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Species distribution modelling in the Southwestern Atlantic Ocean: A systematic review and trends

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ABSTRACT

Species distribution modelling (SDM) of marine organisms is widely developed for biogeography, ecology and management purposes. However, most studies continue to focus on the Global North, with fewer examples for the Global South. We carried out a bibliometric analysis to characterise aspects of studies conducting SDM for species in the Southwestern Atlantic Ocean (SWAO), focusing on the type of input data, taxonomic groups studied, focus of research, methods applied, and international collaboration between countries. Studies on megafauna and fisheries resources, based on presence-only and scenopoetic input data, applying Maximum Entropy (MaxEnt) and generalized linear/additive models (GLM/GAM) predominate. Models applied to biogeography/current species distribution were the most common, followed by biological invasion. Brazil figures as the most prolific country publishing in SWAO, and has more collaborations with the United States of America, Europe, and South Africa than with its neighbours Uruguay and Argentina, who formed a separate cluster. Research groups based on coauthorship of the 30 most frequent authors seem to be mostly isolated, with only two research groups collaborating to each other. In addition, we fit a Binomial generalised linear model (BGLM) to explore how many predictors (layers) would be sufficient to reach an excellent modelling performance based on Area Under the Curve (AUC) values. The BGLM indicated at least 5–8 layers would be necessary to have a 50 % chance of achieving excellent model performance (AUC $\geq$ 0.9), but we urge caution regarding this result and briefly discuss it. The literature review was used as a baseline to discuss aspects of our findings and highlight the need to increase SDM application in the SWAO and to strengthen international collaboration between Latin American countries. Finally, we provide recommendations on how researchers could approach some of the gaps we found.

1. Introduction

Understanding species distributions is the starting point for several ecological studies and management decisions. For instance, by understanding species distribution and its drivers, one can predict changes in its distribution given different landscape uses due to anthropic activities or climate changes (Krüger et al., 2018; Kopp et al., 2023). Distribution data also holds the potential to inform decisions when implementing marine protected areas and giving directions to create new policies to protect specific species or complex habitats (Guisan et al., 2013; Paradinas et al., 2022). Nonetheless, many species still lack basic information regarding their occurrence. This is particularly noticeable in the marine environment, where collecting data *in situ* is costly, time-consuming, and challenging due to weather constraints. To overcome data-deficient scenarios, statistical models to predict species distribution have been developed based on ecological theory (Guisan and Zimmermann, 2000; Ferrier and Guisan, 2006; Warton et al., 2015).

Species distribution models (SDM; *sensu lato*) became a popular tool

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in spatial ecology. They are centralised around niche theory, which has a long history in ecology (Grinnell, 1917; Elton, 1927; Hutchinson, 1957). The underlying idea of any SDM is to capture the species-environment relationship, which in turn represents the spatial dimension of the niche of a species. Depending on the chosen modelling framework, one could estimate the 'potential niche' of a species—the geographic space that could be occupied by a species, for its optimal population growth, given its ability to dispersal—or its 'realised niche'—the geographic space actually used by the species due to resource availability and competition (Peterson et al., 2011; Sillero, 2011). To effectively translate this theory into statistical models, Soberón and Peterson (2005) encapsulated these concepts into the famous BAM (Biotic-Abiotic-Movement) diagram. In addition, we must distinguish niche as a 'condition' or a 'resource' (see Soberón 2007 for an in-deep discussion). The former can be understood as the environmental conditions influencing species distribution without competition (named 'scenopoetic' variables, or 'Grinnellian niche'), whereas the latter refers to the biological interactions shaped by resource consumption/competition and several mechanisms influencing demographic parameters such as predation and prey depletion (often named 'bionomic' variables, or the 'Eltonian niche').

Climate envelopes, habitat suitability models, ecological niche models and species distribution models are a few examples of how different methods are named, which also reflect how they approach and estimate different niche or BAM components (but see Araújo and Guisan 2006; Peterson and Soberón 2012). For simplicity, hereon we use the term 'SDM' in its broad scope, encompassing several methods developed to estimate niche and distribution of species (*sensu* Elith and Leathwick 2009). The reasons that make SDMs widely applied in ecology range from their low data requirement, to being relatively simple to use given several free software available (Sillero et al., 2023). SDMs' input for the response variable is georeferenced species observations, such as species presence or species counts. As predictors, SDMs use spatial layers of environmental data. This information is now increasingly in digital format and freely available. For instance, the Global Biodiversity Information Facility (GBIF) and the Ocean Biodiversity Information System (OBIS) allow users to download biodiversity records, and remote sensing products can be found in many online platforms (e.g., the European Unions' Earth observation programme Copernicus). The complexity of the modelling framework varies a lot, from ordinary regression models to sophisticated Bayesian hierarchical models and machine learning methods (Elith and Leathwick, 2009), including merging different models into an ensemble framework (Araújo and New, 2007). Furthermore, complex models can go a step further by including spatial effects (Pennino et al., 2014; Paradinas et al., 2023a) and/or co-occurrence patterns of a given species in the presence of the modelled species (Wilkinson et al., 2019; Paradinas et al., 2020; Poggiato et al., 2021), thus encompassing other facets of niche theory. Regardless of the modelling choices, SDMs can be used to project the predictions over a spatial grid, thereby helping to fill in the gaps of lacking distribution data (Carmezim et al., 2022; Sarzo et al., 2023).

