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Temporal and spatial transferability in telemetry-based dynamic species distribution models: The effects of algorithms and pseudo-absence techniques

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ABSTRACT

Species distribution models using animal tracking data to predict foraging habitat suitability can inform dynamic ocean management techniques that respond to changing environmental conditions. Such models require accurate transferability in time (and sometimes space), often involving extrapolation into new environmental conditions. However, the impacts of modelling configuration on transferability are unclear. Here we built species distribution models using animal tracking studies from the Southern Ocean and projected them in time and space. We tested 24 different model configurations to assess how the choice of pseudo-absence technique and algorithm influences temporal and spatial transferability. Using data from a variety of seabird and marine mammal species with differing ecological traits, we aimed to identify 1) which model configurations produce consistently high transferability scores and 2) whether any tested algorithms or pseudo-absence techniques were better equipped to deal with environmental extrapolation and small sample sizes. Models consistently achieved high temporal transferability scores. Of all tested configurations, background sampling combined with tree-based machine learning algorithms or models accounting for autocorrelation performed best in this context. Conversely, no model configuration consistently attained high spatial transferability scores, with all exhibiting poor predictive capacity in many cases. The impacts of environmental extrapolation and sample size on transferability were also assessed. Most models exhibited greater temporal transferability when built with larger datasets that required lesser environmental extrapolation. We recommend that researchers use data-rich ensembles of the most reliable algorithms built with background sampling when looking to predict near real-time distributions and, where possible, avoid spatial extrapolation when data do not cover every population within the target area.

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1. Introduction

Tracking data offer unique insights into animal movements as individuals navigate their environments. Since the invention of the first bio-logging devices in the 1960s, the use of biotelemetry data has proliferated (Watanabe and Papastamatiou, 2023). These data are used to address a diverse array of questions, from broad-scale mapping of distribution and migration routes to fine-scale assessments of individual movement decisions (Beltran et al., 2024). Interactions between tagged animals and their environments can also provide insights into ecosystem structure and dynamics, serving as sentinels of ecosystem health (Hazen et al., 2024).

The use of tracking data as occurrence data in species distribution models (SDMs) has also become increasingly common. These models statistically relate locations of focal species to spatial environmental covariates, such as temperature or depth (Guisan et al., 2017), and are primarily used to assess species-habitat relationships, predict existing distributions, and project future suitable habitats (Zurell et al., 2020). SDM outputs support environmental management, policy, and biodiversity assessments, although many SDMs are built with methodological flaws that limit their suitability for these purposes (Araújo et al., 2019). This has necessitated the development of best-practice standards, one of which states that "temporal resolution should match the biology of the response variable" (Araújo et al., 2019). Essentially, if animals respond to daily, weekly, monthly, or seasonal changes in environmental conditions, the temporal resolution of model covariates should reflect that. Although marine species are subject to environmental changes on these timescales, many SDMs opt to use long-term averages of environmental predictors, or climatologies, instead of dynamic predictors (Mannocci et al., 2017; Melo-Merino et al., 2020). Recognition of this limitation has led to an uptake in dynamic SDMs, where locations are matched with daily measurements or weekly averages of covariates (e.g., Hückstädt et al., 2020; Green et al., 2023; Welch et al., 2023).

One benefit of dynamic modelling is the opportunity for dynamic ocean management (Karp et al., 2025). By matching locations with covariates on daily or weekly scales, predictions can be made at the same temporal resolutions. Along with advances in remote sensing, vessel monitoring, and animal tracking technologies, dynamic SDMs allow for spatiotemporal predictions of threats to populations (Sequeira et al., 2019a). Several studies have already put this into practice, modelling exposure to fisheries (e.g., Reisinger et al., 2022; Warwick-Evans et al., 2022), ship strike risk (e.g., Hazen et al. 2017; Abrahms et al., 2019), and responses to interannual variability (e.g., Niella et al., 2022; Welch et al., 2023). Dynamic predictions can then be used to inform practitioners and resource users, so that species can be protected through legislative enforcement or voluntary action. With growing calls for dynamic management for highly mobile species and species undergoing range shifts (Maxwell et al., 2020), such predictions will be vital to inform spatial management measures.

Although dynamic predictions are promising, their effectiveness is limited by transferability, defined as the ability of a model trained on data from one region and time to predict distribution in another region and/or time (i.e. spatiotemporal extrapolation). If predictions are to inform dynamic ocean management, accurate temporal transferability is essential. A key factor in this is the degree of environmental extrapolation. The greater the dissimilarity between the covariate values of the training data and the covariate values to which the model is projected ("testing data"), the poorer a model will generally perform (Rousseau and Betts, 2022). Model performance also degrades due to non-stationarity of species-environment relationships, since the preferred habitats of species may change in response to changing conditions (Hirtle et al., 2026). When transferred through time, SDMs yield mixed results, with the best-performing models being trained on more recent data and data recorded over many years (Zhang et al., 2020). As models are transferred further in time, uncertainty increases because models are extrapolated into increasingly novel environmental space (Brodie et al., 2022).

Furthermore, if tracking data do not encompass the entire range of a species within a target area, spatial transferability may be necessary. Models transferred through space generally perform poorly because, in addition to dealing with environmental extrapolation, interspecific relationships, anthropogenic pressures, environmental niches, and other ecological traits may vary between populations (Torres et al., 2015; Liang et al., 2018; Reisinger et al., 2021; Bentley et al., 2024). Many model parameters and tracking data properties also influence temporal and spatial transferability, a number of which remain unclear (Sequeira et al., 2018; Yates et al., 2018). For dynamic SDMs to be useful in ecosystem management, the modelling choices and data properties that optimise transferability must be better understood.

Several studies have attempted to identify which model algorithms provide the greatest transferability, but results are varied, and it is unlikely that any single algorithm is best in all scenarios (Yates et al., 2018; Takolander et al., 2025). One suggestion has been to use an ensemble approach, employing a weighted average of predictions from multiple models, to avoid reliance on any single model (Zhu and Peterson, 2017). Ideally, these ensembles should be composed of multiple reliable algorithms rather than averaging predictions from a random collection of algorithms.

SDMs that only use presence locations as input data, such as those built on telemetry data, can be formally expressed as inhomogeneous spatial Poisson point process models (IPPs) in that an IPP model also relates the density of points to a set of spatial covariates (Renner et al., 2015; Hooten et al., 2017; Matthiopoulos et al., 2023). For greater detail, Matthiopoulos et al. (2023) connect SDMs and other species-habitat association models to IPPs. One method for estimating an IPP model is through a use-availability design, where the available environment is sampled to generate control points and construct a binomial response variable, with observed presences classified as 1s and available locations classified as 0s (Aarts et al., 2008; Warton and Shepherd, 2010). However, this raises conceptual questions as to what constitutes the available environment and which methods are most appropriate to sample locations available to an animal in space and time (Northrup et al., 2022). In SDM terminology, these sampling methods are broadly known as pseudo-absences. Both the type of pseudo-absence sampling technique and the number of pseudo-absences can have profound impacts on SDM performance and predictions (Barbet-Massin et al., 2012; O'Toole et al., 2021; Hysen et al., 2022).

