compiled from a recently updated database, thoroughly scrutinised with the World Register of Marine Species (WoRMS Editorial Board 2016), to delete potential discrepancies, update taxonomy and correct for georeferencing errors (Moreau et al. 2018).

Models were generated for the different species using 298–851 presence-only records, and projected at different depth ranges (Table 1). The distributions of these presence-only records are contrasting between species (Appendix 1), with *A. hodgsoni*, *B. loripes* and *G. antarctica* having an Antarctic and sub-Antarctic distribution, with an important number of data available for *B. loripes* and *G. antarctica* but less data for *A. hodgsoni* (respectively 591, 851 and 298 presence-only records). *Labidiaster annulatus* has a distribution mainly gathered in the sub-Antarctic region with few data available (375 presence-only records). *Odontaster validus* and *P. charcoti* are mainly present on the coasts of the Antarctic shelf.

Environmental descriptors were selected from the dataset provided at https://data.aad.gov.au/metadata/records/environmental_layers. These are oceanography raster layers that mostly describe the physical and geochemical environment south of 45°S with a 0.1° grid-cell resolution (approximately 11 km wide in latitude). Among the 58 environmental descriptors provided, only those that fulfilled the analysis performed by Guillaumot et al. (2020) were selected: 'distance' layers and 'extreme' layers were not selected because the interpretation of their respective contributions to niche models is complex or weak and collinear descriptors were also discarded for a Variance Inflation Factor (VIF) > 10 (Naimi et al. 2014). A set of 14–16 species-specific layers that characterise temperature, salinity, food availability and habitat characteristics were therefore used for model calibration (Table S2).

Table 1

Sea star species investigated in the present study. The number of presence-only records available was summed up after removal of duplicates from each grid cell pixel. Image sources: Bruggeman 1998, BIOMAR ULB database (P. Pernet), proteker.net, B121 expedition (Q. Jossart).

	<i>Acodontaster hodgsoni</i> (Bell, 1908)	<i>Bathybiaster loripes</i> (Sladen, 1889)	<i>Glabraster antarctica</i> (Smith, 1876)	<i>Labidiaster annulatus</i> Sladen, 1889	<i>Odontaster validus</i> Koehler, 1906	<i>Psilaster charcoti</i> (Koehler, 1906)
						
Presence-only records number	298	591	851	375	337	353
Model maximum depth	1500 m	4000 m	4000 m	1500 m	1500 m	4000 m

2.2. Models calibration

Species Distribution Models (SDMs) were generated using the Boosted Regression Trees (BRT), a machine-learning approach that was already calibrated for Southern Ocean case studies (Guillaumot et al. 2018a, 2018b, Guillaumot et al. 2019) and was proved efficient to provide accurate models with good transferability performance, that is good ability to project model in space and time (Elith et al. 2008, Reiss et al. 2011, Heikkinen et al. 2012, Guillaumot et al. 2019). In order to minimize the effect of presence-only records aggregation on model predictions, background data were randomly sampled in the environment following the probabilities defined by a Kernel Density Estimation (KDE) (see Phillips et al. 2009 for general principles, Guillaumot et al. 2018a, 2018b; Fabri-Ruiz et al., 2019 for applications). The number of background records was selected equal to the number of presence-only records (Barbet-Massin et al. 2012). The KDE was established based on the aggregation of benthos sampling effort provided in the Biogeographic Atlas of the Southern Ocean (De Broyer et al. 2014, map available in supplementary material of Guillaumot et al. (2019)). One hundred SDMs were generated and averaged for each species, with background data randomly sampled following the KDE for each replicate.

SDMs were calibrated and reliability tested using a spatial cross-validation procedure. For each species, several procedures were compared following Guillaumot et al. (2019). The studied area was randomly subdivided into 2 to 6 areas of similar surfaces (longitude-split spatial folds), with presence and background data selected from one to three areas for model training and from the remaining areas for model testing. The “6-fold CLOCK” cross-validation approach was selected for *B. loripes*, *G. antarctica*, *L. annulatus* and *O. validus* and the “2-fold CLOCK” procedure was selected for *A. hodgsoni* and *P. charcoti*, according to the best percentage of test data correctly classified (Appendix 3).

The Maximum sensitivity plus specificity threshold (MaxSSS), considered the most appropriate threshold for presence-only SDM (Liu et al. 2013) was used to binarize models into suitable (>MaxSSS value) and unsuitable areas (<MaxSSS value). This threshold was used to measure the proportion of test data correctly classified. Modelling performances were also assessed using the three following metrics: Area Under the Receiver Operating Curve (AUC, Fielding and Bell 1997), the Point Biserial Correlation between predicted and observed values (COR, Elith et al. 2006) and the True Skill Statistics (TSS, Allouche et al. 2006).

Two analyses were performed: in Analysis #0 (‘no-depth limited’), SDMs were projected on the entire Southern Ocean surface (south of 45°S) and in Analysis #1 (‘depth limited’), SDM projections and background samplings were restricted to areas limited by a maximum depth threshold defined for each species based on the available species presence-only records (Table 1).