Bibliometric analysis is a systematic approach to analyse scientific literature. These analyses help not only to understand emerging trends in a field of research and collaboration networks, but also to uncover its gaps and needs (Donthu et al., 2021; Liu et al., 2022). For instance, to understand SDM-related topics, bibliometric studies have been used to analyse top-cited papers (Barbosa and Schneck, 2015) and trends for specific regions (e.g., Latin America; Urbina-Cardona et al., 2019) or groups (e.g., fish; Pickens et al. 2021). In the marine environment, recent bibliometric analyses revealed that hundreds of articles on SDM have been published in the northern hemisphere, while there is noticeable less publications in the southern hemisphere (Robinson et al., 2017; Rodrigues et al., 2023). In their literature review, when Melo-Merino et al. (2020) broke down SDM applied in the marine environment to different taxonomic groups (their Fig. 5), it became clear that only seabirds were studied more in the southern hemisphere compared to other taxa. While these reviews show global trends, a regional perspective can find out about gaps and be more informative to support management decisions.

In the southern hemisphere, the Southwestern Atlantic Ocean (SWAO; defined as between 22 and 55ºS and 40–70ºW *sensu* Franco et al., 2017) covers the adjacent coastal and oceanic zones of southern Brazil, Uruguay and Argentina. The SWAO waters are dominated by the warm tropical waters of the Brazil Current flowing south and the cold subtropical Antarctic waters carried by the Malvinas/Falklands Current flowing northward, generating the Subtropical Confluence (Acha et al., 2004; Mendonça et al., 2017), and by the outflow of the Río de la Plata and Lagoa dos Patos estuaries (Piola et al., 2018). The movement of these water masses along the undulated topography of the upper slope induces shelf upwellings which, combined with the nutrient-rich continental waters outflow, results in a highly productive area. The region is recognized as a global marine biodiversity hotspot (Ramírez et al., 2017), and a hotspot for marine megafauna (Croxall and Wood, 2002; Tittensor et al., 2010; González Carman et al., 2016)—essentials for maintaining healthy ecosystems (Heithaus et al., 2008; Hazen et al., 2019). The SWAO is also an important fishing area for international industrial fishing fleets (Tickler et al., 2018; Rodríguez et al., 2021; Welch et al., 2022) as well as industrial and artisanal domestic fleets from Brazil, Uruguay, and Argentina (Gianelli and Defeo, 2017; Haimovici and Cardoso, 2017). Decades of intense fishing exploitation have driven some essential stocks to reach unsustainable biomass levels (Haimovici et al., 2021, 2022), which lead to calls for fishing effort decreases (Cardoso et al., 2021). Notwithstanding its importance, SWAO still lacks a fundamental understanding of how its ecosystem functions, and information regarding species distribution dynamics is poorly known.

In this study, we carried out a bibliometric analysis of distribution studies applying SDM in SWAO. The analyses revealed regional temporal and spatial trends of publication growth and research focus, the area used for model predictions, the most studied taxonomic groups, and technical choices such as the biological and environmental data used in the models and analytical methods applied. In addition, based on the selected literature, a collaborative network between countries and co-authors was also built to understand the degree of international collaboration. Besides, using the selected literature, we also performed an exploratory analysis estimating the number of environmental predictors (layers) necessary to reach an excellent model performance, which may have transboundary interest. We thus aim to set the scene of SDMs applied in the SWAO, highlighting methodological and taxonomic gaps, the need for increasing international collaboration, and research opportunities for Latin American researchers, especially those in SWAO.

2. Methods

We used the Science Citation Index Expanded (SCI-EXPANDED) database of Clarivate Analytics Web of Science (WoS) and Scopus database to search for the scientific literature (on the 10th of May 2023), following the preferred reporting items for systematic reviews and meta-analyses (PRISMA) statement (Moher et al., 2010). We combined two groups of terms, one regarding the modelling framework ("ecologic* niche model*" or "specie* distribution model*" or "habitat suitability" or "bioclimatic envelop" or "habitat model*" or "spatial model*" or "spatio-temporal model*" or "spatiotemporal model*" or "spatial prediction*"), and another for the geographical scope ("southwest* Atlantic" or "southwest* south Atlantic" or "west* Atlantic" or "west* south Atlantic" or "south-west* Atlantic" or "south-west* south Atlantic" or "SW Atlantic" or "SW south Atlantic" or "south Atlantic"). The terms were searched in title, abstract and author keywords in both databases. Only scientific articles published in English, Portuguese and Spanish until December 2022 were considered. All searches, filters, and data summarisation were carried out by one author (LdSR) to maintain consistency across criteria.

The search resulted in 204 articles, of which 107 were from the WoS and 97 from Scopus databases. Firstly, we checked for duplicate records among both databases and removed them (84 documents). Next, we manually revised each document (120 articles; Supplementary Material 1, Table S1) to exclude studies (i) carried out outside SWAO boundaries (as defined above), (ii) that did not include marine species modelling, or (iii) that were not in the scope of SDM as defined here (e.g., physical oceanography modelling). Articles retained after these filter procedures (Supplementary Material 1, Table S2) were then subject of analysis (Supplementary Material 2, Fig. S1).

