Refining seabird marine protected areas by predicting habitat inside foraging range - a case study from the global tropics

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Abstract

Conservation of breeding seabirds typically requires detailed data on where they feed at sea. Ecological niche models (ENMs) can fill data gaps, but rarely perform well when transferred to new regions. Alternatively, the foraging radius approach simply encircles the sea surrounding a breeding seabird colony (a foraging circle), but overestimates foraging habitat. Here, we investigate whether ENMs can transfer (predict) foraging niches of breeding tropical seabirds between global colonies, and whether ENMs can refine foraging circles. We collate a large global dataset of tropical seabird tracks (12000 trips, 16 species, 60 colonies) to build a comprehensive summary of tropical seabird foraging ranges and to train ENMs. We interrogate ENM transferability and assess the confidence with which unsuitable habitat predicted by ENMs can be excluded from within foraging circles. We apply this refinement framework to the Great Barrier Reef (GBR), Australia to identify a network of candidate marine protected areas (MPAs) for seabirds. We found little ability to generalise and transfer breeding tropical seabird foraging niches across all colonies for any species (mean AUC: 0.56, range 0.4-0.82). Low global transferability was partially explained by colony clusters that predicted well internally but other colony clusters poorly. After refinement with ENMs, foraging circles still contained 89% of known foraging areas from tracking data, providing confidence that important foraging habitat was not erroneously excluded by greater refinement from high transferability ENMs nor minor refinement from low transferability ENMs. Foraging radii estimated the total foraging area of the GBR breeding seabird community as 2,941,000 km2, which was refined by excluding between 197,000 km2 and 1,826,000 km2 of unsuitable foraging habitat. ENMs trained on local GBR tracking achieved superior refinement over globally trained models, demonstrating the value of local tracking. Our framework

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Keywords

Foraging Radius, Foraging niche, Great Barrier Reef, Ecological Niche Model, Marine Protected Area, Transferability

Introduction

To counter the biodiversity crisis, there is an urgent need to protect important habitats to ensure the stability of global ecosystems. In response, the International Union for Conservation of Nature (IUCN) has called for 30% of the Earth's overall land and sea area to be protected by 2030. However, as of April 2023 only 2.9% of the ocean was highly protected (www.mpatlas.org; Morgan et al. 2018). There is also concern that protected areas could be situated in locations where increased protection offers marginal benefit for biodiversity (Devillers et al. 2015, Woodley et al. 2021). One barrier to protected area implementation is

that limited knowledge of animal distributions and abundance hampers the identification of the most critical locations. In the marine realm, data collection is logistically and financially challenging; however, there are numerous, pressing threats to biodiversity that include fishing, climate change, pollution, shipping and energy generation (Halpern et al. 2008).

Seabirds are a highly threatened animal group (Croxall et al. 2012) with a marine foraging niche (they depend upon the sea for food). Their relative detectability and accessibility (i.e. above water, colonial, terrestrial breeding) compared to other marine species has provided sufficient data to merit global analyses of conservation priority (Dias et al. 2019a) and designate marine protected areas (MPAs) (e.g. North Atlantic Current and Evlanov Sea-basin MPA; Davies et al. 2021). During the breeding season, seabird distribution is focussed around colonies, as birds regularly return to perform parental duties such as incubating eggs and feeding chicks, and area-based conservation measures, such as MPAs, are more feasible than during more dispersive migratory and non-breeding seasons (Oppel et al. 2018). To identify MPAs for seabirds, a spatial representation of their marine foraging niche is required. This can come directly from bird-borne tracking devices or at-sea surveys, which locate hotspots of occurrence or abundance to delineate candidate MPAs (Lascelles et al. 2016). Alternatively, such data can be entered into Ecological Niche Models (ENMs), also known as species distribution models, to make predictions beyond surveyed areas. ENMs build statistical relationships between species space use and remotely-sensed environmental variables, and then predict these relationships over broad areas sampled by remote sensors (e.g. satellite imagery). For seabirds, these environmental variables describe important marine habitat and bio-physical processes such as seamounts, frontal systems and productivity blooms, which can characterise their foraging niches, for example the foraging niche of a seabird population could be described as specialising on upwellings at pelagic seamounts. The ability of ENMs to predict seabird foraging niches beyond surveyed areas, has seen them regularly used for marine spatial planning and identification of priority conservation areas (Nur et al. 2011, Žydelis et al. 2011, Lavers et al. 2014, Dias et al. 2019b).