2.3. MESS calculation

The MESS was measured using the *dismo* R package (Hijmans et al. 2017) and following the guidelines provided in Elith et al. (2010). Pixels for which at least one environmental descriptor has a value that is outside the range of environmental values defined by presence-only records (calibration range) were considered to be extrapolation (i.e. when MESS gets negative values, Appendix 4). The proportion of extrapolation areas (i.e. the proportion of cells defined as extrapolations over the total projection area) was calculated and compared between species. On SDM projection maps, extrapolated pixels were displayed in black.

Environmental parameters responsible for extrapolation were estimated by modifying the code provided in Elith et al. (2010). Detailed R scripts are available at <https://github.com/charleneguillaumot/THESIS>. Methodological details are provided in Appendix 4.

2.4. Influence of the number and distribution of presence-only records on extrapolation

The proportion of extrapolation areas may vary with presence-only sampling effort. In order to study the influence of the number and distribution of these presence-only records on the proportion of extrapolation areas, two analyses were performed. First, several SDMs were generated with different numbers of presence-only records, following the chronological addition of new presence-only records through time, from 1980 to 2016. Second, SDMs generated with 10–100% (10% increments, so 10 subsets) of the entire presence-only dataset were compared. In this analysis, in contrast to the previous one, presence-only records are randomly sampled among the datasets available.

In these two analyses, SDMs were projected on the environmental space limited by the maximum depth defined for each species (Table 1), 100 model replicates were generated and averaged in each case and spatial autocorrelation (SAC) was estimated to assess the influence of presence-only records aggregation on modelling performances. The significance of SAC was tested using the Moran I index computed on model residuals (Luoto et al. 2005, Crase et al. 2012).

The relationship between the number of presence-only records used in SDM and the relative proportion of extrapolation areas was characterised using linear regressions. This allowed, for each model, estimation of the minimum number of presence-only records required to obtain a ‘reasonable’ proportion of extrapolation area arbitrarily set to a 10% threshold.

3. Results

3.1. Extrapolation and the extent of projection areas

All generated SDMs are accurate and performant, with high AUC (AUC > 0.91), TSS (TSS > 0.559) and COR (COR > 0.68) values, low standard deviations and good percentages of correctly classified presence-only test data (77–90%) (Table 2). Descriptors that contribute the most to SDMs are depth (22–34%), minimum POC (6–21%), POC standard deviation (8–20%), mean ice cover depth (7–17%) and mixed layer depth (3–10%). Contrasts between species are in the respective percentage of contribution of these descriptors. Descriptors that drive the most species distribution are similar between species (Appendix 5).

Models projected on the entire Southern Ocean (Analysis #0, ‘no-depth limited’) extrapolate on an area covering between 15 and 78% of the entire projection area, and 19–45% of the area initially predicted as suitable to the species distribution (Table 2, Fig. 1). Extrapolation areas cover more than 50% of the projection area for *A. hodgsoni* (78.6%), *P. charcoti* (67.8%), *L. annulatus* (64.8%) and *O. validus* (51.9%) and more than 30% of suitable areas (Table 2). For these four species, depth is responsible for 25 to 68% of extrapolation (Appendix 5). Geomorphology, mean ice cover and POC standard deviation are layers also contributing to 2–7% for extrapolation (Appendix 5). These descriptors that highly contribute to MESS also contribute to the model, and there are no descriptors for which the contribution to MESS is important whereas the contribution to the model is not substantial (Appendix 5).

In models projected on areas restrained in depth (Analysis #1, ‘depth limited’), the percentage of extrapolation area sharply decreases from 59 to 18% according to the species (Table 2). However, model performances also decrease, with AUC values going down to 0.885, TSS values to 0.419 and COR values to 0.475. The percentage of correctly classified test data is much lower and more variable for the shallowest species *A. hodgsoni* (from 90 ± 6.26% to 45.5 ± 8.1%), *L. annulatus* (77.7 ± 15.2% to 57.98 ± 20%) and *O. validus* (from 85.4 ± 9.6% to 57.68 ± 21%). For all species, predicted suitable areas increase two-fold.

Overall, descriptor contributions to the model remain unchanged between the two analyses, except for depth contribution that decreases to around 10% on average for all the species. In contrast, in Analysis #1, depth contribution to the MESS is very low (0.64–5.8%), except for

Table 2

Modelling performances for each species. Average and standard deviation values of the 100 model replicates. Pres. NB: number of presences-only records available for modelling (duplicates excluded); AUC: Area Under the Curve; TSS: True Skill Statistics; COR: Biserial Correlation.