Each article was classified by (i) year of publication, (ii) research topic (e.g., biogeography/current distribution, climate change), (iii) large taxonomic groups, (iv) type of response variable (biological data; i.e., presence-only, presence-absence, count, catch rate, biomass), (v) type of explanatory variables (environmental data; i.e., abiotic, biotic$_{\text{non-interactive}}$, biotic$_{\text{interactive}}$; based on Soberón and Nakamura 2009), (vi) number of explanatory variables used, (vii) method(s) applied (e.g., MaxEnt, Generalized Linear/Additive Models [GLM/GAM]) and (viii) number of methods applied, (ix) sub-region where the predictions were made (Argentina, Brazil, Uruguay, or a combination of them; we considered the seas around Malvinas/Falkland Islands as Argentineans). If any retained article fitted in more than one category among the selected criteria (e.g., more than one taxonomic group was analysed), data were classified in both categories and the results are shown in percentages (%). Detailed categories used to classify each article can be found in the Supplementary Material 1 (Table S3).

The collaboration network among countries was accessed and quantified through the first author' affiliation, where bubble size refers to the number of internal collaborations, line width refers to the number of international collaborations, and the axis arrangement was done through multidimensional scaling. A similar analysis was also conducted to access coauthors' collaboration networks and identify research groups and possible collaborations between them; for this, we selected the 30 most frequent authors. In the network plots, each group is linked by intra-group solid lines (groups are colored) while inter-group collaborations are linked by dashed gray lines (Aria and Cuccurullo, 2017).

We also explored the relationship between the number of environmental predictors (layers) and the quality of prediction. Despite criticisms around the indiscriminate use of Area Under the Curve (AUC) (Jiménez-Valverde, 2012), it is the most used metric to measure prediction accuracy in SDMs (Melo-Merino et al., 2020). We classified as an 'excellent prediction' model output that presented AUC $\geq$ 0.9. Following, we fit a Binomial Generalized Linear Model (BGLM) with a logit link function. We considered as response variable the number of outputs with excellent prediction over the total number of outputs by the number of environmental predictors (layers) as the linear predictor (grouped in classes: 0, 1–4, 5–8, 9–12, 13–16, 17–20, 21–24, 32, 34). In our analysis, outputs are the different model outputs that a study may present, as studies may have applied more than one analytical method (i.e., one study may present several 'outputs'). The model is expressed as follow:

$$Y_i \sim Bin(n_i, \mu_i) \mid i \in 1, \dots, 9$$

$$logit(\mu_i) = \eta_i$$

$$\eta_i = \alpha + \beta_i X_i^{LayerClass}$$

where Y_i is the response variable, μ_i is the parameter of interest, n_i the total number of trials (outputs), η_i is the linear predictor linked to the random component by logit function, α is the intercept and $\beta_i X_i^{LayerClass}$ is the linear predictor (parameter and number of layers). We assumed zero layers would return a probability value of zero. Finally, based on the fitted model, we estimated the number of environmental predictors (layers) necessary to reach 50 % (Layer$_{50}$) to 90 % (Layer$_{90}$) chance of excellence in quality of prediction.

The literature search was carried out directly in WoS and Scopus platforms. After articles had been downloaded, all descriptive analyses and plots were developed in R 4.2.0 (Core Team, 2023), using mainly the *tidyverse* v.2.0.0 (Wickham et al., 2019) and *bibliometrix* v.3.2.1 (Aria and Cuccurullo, 2017) packages. The BGLM was fitted using base R *stats* and *emmeans* v.1.8.6 (Lenth, 2023) packages, and the network analysis was carried out using *bibliometrix::biblioNetwork()* function. All Supplementary Material can be found online in a GitHub repository (https://github.com/lvcasrodrigues/RodriguesDaudt_SDM_SWAO/). In the Supplementary Material 1 the reader can find the references for the 120 screened and the 62 retained articles, the criteria for classifying articles, and the R code; in the Supplementary Material 2 are the supplementary results.

3. Results

3.1. Bibliometric analysis

Sixty-two articles were retained (complete reference list in Supplementary Material 1, Table S2), all published between 2008 and 2022 (Fig. 1). There is an overall growing rate of ≈ 2 articles/year, but there is a noticeable increase in published articles from 2015 onwards (2015–2022 growing rate of ≈ 6 articles/year; Fig. 1). The top-10 most-cited articles and the top-10 journals where articles were published can be found in the Supplementary Material (Supplementary Material 2, Tables S1, S2). The majority of studies focused on biogeography/current species distribution (74 %), followed by projecting invasive species habitat suitability (15 %). Studies addressing climate change, conservation/management and past climates were also found, although in smaller numbers (Fig. 1). Models were applied to fourteen taxonomic groups, with marine mammals, seabirds, molluscs, cartilaginous and bony fishes making up 77 % of the total, followed by corals, crustaceans, red algae, cnidarians, starfish, ascidians, kelps, polychaetes and sea turtles (Fig. 2).

Regarding the type of data used to fit the models, presence-only was the most popular type of biological data (Fig. 3a), with GBIF and OBIS as the main data sources for biological observations. As for the predictors, abiotic and biotic$_{\text{non-interactive}}$ (scenopoetic variables) were the most popular types of environmental data (Fig. 3a), with temperature, depth and sediment size as common examples of abiotic data used, and chlorophyll-*a* (as a proxy for biological productivity) or phytoplankton

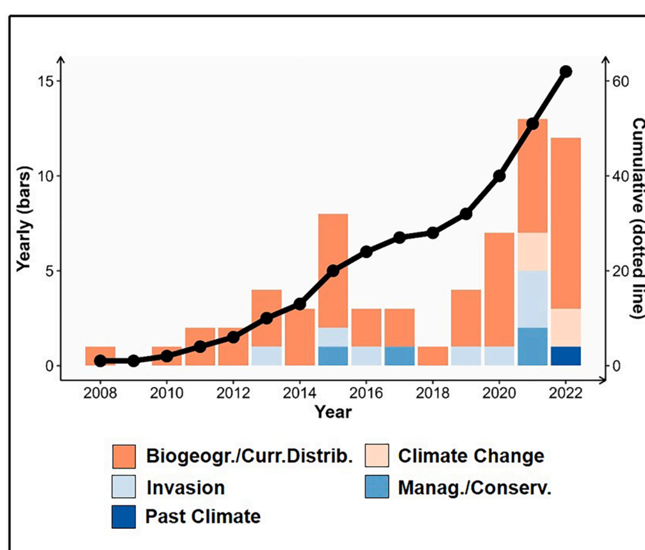

Fig. 1. Yearly and cumulative number of articles among five focuses of research applying species distribution modelling in the Southwestern Atlantic Ocean.