Three sampling techniques are commonly used (Hazen et al., 2021): Background sampling, where pseudo-absences are randomly sampled across the track extent; buffer sampling, where pseudo-absences are sampled within a set radius of each recorded location to represent the immediately available environment; and correlated random walks (CRWs), where tracks are simulated based on the movement parameters of the real track. Studies that have assessed how these different techniques affect dynamic SDM accuracy concur that background sampling methods achieve the highest model validation scores, while CRWs in some instances offer more biologically realistic predictions (Hazen et al., 2021; Fernandez et al., 2022; Braun et al., 2023); however, these models were tested using data from the same region and period as the training data. Accurate projections are vital for transferability, and whichever pseudo-absence technique provides the best transferability should be used when looking to extrapolate SDMs in space and/or time.

In this study, we investigated the temporal and spatial transferability of dynamic SDMs built using tracking data from 10 species of marine mammal and seabird from the Southern Ocean. We trained models on tracks from one period, or region, and projected them to different periods, or regions, where tracking data were available to validate the results. Eight different model algorithms and three pseudo-absence techniques were tested for each scenario to identify whether any combination of algorithm and background sampling method might achieve consistently high transferability scores. We also sought to understand how sample size and environmental extrapolation between the testing and training data influenced model transferability. By identifying modelling choices that consistently yield high performance in novel periods and regions, researchers can be guided when creating dynamic predictions of species distributions for conservation purposes.

2. Materials and Methods

2.1. Tracking Data

Species occurrence data were sourced from the Retrospective Analysis of Antarctic Tracking Data (RAATD; Ropert-Coudert et al., 2020). RAATD consolidated tracking data for 17 Antarctic and Subantarctic marine predator species tracked between 1991 and 2016 in the Southern Ocean. All selected data were standardised and underwent quality-control checks to remove erroneous tracks. A correlated random walk state-space model was then fitted to estimate locations at regular intervals (1 hour for GPS, 2 for PTT) and smooth errors. These were constructed with a custom state-space-model package called *duckConfit* (https://github.com/ianjonsen/duckConfit), a precursor to the widely used *aniMotum* R package (Jonsen et al., 2023). After filtering, the dataset includes data from 2,823 individual animals and over 2.3 million observed locations (Ropert-Coudert et al., 2020). Due to the ~186km error radius of light-geolocation (GLS) tags (Phillips et al., 2004), data from GLS devices were removed from this study to ensure that the error

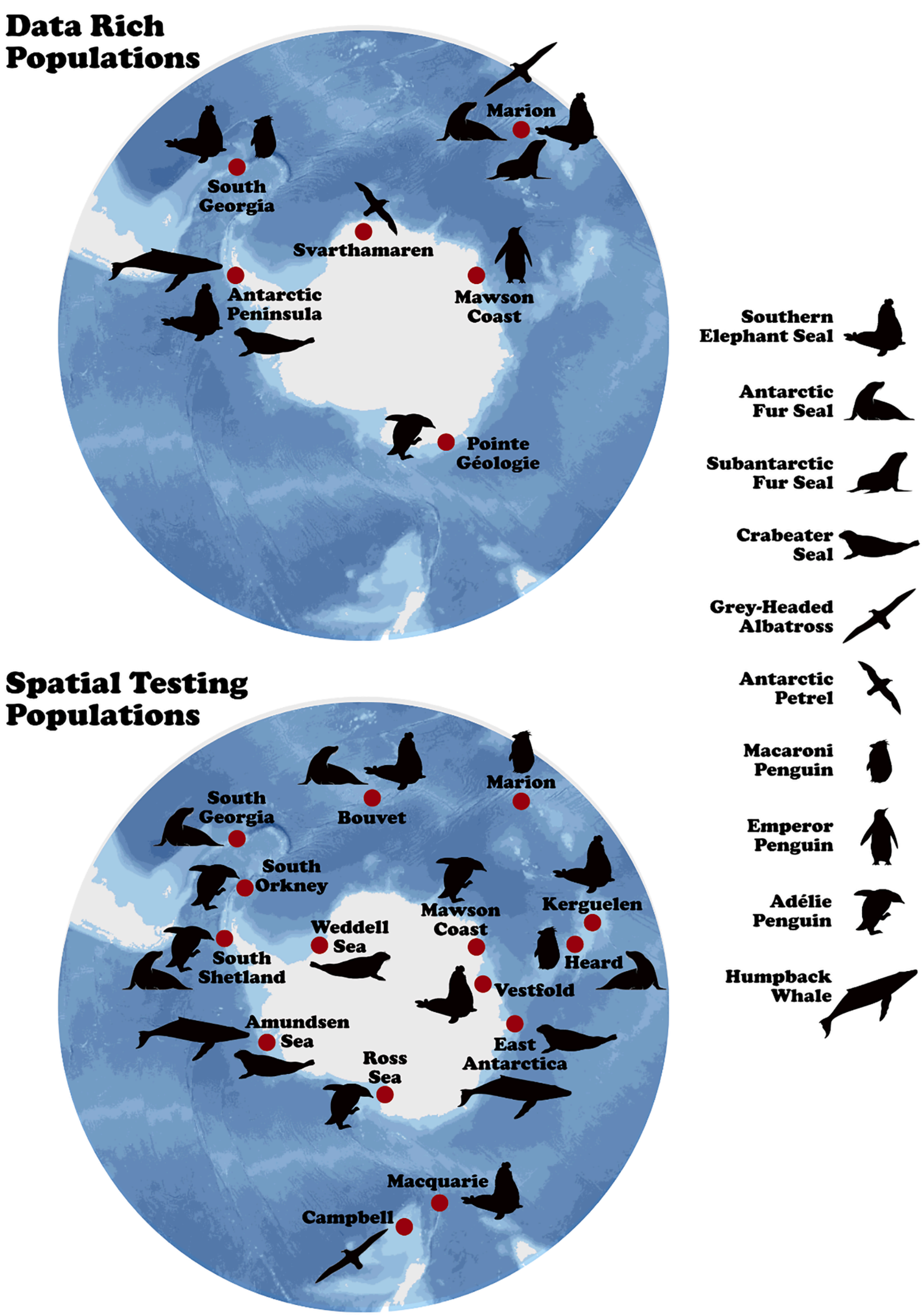

Fig. 1. The study sites and species used to assess model transferability. Models were built on the data-rich populations (top) and temporal transferability was also assessed on these populations. Spatial transferability was assessed by building models on the data rich populations and predicting them to other populations for which data were available (below). Information on the temporal coverage and breeding stages for each population is available in Table S1.

of the response data did not exceed the predictor covariate resolution (Araújo et al., 2019). The associated error of other devices was far smaller, at under 1km for GPS tags and between 0.25km and 60km for PTT data dependent on the location quality class. Coarser PTT location estimates were accounted for in the state-space modelling process to reduce the influence of erroneous locations. The final dataset consisted of approximately 2 million locations from 2280 individuals across the 17 species.

To explore temporal transferability, suitable populations were identified from RAATD that contained tag deployments from multiple years during the same breeding stage. Data were first subset for each species by tagging location and life-history stage, as habitat preferences vary among populations (Torres et al., 2015; Reisinger et al., 2021) and breeding stages (Phillips et al., 2017). Life-history stage dates were obtained from RAATD metadata, with tracks automatically assigned to a life-history stage by date, and manually reassigned where necessary after examining individual movement patterns (Hindell et al., 2020). 12 populations across 10 species were suitably extensive, containing data for at least one breeding stage from three or more unique deployment years (Fig. 1). These same data-rich populations were used to explore spatial transferability by building models on the full data for each population and predicting them to data from other populations (Fig. 1). A graphical overview of the methods from here on is provided (Fig. 2).