Analysis #0, no-depth limited								
Species	Pres. NB	AUC	TSS	COR	Correctly classified test data (%)	Suitable area (% total area)	Extrapolation area (% total area)	Extrapolation area (% total area)
<i>Acodontaster hodgsoni</i>	298	0.925 ± 0.02	0.579 ± 0.04	0.735 ± 0.06	90 ± 6.26	8.86	78.6	35.3 ± 4.1
<i>Bathybiaster loripes</i>	591	0.910 ± 0.02	0.559 ± 0.07	0.68 ± 0.09	80.6 ± 10.9	8.55	29.1	21.9 ± 4.4
<i>Glabraster antarctica</i>	851	0.929 ± 0.01	0.58 ± 0.05	0.719 ± 0.07	85.45 ± 6.34	7.95	15.73	19.9 ± 3.9
<i>Labidiaster annulatus</i>	375	0.95 ± 0.03	0.598 ± 0.07	0.730 ± 0.14	77.7 ± 15.2	3.33	64.83	42.1 ± 10.5
<i>Odontaster validus</i>	337	0.953 ± 0.01	0.605 ± 0.05	0.746 ± 0.09	85.4 ± 9.6	6.89	51.9	45.2 ± 5.65
<i>Psilaster charcoti</i>	353	0.911 ± 0.02	0.58 ± 0.03	0.723 ± 0.04	87.7 ± 4.8	8.90	67.9	32.5 ± 4.71
Analysis #1, depth limited								
Species	Pres. NB	AUC	TSS	COR	Correctly classified test data (%)	Suitable area (% total area)	Extrapolation area (% total area)	Extrapolation area (% total area)
<i>Acodontaster hodgsoni</i>	298	0.823 ± 0.05	0.419 ± 0.1	0.475 ± 0.14	45.5 ± 18.1	17.49	40.6	27.5 ± 8.5
<i>Bathybiaster loripes</i>	591	0.887 ± 0.03	0.513 ± 0.08	0.607 ± 0.12	78.4 ± 11	15.75	18.2	20.8 ± 4.8
<i>Glabraster antarctica</i>	851	0.915 ± 0.01	0.537 ± 0.08	0.654 ± 0.1	81.8 ± 7.7	14.08	23.9	18.64 ± 3.5
<i>Labidiaster annulatus</i>	375	0.918 ± 0.03	0.482 ± 0.16	0.563 ± 0.25	57.98 ± 20	8.88	59.5	38.7 ± 14.6
<i>Odontaster validus</i>	337	0.908 ± 0.03	0.504 ± 0.13	0.586 ± 0.17	57.68 ± 21	11.64	51.5	38.3 ± 6.97
<i>Psilaster charcoti</i>	353	0.885 ± 0.02	0.546 ± 0.04	0.665 ± 0.06	83 ± 6.6	15.40	35.78	33.2 ± 5.1

P. charcoti (16.3%). Mean ice cover is the layer that contributes the most to extrapolation, extrapolation areas mainly corresponding to Weddell and Amundsen seas.

3.2. Extrapolation and the number of presence-only records

Model performance and size of extrapolation area were compared between models run with different numbers of presence-only records, following the chronological addition of new samples (from 1980 to 2016). From 1980 to 2016, the number of presence-only records collected during oceanographic campaigns has increased from 1.9–3.3 times according to the species (1.9 times for *O. validus*, 3.3 times for *A. hodgsoni*) (Fig. 2A). Spatial autocorrelation between presence-only records varies between species, with the highest Moran's I scores obtained for *L. annulatus*, *O. validus* and *A. hodgsoni*. The highest Moran's I values were mainly calculated for the oldest presence-only subsets (1980), strengthening the fact that the addition of new presence-only records with additional campaigns reduces spatial autocorrelation (Table S6).

Model performance increases (higher AUC scores) with the addition of new presence-only records, for all species except for models of *A. hodgsoni* and *B. loripes* for which AUC values are stable (Table S6). Similarly, the percentage of correctly classified test data presents important standard deviation values and improves with the addition of new presence-only records, except for *O. validus* (10% decrease) (Fig. 2).

For all species, the addition of new data reduces the percentage of extrapolation over the total projection area (-30.7% for *A. hodgsoni*, -12.7% for *B. loripes*, -20.5% for *G. antarctica*, -17.6% for *L. annulatus*, -10.2% for *O. validus* and -11% for *P. charcoti*, i.e. differences between the two extrapolation % values) and over the species suitable area as well (Fig. 2, Table S6).

The decrease of extrapolation with the addition of presence-only records was tested by running, for each species a series of models with different subsets of presence-only records randomly sampled from the

total dataset. One hundred model replicates were progressively run with 10–100% of the total dataset and proportions of extrapolation areas were computed accordingly (Fig. 3, Table S7). Results confirm that the addition of presence-only records strongly reduces proportions of extrapolation areas. Proportions of extrapolation areas also vary between species models as a function of depth. Low proportions of extrapolation areas are obtained in models run for deep species and large datasets (e.g. 8.2% for 591 records in *B. loripes* and 23.9% for 851 records in *G. antarctica*). In contrast, models run for shallower species show higher proportions of extrapolation areas (40.6% for 298 records in *A. hodgsoni*, 51.5% for 375 records in *L. annulatus* and 35.8% for 337 records in *O. validus*). For these last species, spatial autocorrelation values are also higher compared to other species (Table S7).

A linear regression model was fit to the relationship between the number of presence-only records and proportions of extrapolation areas. For all species, regression coefficients are all negative and tested significant showing that proportions of extrapolation areas decrease with the addition of new records (Table 3). The intersection point between regression models and the (arbitrary) 10% extrapolation threshold was used to provide an estimate of the minimum number of records required for each species model to have an “adequate” proportion of extrapolation areas of 10%. This minimum number of presence-only records is reached for none of the studied species, and according to species, the number of presence-only records available should be increased at least by 1.6–3.3 times (Table 3).