However, a key hurdle for ENMs is to extrapolate predictions beyond the geographical and temporal range of training data, known as model 'transferability' (Randin et al. 2006, Yates et al. 2018). A growing body of literature suggests limited ENM transferability between different regions (Redfern et al. 2017, Mannocci et al. 2020). In seabirds, Warwick-Evans et al. (2018) found that the foraging niche of chinstrap penguins *Pygoscelis antarcticus* was transferable between colonies at <100 km, while Péron et al. (2018) found that foraging niche of Scopoli's shearwater *Calonectris diomedea* was transferable locally but not regionally (>200 km). Transferability at large scales (>1000's of km) does not apply in grey petrel *Procellaria cinerea* wintering distributions (Torres et al. 2015), nor red-billed tropicbird *Phaethon aethereus* foraging niches (Diop et al. 2018). These studies support contrasting regional marine habitats and differing associations with habitat by different populations (local adaptation) as major barriers to transferability. Local adaptation is driven by strong philopatry in seabirds, many of which have evolved population-specific foraging behaviours suited to local biotic and oceanographic conditions (Peck & Congdon 2005, Mendez et al. 2017, Gilmour et al. 2018). To improve transferability, ENMs can be trained with data from different regions to extract commonalities in local adaptation and better generalise a species' niche (Matthiopoulos et al. 2011). With the growing availability of multi-colony seabird tracking datasets (e.g. Ropert-Coudert et al. 2020; www.seabirdtracking.org), it is now feasible to train such ENMs and conduct a comprehensive evaluation of the transferability of breeding seabird foraging niches. This assessment is particularly warranted in tropical regions, which have received significantly less effort from seabird tracking studies relative to higher latitudes (Bernard et al. 2021), and ENMs could be particularly important for filling gaps in knowledge on seabird distributions.

A simple, pragmatic and generally effective alternative to ENMs for defining important areas of seascape for breeding seabirds is the foraging radius approach (Birdlife International 2010, Thaxter et al. 2012, Soanes et al. 2016, Critchley et al. 2020). At-sea observations and/or tracking data are used to calculate the distance breeding seabirds forage from their colony (hereafter a "foraging radius"), this is mapped with a circle centred on the colony to represent the sea area within which the breeding seabird population feeds (hereafter a "foraging circle"). Averaging foraging radii from multiple colonies can generalise a species' foraging radius

which can then be applied to colonies lacking information on the at-sea distribution of breeding residents (Thaxter et al. 2012). With a representative sample of colonies, the process can be applied globally (e.g. https://maps.birdlife.org/marineibas). However, the foraging radius approach overestimates foraging habitat, as not all areas within the foraging circle will be used. A foraging circle can be refined with information relating to habitat preference, such as bathymetry (Birdlife International 2010, Soanes et al. 2016) or prey availability (Grecian et al. 2012), where unsuitable habitat is 'cut out' from the circle. Extending this approach by using a range of remotely-sensed variables commonly used in ENMs allows a more holistic approximation of unsuitable habitat, which could improve the accuracy of foraging circle refinement. As such, this new approach better meets a key goal of systematic conservation planning, minimising the cost (in terms of size) of protected areas while maximising the confidence they contain core habitat (Margules & Pressey 2000).