2.2. Pseudo-Absences

For each population, pseudo-absences were generated using three techniques: Background sampling, buffer sampling, and correlated random walks (CRWs) (Fig. 3). 10,000 pseudo-absences were generated initially, but for tree-based machine learning algorithms, the number of pseudo-absences was downsampled to be equal to the number of presences to avoid class imbalance (Barbet-Massin et al., 2012; Hysen et al., 2022; Valavi et al., 2021). Each pseudo-absence location was associated with a date from the tracking data. Background points were generated within minimum convex hulls. This creates an even spatial distribution of points to sample the full range of environmental conditions in both used and unused locations across the track extent.

Buffer samples were randomly generated within a set distance from each location fix, representing unused locations available to the individual at that time. Buffers are typically produced within a radius equal

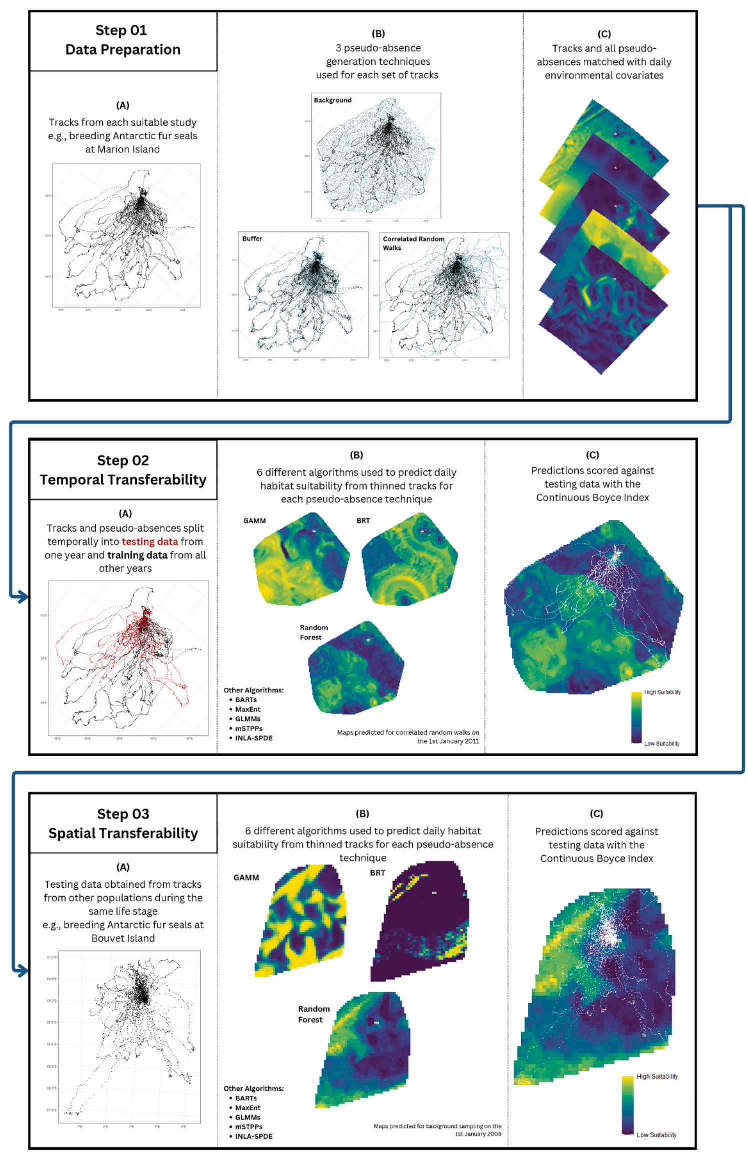

Fig. 2. Visual overview of the modelling process using breeding Antarctic fur seals (Arctocephalus gazella) from Marion Island and Bouvet Island as an example. Overlays of tracks on predictions are purely illustrative, as not all tracking data overlap with the prediction date provided. Blue arrows connecting steps show the order of progression in the workflow, with both step 2 and step 3 continuing from step 1 and not sequentially.

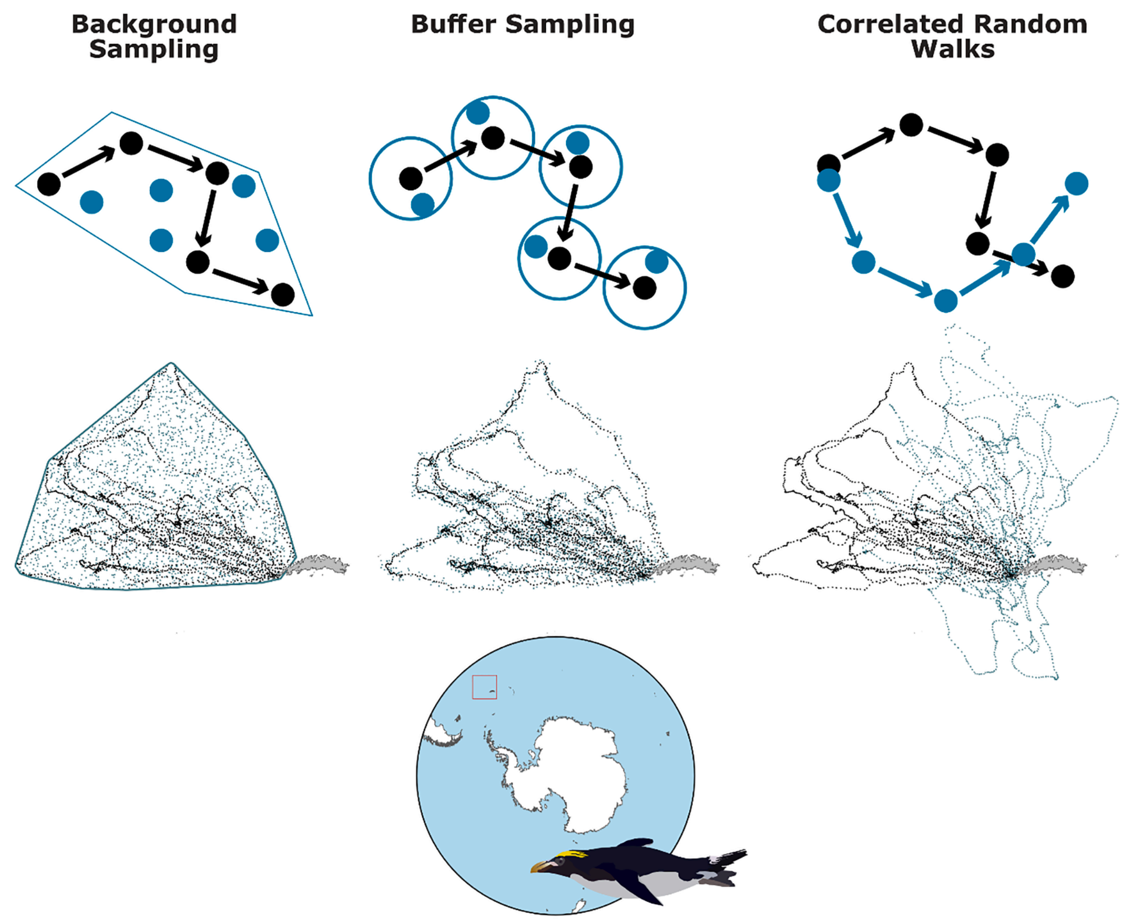

Fig. 3. The conceptual basis (top) of each pseudo-absence technique used in this study, alongside examples of each pseudo-absence (middle) for incubating macaroni penguins (Eudyptes chrysolophus) from Bird Island, South Georgia. Real tracks are in black and pseudo-absences are in blue in each instance. The map (bottom) highlights South Georgia and the surrounding waters with a red bounding box. Concept graphics adapted from Hazen et al. (2021).

to the average step length (Hazen et al., 2021), but we opted to use the 75th percentile daily step-length for each species. This still represents areas that animals could feasibly reach without neglecting points at further yet accessible distances. Radius distance values ranged from 24.7km (crabeater seals; *Lobodon carcinophaga*) to 385.6km (grey-headed albatross; *Thalassarche crysostoma*), reflecting the contrasting ecology of the species (Table S2). This variance could influence buffer performance as the radii for flying birds is typically larger than the scales of environmental data decorrelation, whereas most swimming species have radii of a similar size. A minimum distance of 11.3km was also employed so that buffer samples fell in a different grid cell to the corresponding presence during extraction of environmental covariates.