4. Discussion

4.1. Modelling performances and extrapolation

SDMs were generated for Southern Ocean sea star species, with contrasting distributions and different numbers of presence-only records available (Table 1, Appendix 1). Overall, species presence-only records are spatially concentrated in the most accessible and visited areas of the

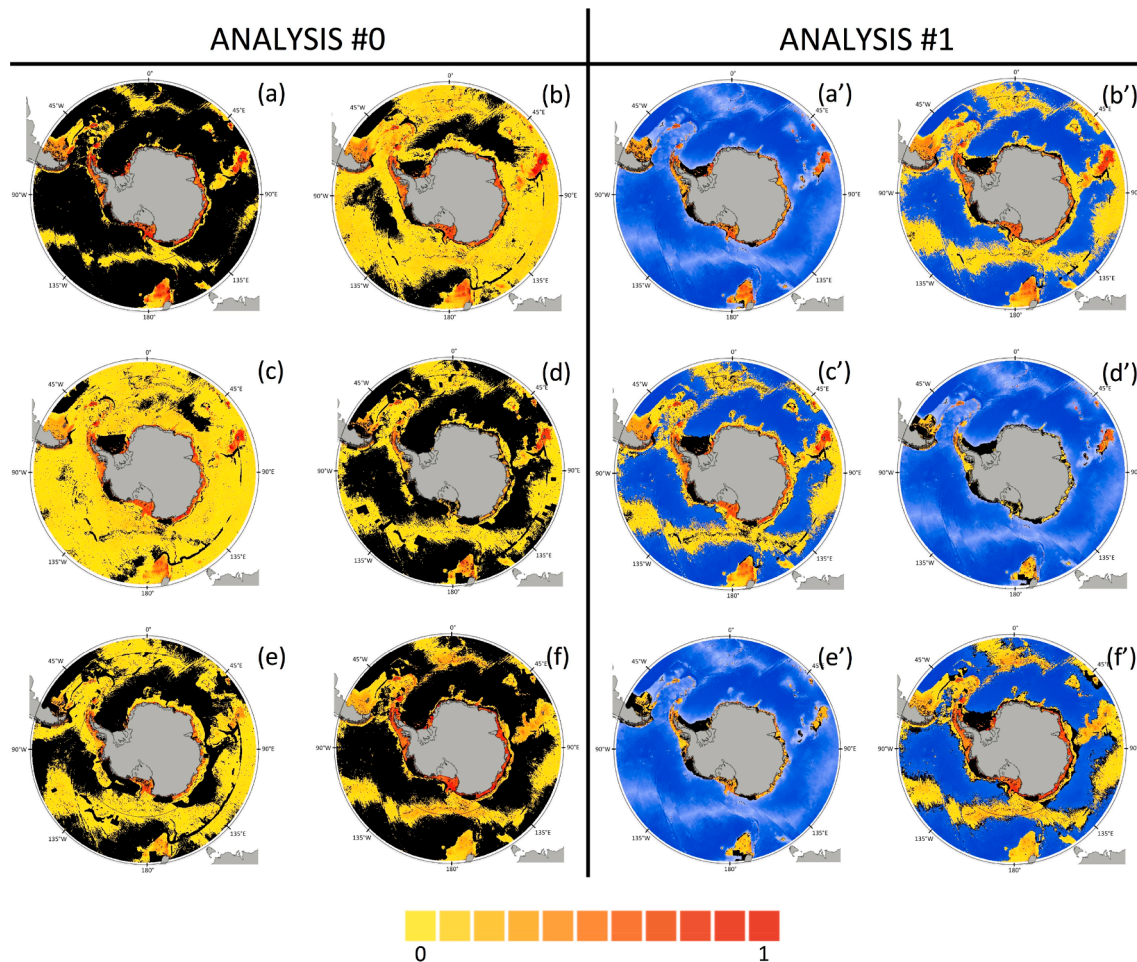


Fig. 1. Maps of extrapolation areas covering SDM predictions, generated with all presence-only records available for the studied species. Left panel: projection area not limited in depth (Analysis #0), right panel: projection area limited to -1500 m and -4000 m depth (Analysis #1), according to the species (*A. hodgsoni*, *L. annulatus*, *O. validus* until 1500 m; *B. loripes*, *G. antarctica*, *P. charcoti* until 4000 m; Table 1). (a) *Acodontaster hodgsoni*, (b) *Bathybiaster loripes*, (c) *Glabraster antarctica*, (d) *Labidiaster annulatus*, (e) *Odontaster validus*, (f) *Psilaster charcoti*. Extrapolation areas displayed in black; pixels colored by the yellow-red color palette provide SDM distribution probabilities (comprised between 0 and 1); bathymetric chart in shades of blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Southern Ocean. Most of the sea star samples were collected close to the coasts of the Western Antarctic Peninsula, the Ross Sea and sub-Antarctic Islands such as the Kerguelen Islands. Consequently, high spatial autocorrelation values were computed, for *L. annulatus* and *O. validus* in particular (Table S6).

Overall, models all show good performances (Table 2), the spatial cross-validation procedure ensuring a relevant evaluation of modelling performances when using spatially aggregated data (Muscarella et al. 2014, Dhingra et al. 2016, Guillaumot et al. 2019). However, models show high proportions of extrapolation areas, with extrapolation covering up to 78% of the projection area in *A. hodgsoni* model (Table 2). This means that even if models are evaluated as accurate, model extrapolation area can concern up to three quarters of the projection area! Assessing the proportion of the projection area for which models extrapolate is therefore necessary as a complementary statistic to adapt modelling methods and improve model predictions. Masking projections by extrapolation uncertainties is also important to perform accurate interpretations.