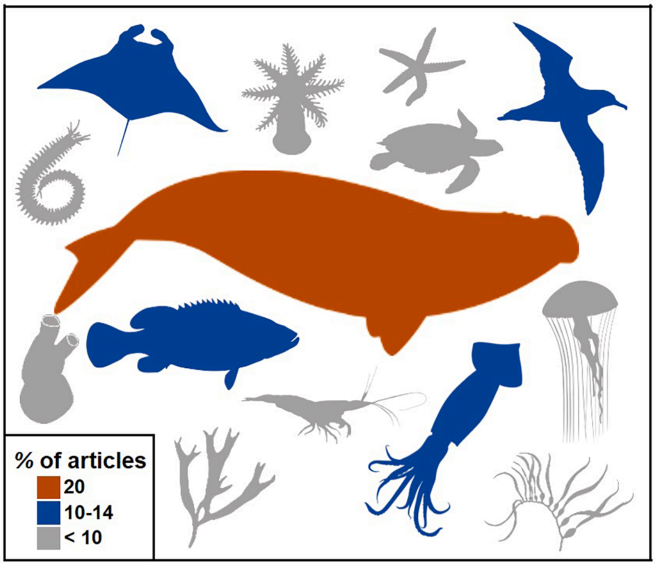

Fig. 2. Frequency of articles applying species distribution modelling in the Southwestern Atlantic Ocean to major taxonomic groups (mammals [orange], seabirds, cartilaginous fishes, molluscs and bony fishes [blue], and corals, crustaceans, red algae, cnidarians, starfish, ascidians, kelps, polychaetes and sea turtles [grey]). Credit for silhouette images, with colour modifications, to Chris Huh, B. Duygu Özpolat, Maija Karala, Harold N Eyster and Qiang Ou downloaded from https://www.phylopic.org/.

concentration as the most common biotic$_{\text{non-interactive}}$ data used. We found no studies using biotic$_{\text{interactive}}$ data as predictors. MaxEnt, GLM and GAM were the most applied algorithms (Fig. 3b), and between one and ten analytical methods were applied per study (median = 1); if more than one method was used (n = 11 studies), authors combined the output through the 'ensemble' approach (n = 8) or presented predictions separately for each method (n = 3).

Most studies predicted their models over the adjacent zones of the three countries (Fig. 4a), but when split by countries, Brazil was the most-studied. The first authors were affiliated to 16 countries. At the country-level, the contribution of Brazilian researchers and their major collaborative network with the United States of America (USA) and a 'European/South African' cluster stood out, compared to its neighbours from SWAO who were clustered together in a separate group (Argentina and Uruguay) (Fig. 4b). When researchers were clustered at the author-level, the collaboration network identified six major research groups (Fig. 4c) where only two of them collaborated with each other. Interestingly, from the six research groups, four are from Brazilian researchers, one is exclusively from researchers based on the United Kingdom (UK) who study the Southern Ocean/Antarctic regions, one is from seabird researchers from European countries, and another from Argentinean researchers (Supplementary Material 2, Figure S2).

3.2. Number of environmental predictors

Studies used between 3 and 34 (median = 8) environmental layers as predictors. There is strong evidence that the number of environmental predictors (layers) improve the probability of 'excellent' model performance ($\chi^2 = 116.27$, df = 1, p-value < 0.001), and that by retaining 5–8 predictors the models could have 50 % of probability to excel (Fig. 5).

4. Discussion

Based on our literature review, we found that SDMs is a growing, relatively new approach to study the distribution of marine organisms in the SWAO. Presence-only biological data explained by scenopoetic environmental predictors through correlative algorithms were the most used set of modelling choices. The majority of these models were applied to megafauna (marine mammals and seabirds) and to commercial fisheries resources (fish and molluscs). Model predictions were mostly done over the whole region, reinforcing the transboundary importance of the region for the marine biota. The network analyses between countries and authors indicated a low degree of international collaboration among the Latin American countries. Our explanatory BGLM model suggests the use of at least 5–8 environmental predictors may guarantee 50 % chance of excellent performance (assessed through AUC). We discuss the gaps found in modelling approaches and how to possibly overcome them, and encourage strengthening Latin America international collaboration to provide robust analyses based on the best available data and local expertise. Finally, we give recommendations to improve SDM applied to SWAO, including taxa that could be modelled, other modelling framework choices that could be explored, and initiatives to foster international collaboration.