Tracking data are autocorrelated because multiple locations are recorded per individual, and each location is limited by the distance an animal can travel within one temporal step from the previous location. CRWs replicate autocorrelation by modelling pseudo-absences similarly, beginning at the same start point and predicting each step from the step lengths and turning angles of the corresponding track. Here, CRWs were modelled with the R package *aniMotum* v1.2-12 (Jonsen et al., 2023). For most species, tracks were first divided into trips, with each trip starting when the animal entered the water and ending when the animal next returned to land. Tracks of humpback whales (*Megaptera novaeangliae*) were treated as one continuous trip as a wholly marine species. Tracks of crabeater seals, which often haul-out on ice, were still split into trips when seals returned to land, but ice haul-outs could not be used to divide tracks with this method. For each trip, 10 simulated trips were generated. Due to the unconstrained nature of these simulations, some simulated tracks can reflect unrealistic movement patterns to inaccessible areas (Jonsen et al., 2023). To limit bias, the distance between the start location and the most distant location was calculated for each simulated trip, and the trip with the most similar distance to the observed trip was retained. Central-place foraging behaviour was replicated for any trip that returned to the same colony from where it began, with the simulated trip programmed to return to its start point. Simulated locations that fell on land were rerouted into the ocean, but any simulated trips that crossed onto continental landmasses were rejected and resampled, as rerouting these trips would condense entire CRWs around the coastline, creating bias.

2.3. Spatiotemporal Autocorrelation

Being equivalent to IPPs, SDMs assume that input data are statistically independent, and spatiotemporal autocorrelation of tracking data violates this assumption, which can influence model outcomes (Boom and Kissling, 2025). To limit autocorrelation, we employed a spatiotemporal data thinning regime for all algorithms that do not explicitly account for autocorrelation. First, points were spatially thinned with the *GeoThinneR* R package v2.0.0 (Mestre-Tomás, 2025) so that only one point per covariate grid cell remained. Then, tracking data were temporally thinned to one point per 24 hour period for most species, or one point per 48 hour period for Antarctic fur seals (*Arctocephalus gazella*), subantarctic fur seals (*Arctocephalus tropicalis*), and southern elephant seals (*Mirounga leonina*). This thinning regime offers substantial reductions in autocorrelation across all species (Figs. S1 and S2).

2.4. Environmental Covariates

Presences and pseudo-absences were matched with three static and eight dynamic covariates (Table 1). All covariates were selected either for their known ecological significance or due to high covariate importance scores in previous SDMs built with RAATD data (Hindell et al., 2020). Seven dynamic covariates were sourced or derived from the Global Ocean Physics Reanalysis Model (GLORYS, Copernicus Marine Environmental Monitoring Service; Lellouche et al., 2021). GLORYS is a data-assimilating ocean model that provides gap-free daily data at a 1/12° resolution, calibrated using remote sensing and in situ platforms. Data-assimilating oceanographic models perform similarly to measured data in species distribution models (Becker et al., 2016), and GLORYS has been successfully adopted in other dynamic SDMs (Braun et al., 2023; Green et al., 2023; Bentley et al., 2024). Chlorophyll-a concentration was obtained from GlobColour (ACRI-ST), which collates multiple satellite observations and uses linear interpolation to improve coverage. Chlorophyll-a concentration was resampled from a 4km to a 1/12° (~8km) resolution using bilinear interpolation to match the resolution of other covariates. All rasters were retained in their native coordinate reference system (WGS 84). GLORYS products are generated through oceanographic modelling that incorporates mesoscale structures such as fronts and eddies, and reprojection would involve interpolation around these structures, potentially obscuring them.

Covariates were not standardised because models were projected to novel environmental conditions, and standardising predictors relative to the training data would anchor responses to the covariate distribution of the training data rather than absolute environmental conditions (Charney et al., 2021). All covariates were used in SDMs, unless over 10% of predictor values were missing from either the testing or training data, in which case incomplete covariates were removed (Table S3 and S4). Additionally, collinearity among covariates was checked using variance inflation factors (VIFs), but since VIFs did not exceed 5 in any tests, no covariates were excluded due to collinearity.

2.5. Species Distribution Modelling

Many algorithms used as SDMs can be equated to IPPs, modelling habitat suitability as a function of environmental covariates (Warton and Shepherd, 2010; Aarts et al., 2012; Fithian and Hastie, 2013; Johnson et al., 2013; Renner and Warton, 2013; Hefley and Hooten, 2016). At the most basic level, regression algorithms model the binomial response of presences (1) and pseudo-absences (0) with a logistic regression framework and a logit link function, where the probability of presence can be expressed as a function *w(x)* of the linear predictor β of each variable x_k:

$$w(x) = \exp\left(\sum_{k=1}^{K} \beta_k x_k \right) \tag{1}$$

This function is then normalised and contrasted with habitat availability to produce final habitat suitability estimates. More advanced algorithms, such as tree-based machine learning methods, estimate this habitat suitability non-parametrically, diverging from this simplified expression.

We tested eight algorithms for each scenario to identify whether any might achieve consistently high performance scores: Generalised Linear Mixed Models (GLMM), Generalised Additive Mixed Models (GAMM), Random Forests (RF), Boosted Regression Trees (BRT), Bayesian Additive Regression Trees (BART), Maximum Entropy (MaxEnt), marginalised Space-Time Point Process models (mSTPP), and Integrated Nested Laplace Approximation with Stochastic Partial Differential Equation (INLA-SPDE).

GLMMs were selected to act as a benchmark model for comparison, as they produce linear estimates of species-habitat relationships, which makes them prone to errors when extrapolated to novel conditions (Conn et al., 2015). GAMMs, RFs, BRTs, and MaxEnt are all among the most widely used algorithms and rank the highest in contemporaneous comparisons of model performance (Valavi et al., 2022). BARTs are Bayesian tree-based models that have gained traction in recent years, and are considered to offer substantial promise for transferability due to their flexibility (Carlson, 2020; Fuster-Alonso et al., 2025; Mestre-Tomás et al., 2026). INLA-SPDE and mSTPPs are both promising but less commonly used methods that use Bayesian approaches and explicitly account for spatiotemporal autocorrelation instead of assuming independence (Johnson et al., 2013; Lezama-Ochoa et al., 2020; Engel et al., 2022; Eisaguirre et al., 2025).