Extrapolation uncertainty maps have already been associated to SDM projections once in the context of the Southern Ocean, by Torres et al. (2015) in their study of the grey petrel *Procellaria cinerea*, performed at the scale of the Southern Ocean. More recently, the MESS approach has been introduced in the methodological paper of Guillaumot et al. (2019), showing an extrapolation area covering 64% of the projection

area for the distribution model of the sea star *O. validus*, the most studied benthic invertebrate of the Southern Ocean. However, uncertainties associated to extrapolation were not provided in most model projections performed for Southern Ocean species studies. For instance, modelled distributions performed for the sea urchins *Sterechinus neumayeri* and *Sterechinus diadema* (Pierrat et al. 2012) were generated using a relative low number of presence-only records (241 and 332, respectively). Based on results of the present study, extrapolation could be expected to cover up to 60% of modelled distribution areas for these last two species. Further Southern Ocean species distribution models were generated with sometimes less than 100 presence-only records (see Guillaumot et al., 2018b; Fabri-Ruiz et al., 2019 for instance), suggesting that extrapolation could cover up to 70% of projection areas as visible in models of *A. hodgsoni* and *P. charcoti* performed in our study with few records (Fig. 2, Tables S6, and S7).

In addition to model uncertainties associated to extrapolation, other biases can alter the performance of SDMs generated at broad spatial scales including the spatial and temporal aggregation of data (Hortal et al. 2008, Tassarolo et al. 2014, 2017), the selection and quality of environmental descriptors (Davies et al. 2008, Synes and Osborne 2011), the choice of modelling algorithms and the definition of model settings (Hartley et al. 2006, Marmion et al. 2009). Providing such uncertainty information, highlighted with some model statistics is very much encouraged here, as they are essential to model interpretation

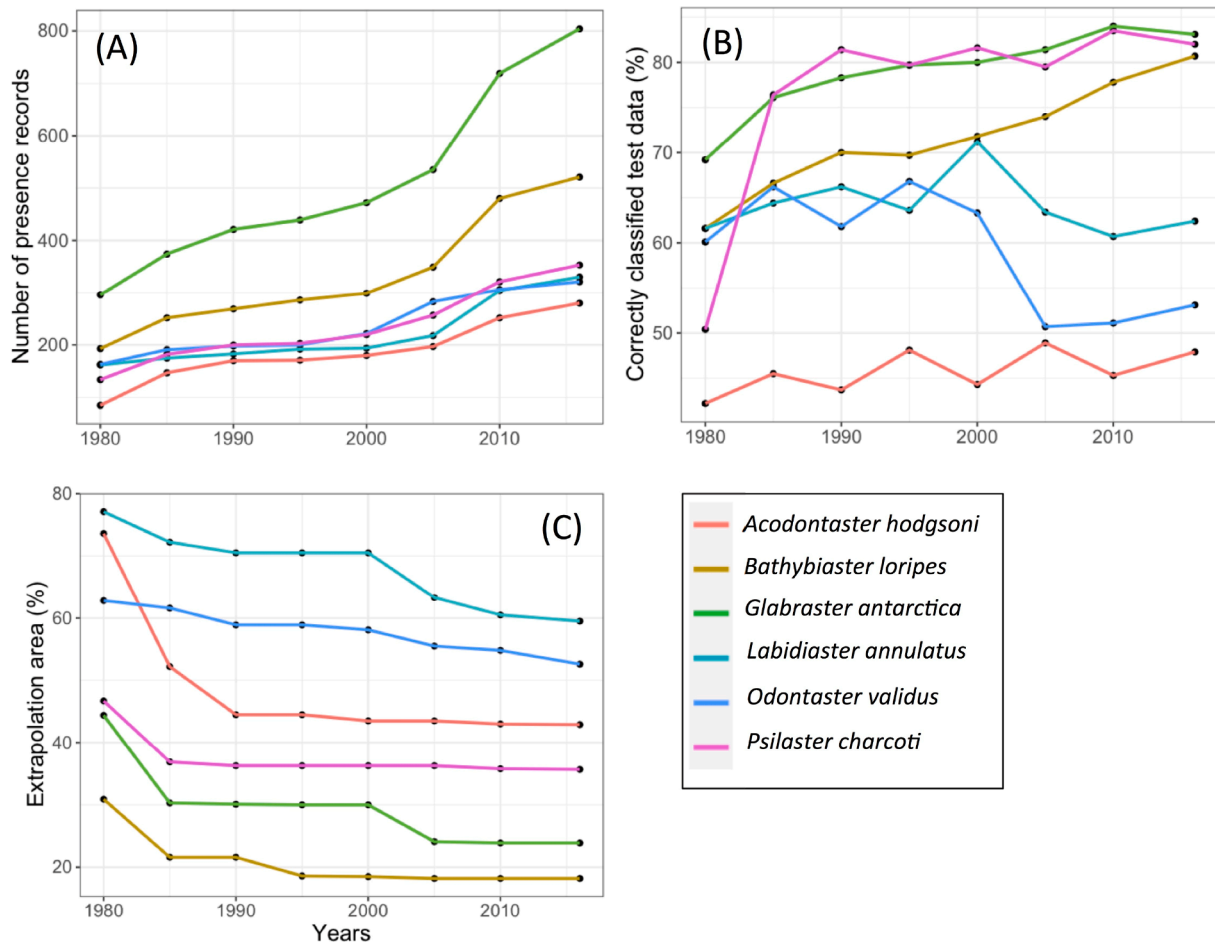


Fig. 2. Evolution of model performances with the increase of data (chronological addition of presence-only records, by 5-year periods, from 1980 to 2016). (A) Number of presence-only records available to generate the model; (B) Mean correctly classified test data (%) (standard deviation values available in Table S6); (C) Proportion of grid-cell pixels of the projection area that are extrapolations (%). The maximal number of presence-only records present in Table 2 may not be reached here because some collection dates remain unknown.