The Great Barrier Reef (GBR) Marine Park, Australia is arguably the most thoroughly managed large MPA in the tropics (Fernandes et al. 2005). In addition to the mega-diverse coral reef community, for which the park was created, the GBR's cays support numerous globally and regionally significant breeding populations of tropical seabirds (King 1993). However, numerous breeding GBR seabird populations are in decline (Heatwole et al. 1996, Batianoff & Cornelius 2005, Hemson 2015, Woodworth et al. 2020). Despite this knowledge of seabird population change, the ability of managers to understand the causes of these changes and respond to them is limited by the lack of information on where they forage. Limited tracking studies underpin much of what we know (Fig. 1), with no standardised boat or aerial-based seabird survey data existing (but see CSIRO (2020) for a survey dataset from the adjacent Coral Sea). Consequently, seabird foraging resources have not been considered in the designation of marine park zoning that dictates the location of permitted activities within the GBR Marine Park. Overcoming these data gaps could inform future amendments to marine park zoning and guide other management interventions, and potentially mitigate seabird population declines.
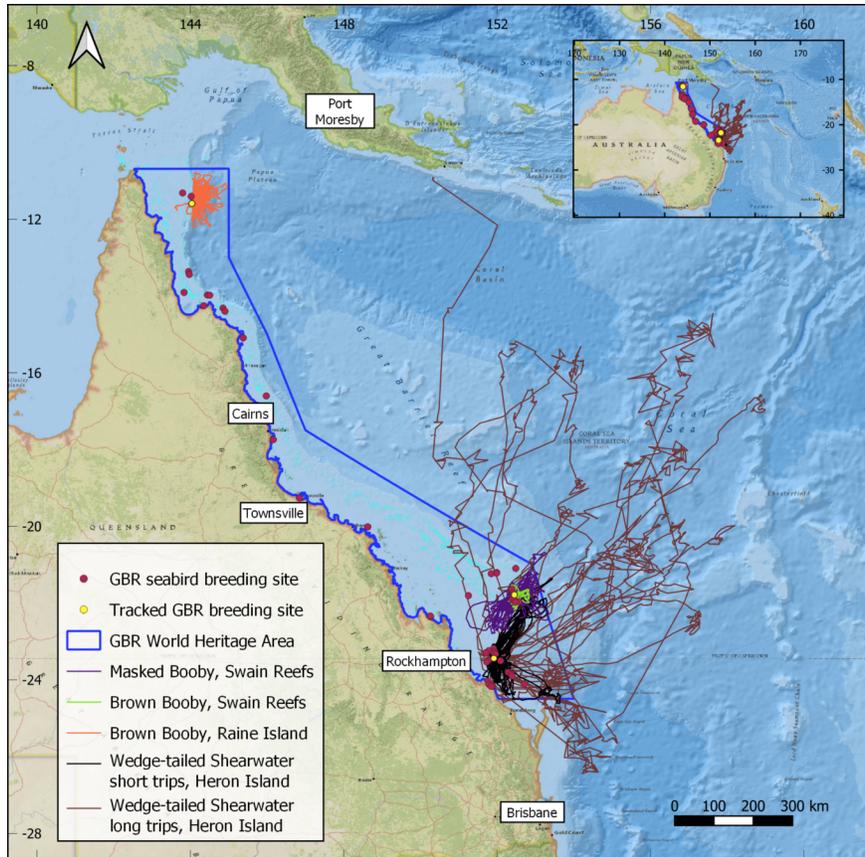
Fig. 1 Extent of published seabird tracking data on the Great Barrier Reef. Displayed GBR seabird breeding sites qualify under globally or regionally significant seabird breeding areas.

Here, we collate the most comprehensive tropical seabird tracking dataset from across the globe to train ENMs, describing foraging niche and to estimate tropical seabird foraging radii. Firstly, we determine whether breeding seabird foraging niches can be transferred (predicted) between global colonies using ENMs. We investigate the influence of local adaptation on transferability by testing whether nearby or oceanographically similar colonies show better transferability, and whether this can be overcome by training ENMs on multiple colonies to generalise a 'global' foraging niche. Secondly, we present a framework combining ENMs with the foraging radius approach to refine foraging circles by excluding areas of predicted unsuitable habitat. We validate our framework's robustness by testing the ability of unrefined and refined foraging circles to include known foraging areas of colonies from our global tracking dataset. Finally, we demonstrate how global models can inform local planning by applying our framework to the breeding seabird community of the Great Barrier Reef to identify a network of candidate MPAs for seabirds, and explore the trade-off between their size and the confidence in their prediction.