GLMMs are parametric linear regression models, while GAMMs are semi-parametric regression models capable of capturing non-linear relationships. As with GLMMs, GAMMs also exhibit extrapolation errors despite allowing for non-linear responses (Conn et al., 2015). Both algorithms incorporate random intercepts and slopes, which can be used

Table 1
Environmental covariates used in the species distribution models.

Variable	Spatial Resolution	Temporal Resolution	Temporal Coverage	Unit	Source
Depth (DEPTH)	0.083° (~9km)	Static	Static	m	GLORYS https://doi.org/10.48670/moi-00021
Slope (SLOPE)	0.083° (~9km)	Static	Static	degrees	Calculated from ETOPO 2022 bathymetry layer using *terrain* function from the *terra* R package (Hijmans *et al.*, 2022) https://doi.org/10.25921/fd45-gt74
Distance to Shelf (dSHELF)	0.083° (~9km)	Static	Static	km	Australian Antarctic Division Accessed using the *raadtools R* package (Sumner, 2023)
Chlorophyll-a Concentration (CHL)	4km (~0.04°)	Daily	1997-2024	mg/m^3	GlobColour https://doi.org/10.48670/moi-00281
Current Velocity (CURR)	0.083° (~9km)	Daily	1993-2024	m/s	GLORYS https://doi.org/10.48670/moi-00021
Eddy Kinetic Energy (EKE)	0.083° (~9km)	Daily	1993-2024	m^2/s^2	U and V Components of CURR $0.5(U^2 + V^2)$
Sea Ice Concentration (SIC)	0.083° (~9km)	Daily	1993-2024	%	GLORYS https://doi.org/10.48670/moi-00021
Salinity (SAL)	0.083° (~9km)	Daily	1993-2024	psu	GLORYS https://doi.org/10.48670/moi-00021
Mixed Layer Depth (MLD)	0.083° (~9km)	Daily	1993-2024	m	GLORYS https://doi.org/10.48670/moi-00021
Sea Surface Height Anomaly (SSH)	0.083° (~9km)	Daily	1993-2024	m	GLORYS https://doi.org/10.48670/moi-00021
Sea Surface Temperature (SST)	0.083° (~9km)	Daily	1993-2024	°C	GLORYS https://doi.org/10.48670/moi-00021

in telemetry-based SDMs to account for individual dependence structures and improve predictive performance (Chambault et al., 2021). GLMMs and GAMMs were fit with the R packages *lme4* v1.1-37 (Bates et al., 2015) and *mgcv* 1.9-4 (Wood, 2015) respectively, treating individual as a random effect. GAMMs featured five knots per variable to avoid overfitting, and a thin-plate spline smoother.

MaxEnt is traditionally viewed as a machine learning model, capable of fitting complex models that transform predictor covariates with a range of transformations (Elith et al., 2011). However, it has been shown to be equivalent to a Poisson regression model (Renner and Warton, 2013), which could limit its transferability as with other regression techniques. RFs, BRTs, and BARTs are non-parametric tree-based machine learning techniques that can handle interaction effects between predictors (Elith et al., 2008; Hastie et al., 2009; Chipman et al., 2010; Elith et al., 2011). While RFs and BRTs are popular algorithms for SDMs, they are inherently designed for interpolation rather than extrapolation and offer limited predictive skill with novel covariate values (Malistov and Trushin, 2019; Milà et al., 2024). BARTs are capable of achieving greater flexibility by using Bayesian priors to constrain trees to shallow depths (Chipman et al., 2010), which may be key for transferability.

All machine learning models were fitted in the *tidymodels* R framework v1.3.0 (Kuhn and Silge, 2022) with the *tidySDM* R package v1.0.0 (Leonardi et al., 2024). During model tuning, the best model hyperparameters were selected using individual block cross-validation, where all data from several individuals were randomly withheld as a testing dataset over 10 iterations. This cross-validation method has been proven to be more appropriate when constructing models with the goal of transferability (Roberts et al., 2017). Data from remaining individuals were used to train models, which were subsequently tested, and the best model was identified with the Continuous Boyce Index (CBI).

MaxEnt models were fitted with the *maxnet* engine (Phillips, 2021), tuning the regularisation multiplier (1, 2, 5, 10, 15, or 20) and the feature class options ("lq", "hq", "lqp", "hqp", "hqt", "hqpt", or "lqhpt"). RFs were fitted with the *ranger* engine (Wright and Ziegler, 2017), tuning the number of covariates to possibly split at each node (2, 3, or 4); all RFs employed 1000 trees, a minimum node size of 1, and the Gini index for node splitting. BRTs were fitted with the *lightgbm* engine (Ke et al., 2017), tuning the number of trees (from 2,000 to 10,000 in increments of 2000), the maximum tree depth (1, 3 or 5), and the learning rate (0.005, 0.01, or 0.5); the minimum number of observations in a node was constant at 20 for each model. BARTs were fitted with the *dbarts* engine (Dorie et al., 2025), tuning the number of trees (50, 100, 200, or 300).

To explore whether accounting for spatiotemporal autocorrelation explicitly within models might improve transferability, we also fit mSTPPs and INLA-SPDE models. These models feature covariates that account for spatial and/or temporal autocorrelation, thus reducing overfitting by representing behavioural and unmeasured environmental processes that would otherwise be attributed to environmental covariates. mSTPPs were fitted to the complete tracking data, using the residuals of a movement-informed covariate rather than data thinning to account for temporal autocorrelation (Eisaguirre et al., 2025). This covariate was constructed through autocorrelated kernel density estimation (Fleming et al., 2015), fitted in the *ctmm* R package v1.3.0 (Calabrese et al., 2016). A logistic regression was then fitted through the INLA Bayesian inference method with the INLA R package v25.10.19 (Rue et al., 2017), using the movement covariate and environmental predictors to estimate habitat suitability. INLA-SPDE models were also fitted to the full tracking dataset, accounting for spatial autocorrelation by leveraging a Gaussian Markov random field approximated with a triangular mesh over the spatial domain (Lindgren et al., 2011). INLA-SPDE then models spatial autocorrelation using a Matérn covariance function. Models were fitted as logistic regressions using all environmental predictors and the random spatial field, also in the INLA R package v25.10.19 (Rue et al., 2017).

2.6. Model Evaluation

To assess temporal transferability, models were evaluated using leave-year-out cross-validation. Within each life stage, one year was iteratively isolated for model testing, and models were trained on data from the remaining years. This emulates real-time prediction by transferring models to different periods within the same region. Because individual tracking devices rarely span multiple years, this ensures independence, as individuals in the training and testing data are distinct from one another. When breeding stage dates spanned multiple calendar years, tracks were grouped into breeding seasons (e.g., December 2012 to January 2013) rather than years to maintain independence. To avoid spatial extrapolation, models were predicted within a minimum convex polygon fitted to all tracks for that life stage. Any test data that contained fewer than 50 points or tracks from fewer than three individuals were removed as these were not considered representative for model validation.

To investigate spatial transferability, models were trained on all the data from the identified data-rich populations before being tested on other populations during the corresponding breeding stage where available (Fig. 1). Again, models were only predicted within minimum convex polygons fitted around the testing data.

Model performance was evaluated using the CBI (Hirzel et al., 2006), a metric which is more suitable for presence-only data than other widely used discrimination metrics (Guisan et al., 2017; Leroy et al., 2018). The CBI assesses whether presences occur disproportionately in areas with high predicted habitat suitability, first by binning habitat suitability within a moving window framework. Then, the ratio between the proportion of presences and the proportion of target cells falling within each bin is determined, and the correlation between habitat suitability and this ratio is calculated. Values range between -1 and 1, with values closer to 1 indicating good model performance.