(Beale and Lennon 2012, Guisan et al. 2013, Yates et al. 2018).

4.2. How can we reduce model extrapolation? Enriching SDMs with knowledge of species ecology

One objective of this work was to provide some methods to mitigate the effect of extrapolation on model uncertainties. Our results show clear contrasts between models generated for “deep” and “shallow” species, with lower proportions of extrapolation areas computed for deep species models (29.1 and 15.73% respectively for *B. loripes* and *G. antarctica*). The model generated for *P. charcoti* departs from this general scheme, with extrapolation reaching 67.9% of the projection area. This is due to the strong spatial aggregation of records and the small presence-only record dataset available in deeper habitats. Depth is indeed responsible for 58.1% of the extrapolation for *P. charcoti* (Appendix 5). Indeed, the erroneous characterization of species occupied space, due to an incomplete sampling, has been identified as a significant source of bias in SDM predictions (Hortal et al. 2007, 2008, Rocchini et al. 2011, Sánchez-Fernández et al. 2011, Titeux et al. 2017, El-Gabbas and Dormann 2018).

Limiting model projection areas to biogeographically, or ecologically “realistic” depth ranges can help reduce extrapolation as exemplified in the present study, for models of *A. hodgsoni* and *P. charcoti*, for which extrapolation was reduced from 78.6 to 40.6% and 67.9 to 35.8% respectively (Table 2). Restraining model projection areas based on species ecological or physiological tolerance thresholds is a common

approach in ecological modelling using experimental data or field observations (Kearney and Porter 2009, Hare et al. 2012, De Villiers et al. 2013). Knowledge of species ecology and physiology can also be useful to delineate transferability areas (Feng and Papeş 2017) and improve distribution models, as recently shown for Southern Ocean species (Guillaumot et al. 2018a, Guillaumot et al. 2019). Feng et al. (2020) developed a new modelling algorithm, called *Plateau*, which uses experimental data to define upper temperature conditions in distribution models. For temperature and salinity, physiological experiments and field observations can be used in models to determine species tolerance thresholds. This requires knowledge about the species ecology and physiology and the input from specialists, all conditions that remain difficult to meet, regarding deep sea species of the Southern Ocean (Gage 2004, Gutt et al. 2010, De Broyer and Danis 2011). Moreover, several studies suggested that some Southern Ocean species might have found refuges in deep-sea habitats in the past, during glacial maxima, which makes species depth range difficult to precise when deep and shallow populations have not been differentiated into distinct taxonomic units yet (Rogers 2007, Arango et al. 2011, Havermans et al. 2011, Near et al. 2012).

4.3. How can we reduce extrapolation? Improving sampling effort

Increased sampling effort over enlarged areas allows the production of larger datasets from which many records can be used to generate reliable models with reduced extrapolation areas. In this study,