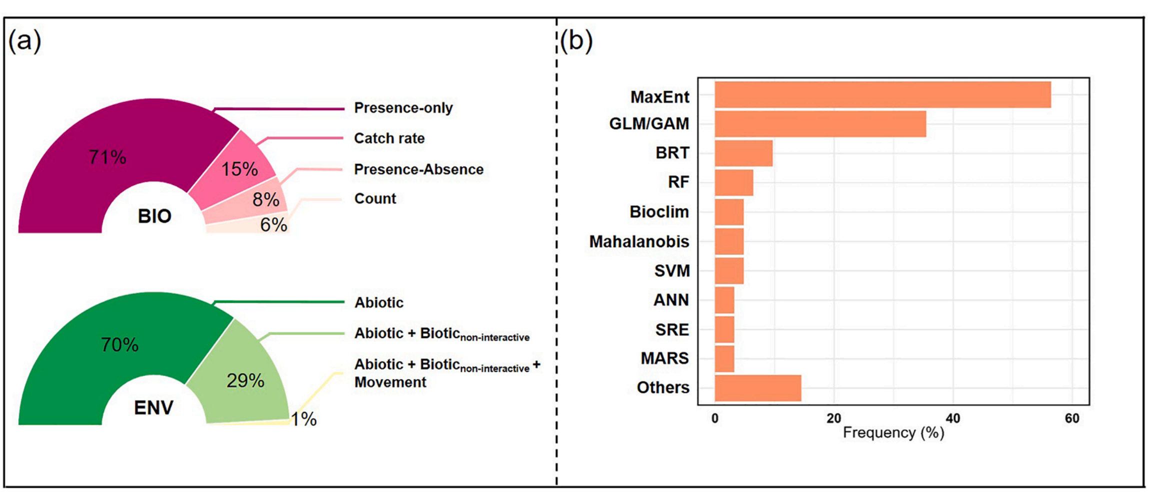

Fig. 3. (a) The most frequent choices of biological (BIO) and environmental (ENV) data used in species distribution models applied in the Southwestern Atlantic Ocean. In (b), the frequency of analytical methods applied (Maximum Entropy – MaxEnt; Generalized Linear/Additive Models – GLM/GAM; Boosted Regression Trees – BRT; Random Forest – RF; Bioclim; Mahalanobis distance; Support Vector Machines – SVM; Artificial Neural Network – ANN; Surface Range Envelope – SRE; Multiple Adaptive Regression Splines – MARS; and others – which includes Classification and Regression Tree, Domain, Ecological Niche Factor Analysis, Flexible Discriminant Analysis, Gower, Habitat Suitability Index, MaxLike, Minimum-Volume Ellipsoids, Non-parametric Probabilistic Environmental Niche).

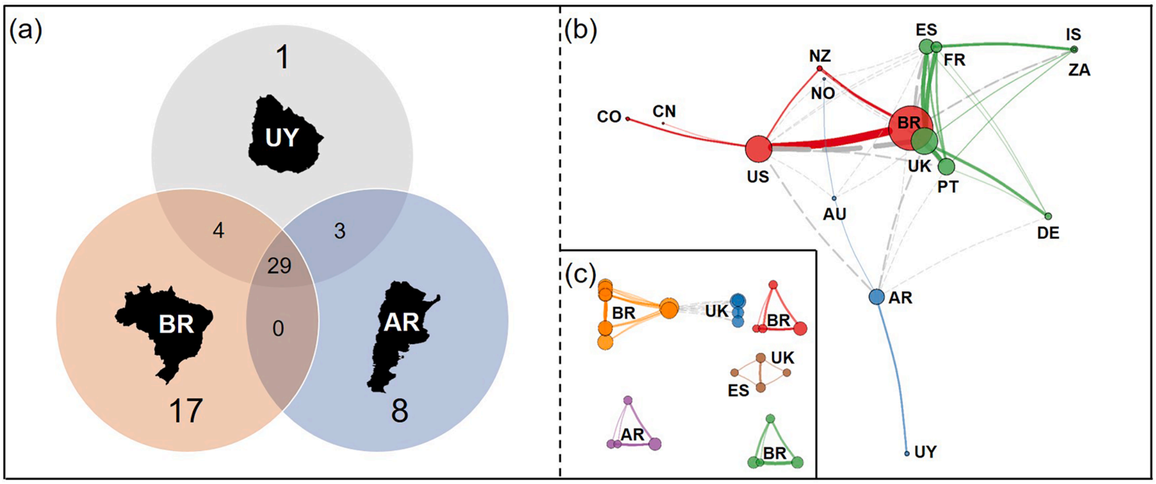

Fig. 4. (a) Venn diagram showing countries where species distribution modelling results were predicted over in the Southwestern Atlantic Ocean (Uruguay – UY, Brazil – BR, Argentine – AR); and the collaboration network among (b) countries and (c) authors of the selected articles (list of countries abbreviation available at https://www.nationsonline.org/oneworld/country_code_list.htm). An expanded version of (c) can be found in the Supplementary Material 2 (Fig. S2).