Methods

Tracking data

The validity of our modelling approach hinges on constructing ENMs from multiple colonies. We thus compiled the most comprehensive database of tropical seabird tracking data to date, featuring 16 species

representing 60 colonies around the globe and totalling ~12000 individual trips (Table 1; Supporting information). Species that had more than 10 tracking studies were modelled individually. Tropicbird *Phaethon* and frigatebird *Fregata* species were grouped respectively (Table 1) to boost sample size and make family level models, acknowledging that foraging differences between species within these families have been observed (e.g. Mott et al. 2016). Noddy *Anous* species were modelled as a family group (following evidence of foraging niche overlap; Surman & Wooller 2003, Shephard et al. 2018), and large tern *Thalasseus* and *Hydroprogne* species were aggregated into a meta-family group for modelling. The exceptions were sooty terns, which were modelled as an individual species (despite few tracking studies) because of their unique, highly pelagic foraging niche among terns (Surman & Wooller 2003). Wedge-tailed shearwaters were also modelled separately for short trips and long trips because we had good a-priori knowledge of dual-foraging behaviours during breeding on the GBR (Congdon et al. 2005, McDuie et al. 2015) and in New Caledonia (Weimerskirch et al. 2020), and sufficient tracking studies to do so. Both individual species (e.g. brown booby BRBO) and family groups (e.g. large terns TERN) are hereafter referred to as "modelled species".

Table 1 Summary of quantity and coverage of tracking data analysed for each species, and the grouping of species with less data.

Species common name	Latin name	Number of colonies	Number of trips	Modelled species (acronym)
Brown booby	*Sula leucogaster*	16	2926	brown booby (BRBO)
Masked booby	*Sula dactylactra*	12	2255	masked booby (MABO)
Red-footed booby	*Sula sula*	13	733	red-footed booby (RFBO)
Great frigatebird	*Fregata minor*	3	1195	frigatebirds group (FRBD)
Lesser frigatebird	*Fregata ariel*	2	732	frigatebirds group (FRBD)
Magnificent frigatebird	*Fregata magnificens*	4	97	frigatebirds group (FRBD)
Red-billed tropicbird	*Phaethon aethereus*	10	1100	tropicbirds group (TRBD)
Red-tailed tropicbird	*Phaethon rubricauda*	1	61	tropicbirds group (TRBD)
Wedge-tailed shearwater	*Ardenna pacifica*	8	313	wedge-tailed shearwater short t
Wedge-tailed shearwater	*Ardenna pacifica*	7	125	wedge-tailed shearwater long tr
Sooty tern	*Onychoprion fuscatus*	3	19	sooty tern (SOTE)
Black noddy	*Anous minutus*	1	7	noddies group (NODD)
Lesser noddy	*Anous tenuirostris*	1	54	noddies group (NODD)
Brown noddy	*Anous stolidus*	3	181	noddies group (NODD)
Caspian tern	*Hydroprogne caspia*	1	313	large terns group (TERN)
Greater crested tern	*Thalasseus bergii*	1	14	large terns group (TERN)
Royal tern	*Thalasseus maximus*	1	253	large terns group (TERN)

Tracking data processing

Tracking datasets were speed filtered (removal of points > 90 km/h; (Mendez et al. 2017), and linearly interpolated using the *AdehabitatLT* (0.3.24) R package (Calenge 2011). Due to differences in temporal resolution of different datasets we interpolated each dataset to either 1, 2, 3, 5, 10, 15, or 20 minute resolutions. We split individual foraging trips from multi-day tracks using the *track2kba* (1.0.0) R package (Beal et al. 2021), removing small foraging trips within 4 km of the colony and under 1 hr in duration. We also manually removed trips that spent too much time away from the colony, indicating breeding failure. Upper trip duration limits were set at five days for boobies (Mendez et al. 2017), 12 days for frigatebirds (Mott et al. 2016) and tropicbirds, 14 days for wedge-tailed shearwater long trips (McDuie et al. 2015) and sooty terns (Neumann et al. 2018), three days for wedge-tailed shearwater short trips (Weimerskirch et al. 2020) and two days for noddies and terns (from inspection of data).