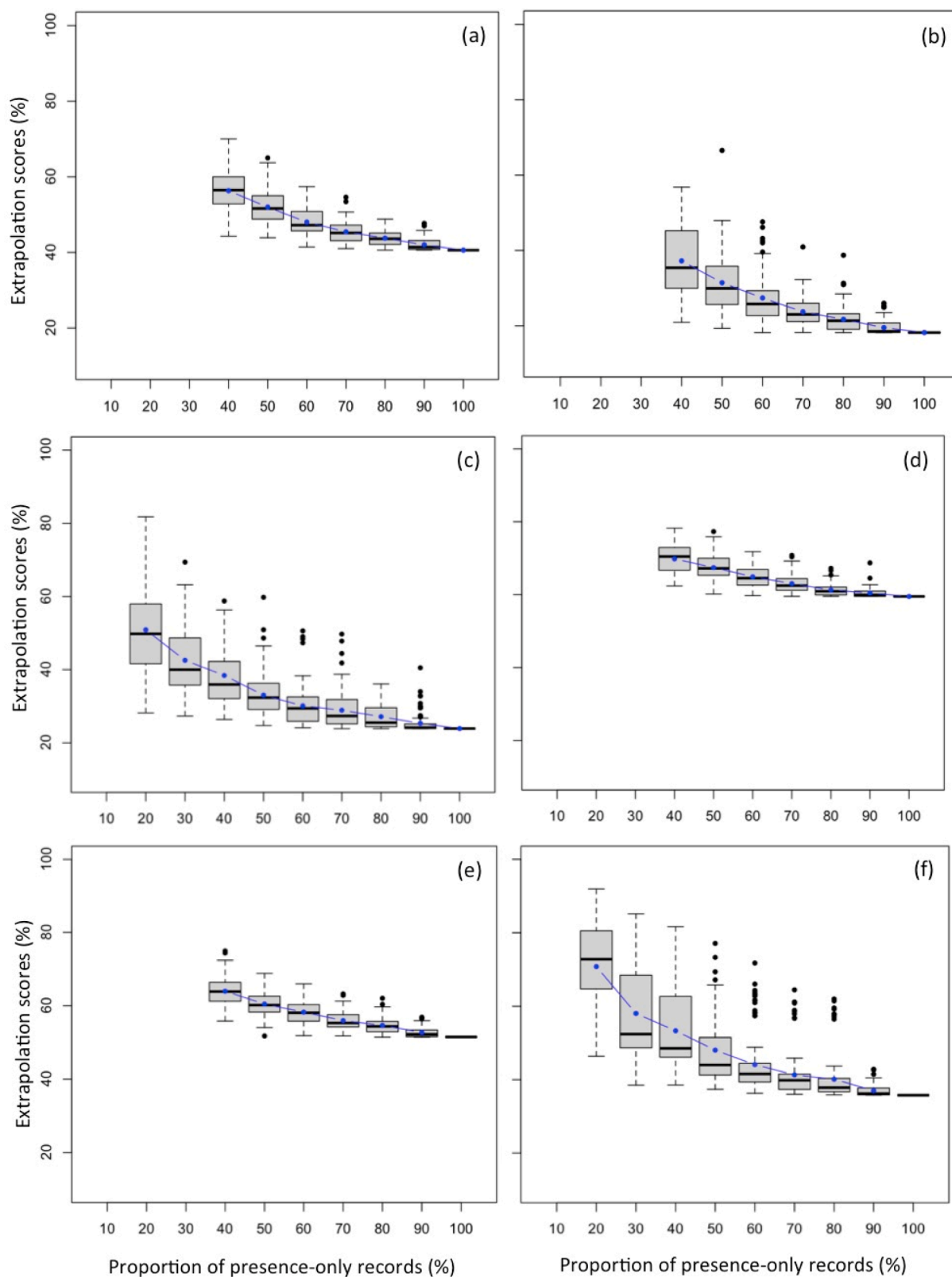


Fig. 3. Boxplot diagrams representing the decrease of proportions of extrapolation areas (in % of the total projection area) with addition of presence-only records used to generate model replicates (in % of data available, see Tables 1 and S7), for: (a) *Acodontaster hodgsoni*, (b) *Bathybiaster loripes*, (c) *Glabraster antarctica*, (d) *Labidiaster annulatus*, (e) *Odontaster validus*, (f) *Psilaster charcoti*. For each box, mean values (blue dots) and outliers (black dots) are shown for the 100 model replicates. Some boxes are missing for low percentages of presence-only records (10–30%, corresponding to close or less than 100 presence-only records) that do not allow models to be generated.

Table 3

Equations of simple linear regressions between the number of presence-only records X and the average proportion of extrapolation areas Y (Table 2, significance levels: * $p < 0.1$, ** $p < 0.05$). The estimate of the number of presence-only records necessary to have a minimum “adequate” arbitrary proportion of extrapolation areas of 10% is given in the last column.

Species	Equation	R ²	Estimated Pres.NB. (with multiplier of actual Pres.NB. available)
<i>Acodontaster hodgsoni</i>	$Y = -0.1358X + 73.616^{**}$	0.60	468 (×1.6)
<i>Bathyiaster loripes</i>	$Y = -0.0249X + 28.974^*$	0.42	762 (×1.3)
<i>Glabraster antarctica</i>	$Y = -0.0304X + 44.991^{**}$	0.61	1151 (×1.4)
<i>Labidiaster annulatus</i>	$Y = -0.0913X + 88.078^{**}$	0.85	855 (×2.3)
<i>Odontaster validus</i>	$Y = -0.0561X + 71.112^{**}$	0.93	1089 (×3.2)
<i>Psilaster charcoti</i>	$Y = -0.0301X + 44.613^*$	0.37	1150 (×3.3)

proportions of extrapolation areas proportionally decreased when increased numbers of presence-only records were used to generate models. The occurrence datasets were significantly augmented between 1980 and 2016, with a number of presence-only records multiplied by 1.9–3.3 times according to the studied species, which allowed reduction of model extrapolation from 10.2 to 30.7% according to the species (Fig. 2, Table S6). However, results suggest that about twice the number of presence-only records actually available would be necessary to reduce extrapolation down to a “satisfactory” threshold of 10% of the projection area (Table 3).

Generating reliable and stable models using a sufficient number of presence-only records is essential. In this study, some models could not be run when the number of presence-only records was too low (approaching 150 presence-only records or less) compared to the broad extent of the projection area and the spatial aggregation of these data (Table S7). Considering that the spatial cross-validation procedure splits the initial dataset into training and test data, and that at each step, 75% of these training data are randomly sampled by BRT to iteratively create a model tree (and generate stochasticity in the procedure), the final number of presence-only records available to describe the presence data - environment relationship becomes too low (around 37.5% of the initial number of presence-only records).