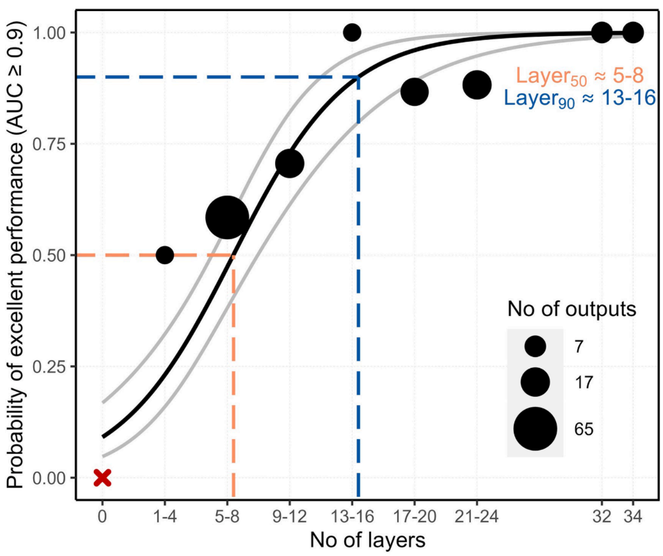

Fig. 5. Probability of excellent model performance given the number of layers, based on a Binomial Generalized Linear Model (BGLM). Dots are the number of successes in N trials (i.e., number of outputs with AUC $\geq$ 0.9 over the total number of outputs), dots sizes are proportional to the total number of outputs, solid lines are the model probability predictions (average in black and 95% confidence intervals in grey), and dashed lines indicate the probabilities of 50 % ($Layer_{50}$) and 90 % ($Layer_{90}$). We assumed a zero probability of excellent performance if zero layers are specified in the models (red cross).

4.1. SDM in SWAO

Most studies focused on 'biogeography/current distribution' of species, followed by 'invasive species'. The former was expected as shown in previous bibliometric analysis (Melo-Merino et al., 2020) and also because it is the inherent aim of SDM itself (e.g., Yesson et al. 2012; Quillfeldt et al. 2013; Fromentin et al. 2014). As for the latter, Brazil has emerged as one of the most prolific countries applying SDMs to study biological invasions worldwide (Melo-Merino et al., 2020). In our study, concerns about biological invasions in the SWAO have become more prevalent since 2013 (e.g., invasive corals *Tubastraea* spp. Riul et al. 2013; Carlos-Júnior et al. 2015; red lionfish *Pterois volitans,* Evangelista et al. 2016; brittle star *Ophiothela mirabilis,* Derviche et al. 2021; and shrimp *Cinetorhynchus erythrostictus,* Alves et al. 2021), pointing out large areas as potential new habitats for invasive species in SWAO, and drawing attention to disrupting ecological interactions as the main potential impact of invasions and settlement. We found a few recent studies that apply SDM to address 'climate change' impacts. These studies have a common, warning message about species poleward displacements by the year 2100 as a consequence of tropicalization of SWAO waters (Anderson et al., 2021; Koerich et al., 2021; Borges et al., 2022; Jiménez et al., 2022). Articles rarely focused on management or conservation topics (Oliveira et al., 2015; González Carman et al., 2016; Prado et al., 2021). SDM is a popular tool used to support management decisions in the Global North (Rowden et al., 2017; Sarzo et al., 2023), and researchers from SWAO could explore such methods to better inform data-driven decisions on a variety of environmental issues (e.g., Sabadin et al. 2022).

Articles on marine mammals were the most frequent. Current distribution and migration are examples of topics addressed by such articles (e.g., do Amaral et al. 2015, 2018; Seyboth et al. 2015; Prado et al. 2021). Seabirds, bony and cartilaginous fishes and molluscs had their distribution modelled to a lesser extent, with topics ranging from current distribution and migration to distribution overlap and niche segregation between species (e.g., Quillfeldt et al. 2013; Mourato et al. 2014; Battini et al. 2019; De Wysiecki et al. 2020, 2022a, 2022b). Many species of these taxonomic groups are threatened by human activities, such as bycatch and overfishing (Bugoni et al., 2008; Haimovici and Cardoso, 2017; O'Hara et al., 2021; Secchi et al., 2021). Due to their role as fisheries resources, and fundamental components of marine ecosystems, it is pivotal to estimate their potential distribution (losses and gains) under multiple human-caused impact scenarios (e.g., Krüger et al. 2018). Such results will allow for a better interpretation of predicted distribution patterns and its possible shifts, helping to guide marine spatial planning and future management recommendations, especially for internationally shared fish stocks (Vogel et al., 2023). Lastly, SDM studies for some taxonomic groups, including invertebrates in general, sea turtles, marine algae and plants were scarce (Riul et al., 2013; Mendoza-Becerril and Marques, 2013; González Carman et al., 2016). Modelling of more taxa is needed in order to create a more realistic picture of spatio-temporal distribution patterns of the organisms inhabiting SWAO.

The most used biological data were presence-only and the most applied method was MaxEnt, as found elsewhere (Melo-Merino et al., 2020). Presence-only has been exponentially growing in the last decades due to large repositories of species records in open-access, online databases (e.g., GBIF and OBIS). In addition, MaxEnt only needs the occurrence data as input to develop its outputs—it basically finds a maximum-likelihood distribution for the species, considering a set of given environmental information recorded at the occurrence data (Phillips et al., 2004). Data from fisheries (count and/or catch rate), can be an important alternative in estimating the abundance of populations through GLM/GAM instead of merely mapping its presence probability (Pennino et al., 2016). However, we highlight that for any kind of data, one needs to consider the residual spatial autocorrelation (Paradinas et al., 2023b). If not, it could lead to a serious biased prediction and, consequently, conclusions (Martínez-Minaya et al., 2018). This could be addressed by considering, for example, spatial effects (Martínez-Minaya et al., 2018; Paradinas et al., 2023b).