To investigate how environmental extrapolation influences transferability, the *Shape* metric was used (Velazco et al., 2024). *Shape* is a model-agnostic approach that calculates the multivariate distance in environmental space between each testing data point and the nearest training data point. To explore the effect of sample size on transferability, we investigated how transferability scores varied with the number of thinned locations in the training data, as this represents both the number of individuals and tag deployment durations.

3. Results

Models generally performed well when transferred through time if pseudo-absences were generated using background sampling or CRWs (Fig. 4). BRTs, BARTs, RFs, and INLA-SPDE fitted with background sampling scored highest with mean CBI scores of 0.793, 0.791, 0.774, and 0.732 respectively, while all other configurations featured detectably lower scores (Table S7). Only BRTs, BARTs, and RFs offered a detectable improvement in transferability over GLMMs using background sampling. Buffer sampling performed poorly in general, reporting mean CBI scores below 0 with all algorithms other than INLA-SDPE (0.446) and mSTPP (0.365).

No combination of algorithm and pseudo-absence technique produced consistently high CBI scores when models were transferred spatially (Fig. 4). The best configuration, mSTPP built with buffer sampling, yielded a low mean CBI of 0.357, which was only detectably better than 13 of the other 23 configurations (Table S8). Each configuration saw at least 21% of the spatial transferability tests report CBIs below 0 and over 40% score below 0.5, suggesting that no configuration could be considered reliable.

Larger sample sizes resulted in improved temporal transferability for most algorithms built with background samples or CRWs (Fig. 5a). At small sample sizes, models built with background sampling far outperformed other model configurations. R^2 values of linear trends were below 0.1 for GLMMs, GAMMs, INLA-SPDE, and mSTPPs built with

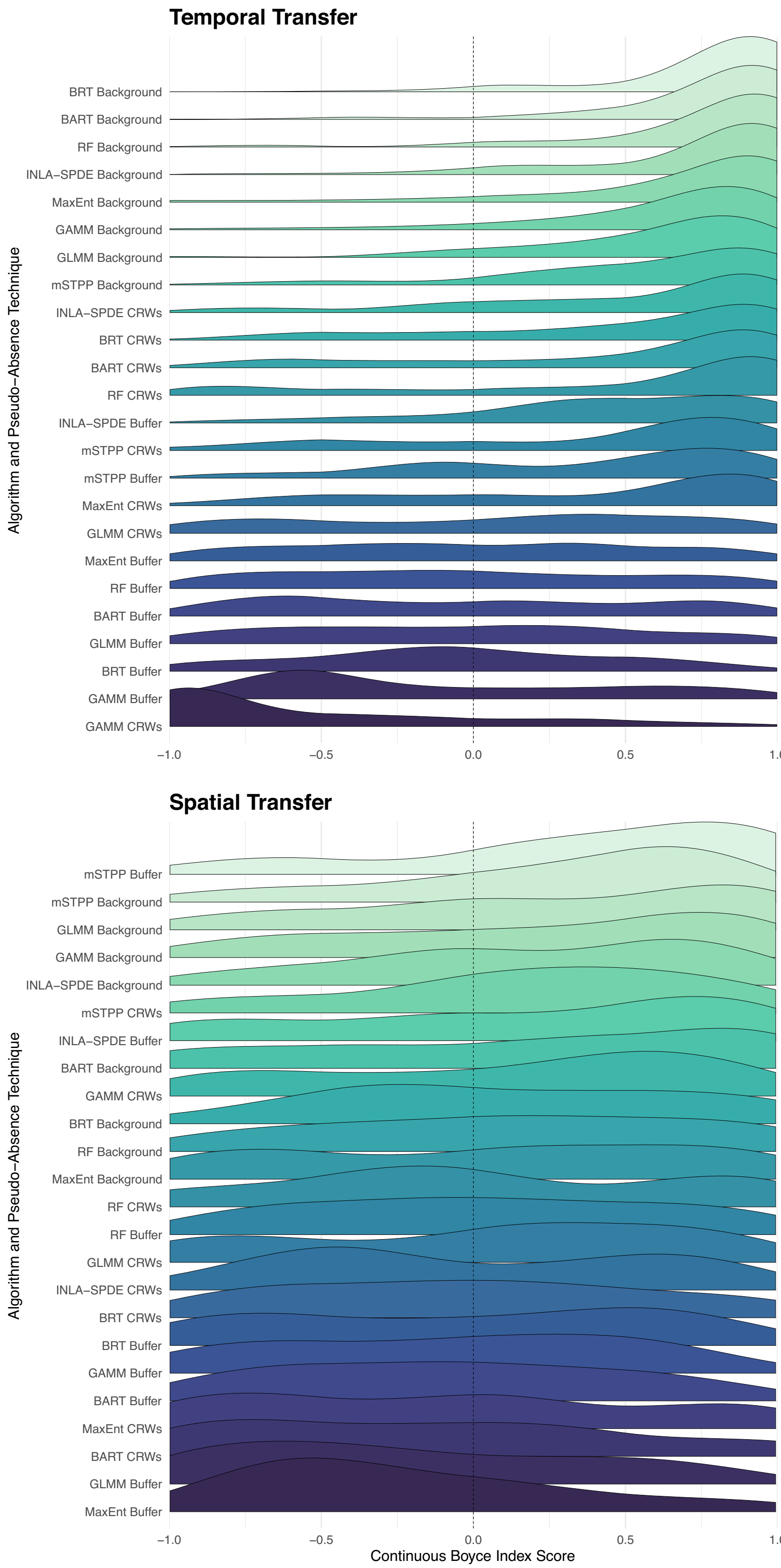

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Fig. 4. Temporal and spatial transferability expressed as Continuous Boyce Index scores for each combination of algorithm and pseudo-absence technique. Combinations are ordered by median score, with the highest scoring configuration at the top and the lowest scoring at the bottom. The dashed vertical line represents a score of 0, below which models are inaccurate, predicting poor suitability in areas of frequent presences. The tested algorithms were Bayesian Additive Regression Trees (BARTs), Boosted Regression Trees (BRTs), Generalised Additive Mixed Models (GAMMs), Generalised Linear Mixed Models (GLMMs), Integrated Nested Laplace Approximation with Stochastic Partial Differential Equation (INLA-SPDE), Maximum Entropy (MaxEnt), marginalised Space-Time Point Process models (mSTPPs), and Random Forests (RFs). CRW stands for Correlated Random Walks. 85 temporal tests per configuration were conducted across 10 species from 12 populations, and 42 spatial tests per configuration were conducted across 7 species from 9 populations.

background samples (Table S9), suggesting that sample size did not explain much of the variation in the data. Increasing sample size also did not have a consistent impact on spatial transferability (Fig. 5c), and again R^2 values were low for these trends (Table S9).

Environmental extrapolation influenced temporal transferability, particularly for the configurations that performed best overall (Fig. 5b). Tree-based machine learning algorithms built with background samples and CRWs attained average CBI scores above 0.8 at low *Shape* values but scores declined with increasing *Shape* values, and CRWs exhibited a sharper decline. However, it should be noted that INLA-SPDE and mSTPPs built with background sampling did not experience declining transferability scores at greater *Shape* values, maintaining average scores above 0.5. As with the effects of sample size, R^2 values of linear trends were generally low for GLMMs, GAMMs, INLA-SPDE, and mSTPPs (Table S9). The effect of environmental extrapolation on spatial transferability was less apparent (Fig. 5d), as little of the variation in transferability could be explained by *Shape* (Table S9).