The lowest number of presence-only records required to build a reliable model is species-dependent as not all presence-only records are equally informative, due to species-specific relationships between records and the environment. When models are generated using BRT, records that bring no new environmental information to the model are dropped because they are not informative enough to improve the construction of BRT trees. Pruning non-informative data also reduces the total number of presence-only records available to generate a model (Elith et al. 2008). This is strongly related to prevalence that is, the ratio between the number of presence-only records and the size of the projection area (Jiménez-Valverde et al. 2009, Santika 2011, Barbet-Massin et al. 2012). In order to accurately describe a vast projection area and be able to create a model, it is necessary to gather a substantial amount of information about the geographic environmental conditions and about species known distribution. If a limited number of records is available and these data are aggregated in space (i.e. weakly informative), the first trees produced by BRT will contain most of the model deviance, but as no new information is provided, the model will quickly overfit because redundant information is provided by close presence-only records. Eventually, this will make the model collapse.

Increasing the number of presence-only records is proved an efficient alternative to generate more relevant models (Stockwell and Peterson 2002, Feeley and Silman 2011, van Proosdij et al. 2016), but the spatial

distribution of these records is of importance as well (Yates et al. 2018). A uniform distribution of records over the entire projection area reduces spatial autocorrelation and optimizes the sampling and representativeness of environmental conditions under which species can thrive. In this study, the spatial aggregation of species records was particularly high for two species, *O. validus* and *L. annulatus*. It was estimated that the number of supplementary presence-only records necessary to reach a proportion of extrapolation areas of 10% should be twice as high as it is for other species (Table 3). Additional data are necessary to improve the establishment of the relationship between species distribution and the environment because species records are less informative when aggregated than when they are evenly distributed.

The Southern Ocean covers contrasting environmental conditions, biogeographic regions and ecoregions (Pierrat 2011, Fabri-Ruiz et al. 2020). Ideally, both species presence and absence should be recorded in each ecoregion for an accurate description of the occupied space (Torres et al. 2015). Because such a sampling effort is usually not achievable, nor realistic, alternatives would consist of (1) a relevant adjustment of projection areas, with for instance the combination of several SDM projections using different grid sizes according to what is available. Generating SDM projections for large areas and combining results with projections zoomed in on areas where more environmental detail is available would provide more relevant and realistic modelled species distributions (Seo et al. 2009, Anderson and Raza 2010). (2) In order to compensate for the lack of presence-record availability, the ‘ensembles of small models’ approach is another alternative. This method fits a set of bivariate models (i.e. generated with two environmental descriptors only), within a hierarchic multi-scale framework (i.e. zooming in and out in space from local to regional predictions), and finally averages this ensemble of models with a weighted ensemble approach, which subsequently provides more accurate and robust model predictions (Lomba et al. 2010, Breiner et al. 2015, Habibzadeh and Ludwig 2019).

4.4. Some limitations to the MESS approach

The MESS approach can reveal parts of projection areas where models extrapolate. Extrapolation however can be over-estimated. Indeed, extrapolation is considered as soon as the value of a single environmental descriptor falls outside the range of the known species environmental requirements. But, some extreme values would not limit but can promote species presence: this is the case for descriptors relating to food resource availability (e.g. chlorophyll *a*, POC concentrations...), for which a high pixel value exceeding the range of values recorded based on species presences will be still considered as extrapolation, although more food usually means suitable conditions for species distribution.

Some fine-tuning of the MESS approach would imply to identify, for each pixel, which descriptor is responsible for extrapolation and filter the conditions for which the model should really extrapolate. Such an approach was developed by Owens et al. (2013), who used the MOP method (Mobility Oriented Parity). Based on multivariate analyses, they determined if pixels contain a combination of environmental conditions that should induce extrapolation. In contrast to the MESS approach, the MOP method can directly differentiate proportions of extrapolation areas according to the combination of descriptors responsible for extrapolation. Another complex alternative is the ExDet tool, developed by Mesgaran et al. (2014), which also accounts for multivariate extrapolation possibilities, i.e. extrapolation linked to novel combinations between covariates.

In this study, the MESS approach was favored as a more strict and conservative method to highlight the importance of extrapolation, the effect of data quantity and quality, and the relevance of the proposed corrections. The MESS is also simpler to apply and well suited to exploratory studies.

5. Conclusions

This study shows that when modelling species distribution on broad scale areas, such as the Southern Ocean, important proportions of predicted distribution probabilities (suitable or not) are model extrapolations. This extrapolation uncertainty relies on the completeness of species sampling, and the definition of its occupied space to calibrate the model. Extrapolation occurs in areas where habitat suitability is unknown as no information on species presence or absence is provided.

Reducing extrapolation is possible by combining SDM with ecological and physiological knowledge of species requirements (e.g. depth range, temperature tolerance thresholds). Increased sampling effort over enlarged areas also allows the production of more reliable models with reduced extrapolation areas and our study shows that doubling the number of presence-only records available to generate the model would help reduce the extrapolation area down to 10% of the projected area.

While more data samples remain unavailable, some methods are increasingly developed to improve model performances, by adjusting the extent of the projection area or by generating and aggregating several ensembles of small models.

Finally, present results call for a widespread use of extrapolation maps and uncertainties associated to model predictions in model outputs, along with information about the quantity of presence-only records available, the quality and resolution of environmental descriptors and the state of our knowledge of species ecology. These are all essential information needed to support model interpretations, as also stated in recent publications that review best practices in ecological modelling (Araújo et al. 2019, Zurell et al. 2020).

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2020.102438>.

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