All studies used abiotic or abiotic plus biotic$_{\text{non-interactive}}$ environmental data and none considered biotic$_{\text{interactive}}$ data. Abiotic and biotic$_{\text{non-interactive}}$ data are 'scenopoetic' variables which refers to "conditions, including aspects of climate, physical environment, edaphic conditions, etc., that impose physiological limits on species' ability to persist" (Soberón and Peterson, 2005; Soberón and Nakamura, 2009). In contrast, 'bionomic' variables refer to biotic$_{\text{interactive}}$ data (Soberón and Nakamura, 2009), a gap found in our study. Bionomic data are scarce and hard to obtain (Wisz et al., 2013), particularly in marine environments where most species are quite elusive compared to the vastitude of the ocean. Species co-occurrence data could be used in the models instead, as distribution estimates are frequently more accurate when accounting for it (Warton et al., 2015; Barber et al., 2021). However, one need to carefully interpret results to not assume biological interactions from it (Dormann et al., 2018; Poggiato et al., 2021). Interestingly, Maricato et al. (2022) was the only study we found incorporating an anthropogenic layer (port activity) to explain the distribution of the common bottlenose dolphin *Tursiops truncatus*, an initiative that weighs in the 'movement' component of the 'BAM' diagram (Soberón and Peterson, 2005).

There were no specific sub-regions (countries) being studied, meaning most studies used the SWAO as their prediction area. Many species of the most studied taxa are migratory or have a wide area of distribution (e.g., dolphins, do Amaral et al. 2015; seabirds, Blanco et al. 2017; sharks, De Wysiecki et al. 2020; fish, Fromentin et al. 2014, Lopes et al. 2019). This may explain why researchers opted to predict their models over the whole region. We see this as a positive fact, which reflects our understanding that the SWAO is subject to the similar ecological/oceanographic forces—ocean phenomena are transboundary—and studies tied to political limits would be senseless.

Although studies predicted results over the whole region, the network analyses, however, showed little international collaboration between the countries within SWAO. The collaborative network at the country-level showed three clusters, on which (i) an 'European/South African' cluster seems to play a big role on SWAO publications, (ii) Brazil has more collaborations with the USA and the 'European/South African' cluster than with its neighbour countries, and (iii) Argentinean researchers are isolated with few collaborations with the Uruguayans, forming their own cluster. The 'European/South African' cluster is mainly related to publications about seabirds. Currently, the Malvinas/Falklands Islands are part of the UK territory, as well as South Georgia, from where many species of seabirds feed in SWAO waters (Croxall and Wood, 2002; Quillfeldt et al., 2013). The collaboration between Brazil and Global North countries may be happening as a result of colonialist science (Haelewaters et al., 2021; Nuñez et al., 2021), where language and financial support barriers may be contributing factors. Another possible explanation is the most significant budget available for science in the North, which results in more methods being developed by northern scientists. Researchers from developing countries seek to learn these methods to use them to respond to their research questions. Urbina-Cardona et al. (2019) have shown that Latin American countries tend to collaborate more with the Global North than with their neighbours, and suggest that increasing opportunities of fellowships, sabbaticals, and supervisions increases international collaboration as researchers return to their home-countries. At the author-level, the network revealed a low collaboration between coauthors as well, as shown by six main research groups isolated to each other. The only exception is a cluster of authors from Brazil who collaborated with authors from the UK; this study was about humpback whale distribution in South Georgia and the South Sandwich Islands Marine Protected Area (Bamford et al., 2022). By increasing collaboration between SWAO countries, researchers could feed complementary data into the models, thus getting more informative results. Also, collaborations could shed light on SWAO knowledge gaps that could be achieved through SDM by integrating the accumulated knowledge of different institutions and their local experiences and needs.

4.2. Number of environmental predictors

Although we did not investigate model complexity in all its facets, our BGLM indicated that between 5 and 8 seems to be the minimal number of predictors (layers) to reach at least 50 % chance of an excellent performance (AUC $\geq$ 0.9), and that using more than 20 predictors could be an overkill. However, the number of predictors is not a metric that guarantees the model's output will have excellent performance; rather, a possible indicator. An useful additional information would be how representative the retained predictors helped explaining the variance of the data, but several studies did not report on this—an information that should be reported under model estimates, as best practice (Zurell et al., 2020). Models can be exploratory, for inference, or for predictions (Tredennick et al., 2021) and modelling choices regarding its framework and parameterization will depend on the research goal and data attributes. As such, other metrics such as Kappa and/or True Skill Static (TSS) should also be accessed (Allouche et al., 2006) depending on the study objective. Ultimately, the models will perform better with improved biological data, ranging from sampling the whole spectrum of environmental gradients that the species may occur to true absence points (Lobo, 2008; Zurell et al., 2012), grounded in sound theory and understanding of data attributes and biological processes (see Merow et al. 2014 for an in-deep discussion on model complexity).

4.3. Limitations of this study

We may have failed to detect all articles that incorporate SDM due to the search terms used. However, for the purpose of this review, we believe that adequate terminology was used in the search terms. Simpler terms, such as "distribution" or "spatial", could have resulted in many articles beyond the scope of this study. Likewise, broader geographical scope, such as "Southern Ocean", could have retained studies only applied to a part of that geographic region; thus, we acknowledge some studies may have been missed (e.g., Krüger et al. 2018). Further, we acknowledge that we might have missed studies published in Spanish or Portuguese by not including the search terms in these languages (native languages from the countries within the scope of our study) (e.g., Ivanoff et al. 2019). In fact, of the 120 screened articles, only one was in Portuguese (Oliveira et al., 2015), and none was in Spanish. Literature in languages other than English play an important role in biodiversity and conservation (Amano et al., 2021). Nonetheless, this is a brief overview and not an exhaustive synthesis nor a meta-analysis, and we do not believe that the revealed trends and conclusions would change significantly.