4. Discussion

Our results show that SDMs can be transferred through time for a single population using appropriate model configurations, but transferring models spatially is more challenging. All algorithms attained mean CBI scores above 0.57 when using background sampling. This concurs with findings from other regions that temporal transferability can be achieved with marine tracking data using background sampling (Abrahms et al., 2019; Welch et al., 2023). An important caveat is that the majority of tests were conducted on data recorded in the year preceding or following some of the training data, and the known improvement in transferability with smaller time gaps (Zhang et al., 2020) means that scores may be greater than if longer intervals were used. Preliminary testing of four long-term datasets found that intervals as large as 5 years between training and testing data consistently yielded high transferability scores, but in some systems transferability declined at longer intervals (Fig. S6). Future work could use simulation studies or long-term datasets from single regions to further understand the limits of temporal transferability, leveraging the model configurations that performed best here. As independent data in our study region are sparse and do not allow for confirmation of breeding stages, we used tracking data to both build and validate models. This has the potential to introduce bias and inflate model scores, and we recommend using multiple data sources to validate models when used for ecosystem management. Nonetheless, SDMs have proven transferable in time when using multiple years of data, including the most recent available data, to yield more accurate model predictions.

Background sampling emerged as the most effective pseudo-absence technique for accurate temporal transfer. Background sampling typically provides the widest sampling of available environmental conditions, and greater environmental separation between presence and pseudo-absence data is known to improve contemporaneous predictions (O'Toole et al., 2021). While new habitats may be experienced in different times, it is plausible that individuals will seek out similar habitat conditions if they are accessible. Models built with CRWs did project well, contributing 22.4% of the top performing models, but CBI scores fell below 0 under increasing environmental extrapolation, which would render predictions unreliable for dynamic ocean management.

Buffer sampling generally exhibited poor temporal transferability. Individually, buffers represent how species select among the conditions immediately available to them. However, the limited distance between presences and buffer samples influences model performance, with larger buffer radii yielding better predictive capacity (Fig. S7). When smaller radii are used, the degree of overlap between the environmental space of the two classes increases with sample size. This is known as class overlap, which causes the performance of machine learning methods to degrade (Vuttipittayamongkol et al., 2021), and may explain why buffers perform so poorly for most algorithms. It is therefore recommended that buffer sampling is not used for real-time predictions.

All eight algorithms performed well with background sampling. RFs, BRTs, BARTs, and INLA-SPDE were most often amongst the highest performing algorithms across all tests (Table S5). This is consistent with findings that tree-based machine learning methods and approaches accounting for autocorrelation outperform traditional regression methods when making contemporaneous predictions (Valavi et al., 2022; Fichera et al., 2023). Higher transferability scores are likely associated with better contemporaneous model performance, since the drop-off in model performance metrics between internal tests and transferability tests was similar across algorithms (Fig. S5).

While declines in performance with increasing environmental extrapolation were observed for all regression and tree-based machine learning algorithms, INLA-SPDE and mSTPP did not experience such declines. This might arise because these models account for residual spatial autocorrelation that arises due to animal behaviour or predictors not included in models, thus reducing the likelihood of overfitting and improving performance in novel conditions. However, environmental extrapolation was generally restricted to below median *Shape* values of 100, showing that dynamic predictions may not often need to extrapolate to completely novel conditions. Therefore, a preferable approach would use an ensemble of multiple tree-based machine learning algorithms (BARTs, BRTs, and RFs) and models accounting for autocorrelation (INLA-SPDE and mSTPPs), which would leverage the benefits and mitigate shortfalls of both approaches. It should be noted that we used a simple logistic regression for both INLA-SPDE and mSTPPs, and that using non-linear statistical models in combination with these methods might further improve transferability scores.

Increasing sample size saw increasing temporal transferability, in part because environmental extrapolation reduces with greater sample sizes (Fig. S4). Tracking data from over 100 deployments are generally needed to assess shifts in space use over time without using SDMs (Sequeira et al., 2019b). When using background sampling, however, differences with sample size were less pronounced and CBI scores over 0.6 were achieved with as few as three tagged individuals (Fig. S11). Temporal transferability may therefore be attainable even in studies where data from fewer tracked individuals are available, though these individuals would need to be representative of the demographics of interest in the study. To account for extrapolation, an approach to quantify projection uncertainty could be to calculate the *Shape* value for contemporaneous conditions and contrast this with the relationship between *Shape* and predictive accuracy (Fig. 5b). If extrapolation is found to be high, then researchers could upweight the importance of robust models like INLA-SPDE and mSTPPs within an ensemble.

Spatial transferability could not be achieved reliably with any model configuration. This is consistent with other studies that report poor spatial transferability in SDMs (Torres et al., 2015; Péron et al., 2018; Rousseau & Betts, 2022). Non-stationarity of species-habitat relationships between regions can stem from different available conditions, variable oceanographic processes, the effects of predation and

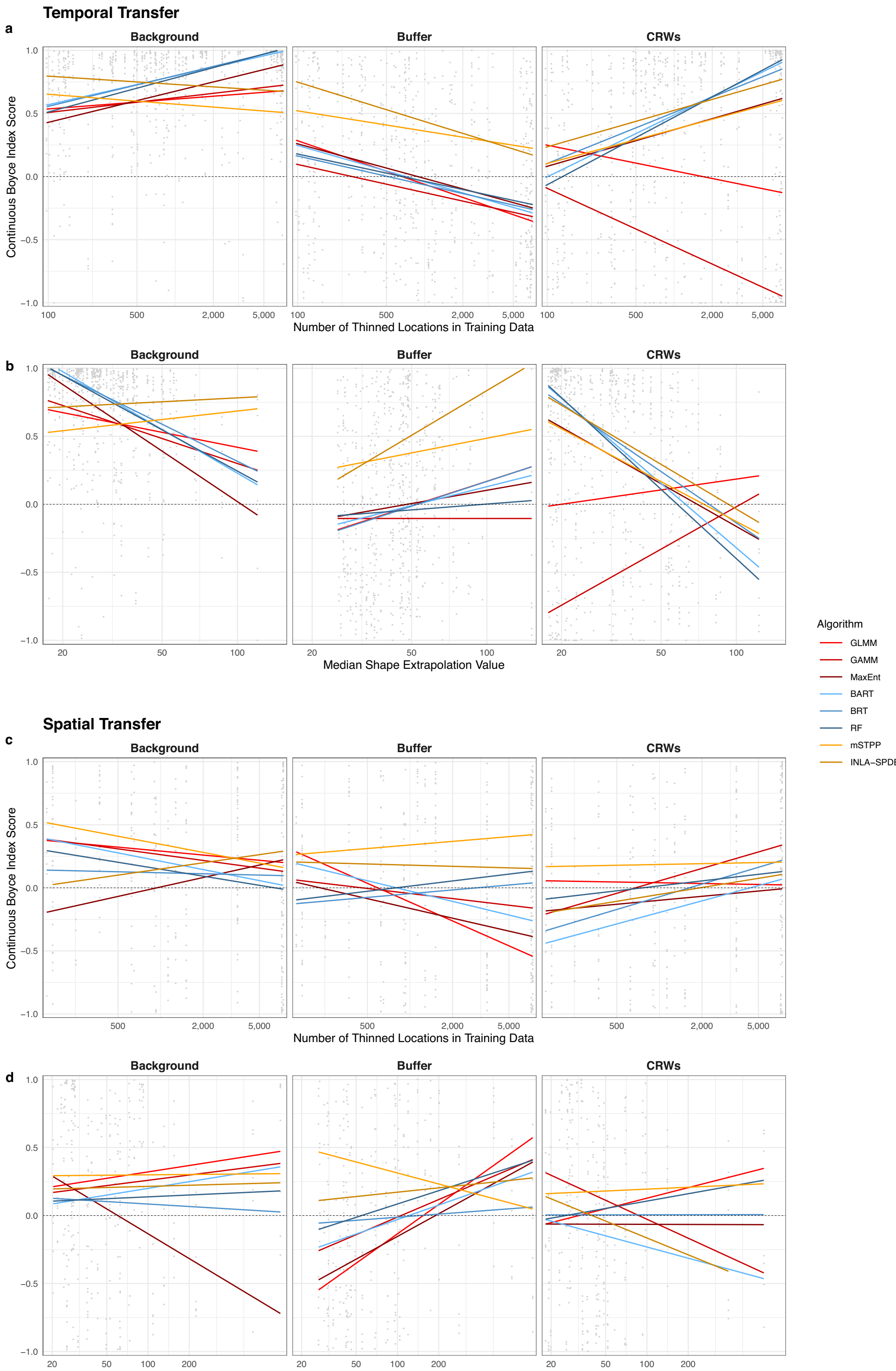

Fig. 5. The influence of (a, c) sample size and (b, d) environmental extrapolation on the predictive skill of models transferred through (a, b) time and (c, d) space. Lines indicate the relationships between extrapolation and transferability for each model configuration, with each colour corresponding to a different algorithm and each subpanel corresponding to a pseudo-absence technique. The tested algorithms were Bayesian Additive Regression Trees (BARTs), Boosted Regression Trees (BRTs), Generalised Additive Mixed Models (GAMMs), Generalised Linear Mixed Models (GLMMs), Integrated Nested Laplace Approximation with Stochastic Partial Differential Equation (INLA-SPDE), Maximum Entropy (MaxEnt), marginalised Space-Time Point Process models (mSTPPs), and Random Forests (RFs). CRW stands for Correlated Random Walks. 85 temporal tests per configuration were conducted across 10 species from 12 populations, and 42 spatial tests per configuration were conducted across 7 species from 9 populations. R^2 values for each of the linear trend lines are reported in Table S9. Note that sample size is based on the number of thinned locations, but that INLA-SPDE and mSTPP models used the full tracking dataset.

competition, differing prey availability, and many other causes (Mannocci et al., 2020; Bentley et al., 2024). Additionally, median *Shape* values were higher on average for spatial than temporal tests, meaning models had to extrapolate further beyond the environmental space of their training data. Future research could assess whether emerging modelling techniques that combine machine learning models with local parametric models, such as Gaussian Process BARTs, achieve greater success than traditional algorithms (Maia et al., 2024; Wang et al., 2024). Another route could be the integration of multiple populations to enable spatial transferability, which has been shown to improve predictive performance in data-poor systems (Redfern et al., 2017). This might also be enhanced using methods such as nested SDMs (Goicolea et al., 2025) or meta-models (Reisinger et al., 2021). Spatial transferability remains an outstanding issue, and future work could use simulation studies or global studies across multiple taxa to identify solutions.

These tests were conducted on a range of marine mammal and seabird species in the Southern Ocean. Although it cannot be guaranteed that the same results would be yielded in other ecosystems, there are several reasons to believe that findings are generalisable to other marine species and environments. First, similar results were found among different taxonomic groups (Fig. S8), varying levels of interaction with sea ice (Fig. S9), and between central-place foragers and unrestricted foragers (Fig. S10). Additionally, there is considerable support in the literature for the superior performance of tree-based machine learning algorithms (Valavi et al., 2022), models accounting for autocorrelation (Fichera et al., 2023; Eisaguirre et al., 2025), and background sampling (Hazen et al., 2021; Fernandez et al., 2022; Braun et al., 2023) in the context of contemporaneous predictions, which theoretically would likely correspond with better transferability. Finally, the considerable sample size of this study for temporal ($n = 85$) and spatial ($n = 42$) tests of transferability limits the likelihood of anomalous results influencing findings.

These findings show that dynamic species distribution models can be used to support dynamic ocean management, provided that the data and model configuration are suitable. This offers a cost-effective alternative to real-time monitoring, using recent historical data to make contemporaneous predictions of habitat suitability that can inform mitigation measures. Dynamic SDMs also allow distributions to be forecast in near real-time (Scales et al., 2017; Dobson et al., 2024), meaning that management can be proactive rather than reactive. Given that dynamic predictions might impact the exposure of species to threats, it is important that methodological recommendations are adopted, using ensembles of tree-based machine learning algorithms and models accounting for autocorrelation, built with background sampling. Although we found that models could be transferred through time successfully, further study is needed to assess the limits of temporal transferability and possible methods to overcome said limits.

To conclude, temporal transferability scores were generally highest for tree-based machine learning algorithms built with background sampling, though models accounting for autocorrelation performed better when there was greater environmental extrapolation. No model configuration produced consistently high spatial transferability scores, and all configurations saw models regularly fail to predict suitable habitat in new regions. Researchers looking to forecast near real-time predictions from tracking data are recommended to use large datasets collected over many years, and to avoid transferring models through space when tracking data do not cover every population within the target area. Future work could expand on this study by assessing model performance over longer intervals, temporal transferability of models using different data sources or data integration, transferability of other point process model equivalents, and spatial transferability when incorporating multiple populations or using emerging modelling techniques. With further refinement, there is clear potential for using telemetry data in SDMs to inform dynamic ocean management.

CRediT authorship contribution statement

Joshua C Wilson: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Philip N Trathan:** Writing – review & editing, Supervision, Data curation, Conceptualization. **Hugh J Venables:** Writing – review & editing, Supervision, Conceptualization. **Horst Bornemann:** Writing – review & editing, Data curation. **Rochelle Constantine:** Writing – review & editing, Data curation. **Daniel P Costa:** Writing – review & editing, Data curation. **Luciano Dalla Rosa:** Writing – review & editing, Data curation. **Louise Emmerson:** Writing – review & editing, Data curation. **Ari S Friedlaender:** Writing – review & editing, Data curation. **Michael E Goebel:** Writing – review & editing, Data curation. **Simon Goldsworthy:** Writing – review & editing, Data curation. **Mark A Hindell:** Writing – review & editing, Data curation. **Mary-Anne Lea:** Writing – review & editing, Data curation. **Mônica M C Muelbert:** Writing – review & editing, Data curation. **Silvia Olmastroni:** Writing – review & editing, Data curation. **Yan Ropert-Coudert:** Writing – review & editing, Data curation. **Colin Southwell:** Writing – review & editing, Data curation. **Ryan R Reisinger:** Writing – review & editing, Supervision, Data curation, Conceptualization.

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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2026.111702.

Data availability

RAATD data are available at DOI: 10.1038/s41597-020-0406-x. The code used in this paper is available at github.com/oshuwilson/pseudoabs_transferability.

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