Regarding our analyses, it is worth mentioning that the country-level collaboration network only takes into account the first author of each article. This could have an influence on the resulting clusters and links. However, we do not believe the pattern would change much by including coauthors' affiliations, as the author-level network showed virtually no links between research groups—an idea reinforced by the lower number of collaborations between Latin American countries than with countries of the Global North (Urbina-Cardona et al., 2019).

Besides, although we trust the framework for our BGLM analysis is robust, it could benefit from additional data, and similar analysis investigating other validation metrics (e.g., Kappa, TSS) may add important insights about SDM model parametrization and complexity.

4.4. Recommendations forward

(i) On the research focus—SDM have the potential to discover unknown populations, estimate extinction risk for species, support conservation planning and link niches to evolutionary processes (Peterson et al., 2011; Guisan et al., 2013), topics we did not detect in our study but whose developments would benefit the understanding of ecological processes driving the complexities of SWAO and support management of living resources. Additionally, studies investigating species occurrences/abundances dynamics (losses and gains) could help unveil the consequences of human-induced changes in SWAO's marine biota, such as climate change, as SWAO already shows signs of tropicalization (Perez and Sant'Ana, 2022).

(ii) On the modelled taxa—To have a better understanding of how the ecosystem functions and links between species occurrences, increasing the number of taxa modelled is needed to fill in distribution gaps and improve our knowledge of their temporal dynamics (e.g., seasonally, monthly). Specifically, given the importance of the SWAO for fisheries and top-predators, SDM exploring plankton and meso-predator distributions would be essential to model and better predict higher-trophic level taxa distribution, including fisheries resources.

(iii) On the chosen algorithms—As presence-only models were the most popular choice of biotic variable, point process models (PPMs), which is a model-based algorithm, could be used to model presence-only data instead of MaxEnt (Warton and Shepherd 2010; Renner et al., 2015). We have found no studies applying PPMs in SWAO. PPMs have several advantages over other presence-only methods, including better interpretability, more control on model parameterization, and tools for checking model assumptions (we refer the reader to Renner et al. 2015 for an in-depth resource on PPMs).

(iv) On the chosen modelling framework—We have found no studies applying joint SDMs, which can be optimal tools to model species co-occurrence (Warton et al., 2015; Ovaskainen et al., 2017). By jointly modelling relationships between multiple species occurrence/abundance against environmental variables, one can, for instance, understand the dynamics of predator-prey (e.g., Sadykova et al. 2017; Barber et al. 2021). In addition, Bayesian hierarchical models could be used more often to control the additional parameters and provide more robust results and predictions (Martínez-Minaya et al., 2018).

(v) On the availability of data—We understand the tough reality of scarce sampling in marine environments of the Latin American region (Miloslavich et al., 2011). However, we believe that presence-only data could be better leveraged (e.g., Ready et al. 2010) given initiatives such as open-access record databases, as well as fishery-dependent data (e.g., Pennino et al. 2014, 2016; but see Goethel et al., 2023). For instance, if Latin America, particularly SWAO, could work on a similar public database such as the Western & Central Pacific Fisheries Commission (https://www.wcpfc.int/scientificdatadissemination), SDM applied to fisheries management could become more accessible and more precise.

(vi) On increasing the international collaboration—We encourage SWAO researchers to strengthening the interactions between their neighboring countries, as this could potentially increase the power of SDMs (by feeding more/better data into the models) and therefore the ecological understanding of the region as well as their applied utility—not to mentioning the sense of a regional scientific community. Initiatives such as the one mentioned above in (v) could facilitate increasing collaboration between researchers. We also motivate Latin American researchers to continue their collaborations with the Global North, as a way of not only to bring resources (financial and expertise) but to also draw international attention to the SWAO as an important ecological and economical region worldwide.

(vii) On expanding the BGLM analysis—Our BGLM analysis estimated the number of predictors needed to increase the probability of an excellent model performance according to the AUC metric. However, we acknowledge that it was an exploratory look at this topic, and expanding such analysis both to other model validation metrics (e.g., explained deviance, TSS) and to studies of other regions/ecosystems would be desirable.

5. Conclusions

In summary, SDM studies in SWAO are recent but growing (few studies have already been published in 2023; Gonzalez et al. 2023; Lemos et al. 2023; Martins et al. 2023; Rondon-Medicci et al. 2023). We have outlined recommendations that may be used as guidance for researchers interested in applying SDM in SWAO, regarding the research focus, taxonomic groups, modelling framework, data availability and encouraging international collaboration. We stimulate researchers to use SDM more frequently, in order to advance the understanding of the species inhabiting SWAO, given all facets these tools can provide. We hope our review serves as an incentive to leverage SDM in SWAO and to foster international collaboration between Latin American countries.

Data availability statement

All data and code are available through a GitHub repository, as well as supporting results, at https://github.com/lvcasrodrigues/RodriguesDaudt_SDM_SWAO

CRediT authorship contribution statement

Lucas dos Santos Rodrigues: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision. **Nicholas Winterle Daudt:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization, Supervision. **Luis Gustavo Cardoso:** Validation, Writing – review & editing. **Paul Gerhard Kinas:** Validation, Writing – review & editing. **David Conesa:** Validation, Writing – review & editing. **Maria Grazia Pennino:** Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare no conflict of interest

Data availability

Data, code, and supplementary results are available at https://github.com/lvcasrodrigues/RodriguesDaudt_SDM_SWAO/

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Supplementary materials

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