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Foraging radii

We estimated radii and mapped foraging circles for each modelled species to predict likely foraging range around untracked colonies (Birdlife International 2010; Thaxter et al. 2012). We first obtained the maximum distance from the colony observed across all the foraging trips made by birds from each tracked colony. We then took the average of these colony-specific maximum distances to generate a 'mean maximum foraging radius' for each modelled species (Thaxter et al. 2012). To provide lower and upper extremes for each modelled species, we also present the minimum and maximum of colony-specific maximum distances observed.

Ecological niche modelling

To model the foraging niche of each modelled species, we assumed a binomial response comparing the oceanographic covariates of known foraging areas (1) against the oceanographic covariates of accessible habitat (0). To identify known foraging areas for each dataset we performed location-based kernel density analyses with a 1 km grid on a subset of tracking datapoints identified as representing foraging behaviour (Miller et al. 2017; see supporting information for further details), and treated all grid points within the 50% utilization distribution (UD) as 'presence' points in the model. The accessible habitat for each colony was defined as the convex hull containing all tracking locations (all behaviours included) and curtailed to marine regions. Areas inside convex hulls were sampled using pseudo-absence datapoints distributed randomly but weighted by inverse distance to the colony (to constrain access to foraging habitat by central-place foraging seabirds). Pseudo-absences were created at a rate of 3:1 to presences (Wakefield et al. 2011) and given the same timestamp as their respective presences for dynamic covariate extraction. To account for the potential influence of random sampling of pseudo-absences on model stability (Barbet-Massin et al. 2012), we repeated the random selection of pseudo-absences five times, generating five replicate presence and pseudo-absence datasets per original dataset. Each of the five replicates was modelled separately and then averaged together for model validation and prediction.

Although tropical seabird prey opportunities are patchily distributed and ephemeral in nature (Weimerskirch 2007), their location and availability are governed by physical ocean processes at broader spatial scales (10-100kms; Wakefield et al. 2009). Ocean covariates for modelling were created to capture broad-scale ocean features representing attractive and/or reliable locations for tropical seabird foraging (Table 2). For dynamic covariates, chlorophyll concentration, sea surface temperature and frontal activity, we created a long-term (~10 year) mean for each month of the year to model whether birds target specific covariate values, and also created the long-term standard deviation over 12 months of the year to describe whether birds target areas that are temporally dynamic/homogenous. The month in which each tracking dataset commenced was used to select the monthly dynamic covariate layer to extract values from. The use of long-term averages in models means that the oceanographic conditions fitted against known foraging areas of tracked birds do not reflect the concurrent oceanography. Rather, they characterise persistent oceanographic features in the seascape. The advantage of this approach is that a global layer for each oceanographic variable can be created, meaning subsequent predictions of seabird foraging at each colony are all built on the same, standardised, comparable oceanography. This is particularly important for assessing model transferability between colonies. Models also included static covariates of bathymetry and seabed slope to allow them to describe the importance of geographical features such as reefs, shelves and seamounts for foraging. Following the seabird foraging niche transferability study of Péron et al. (2018), we did not include a distance-to-colony variable because it is explicitly linked to colony-specific demographic information, such as population size (Lewis et al. 2001), which we lacked for training and test colonies. All data handling and statistical analyses were performed in the statistical software environment R version 3.5.1 (R Core Team 2020). For more detail on tracking and oceanographic data processing see supporting information.

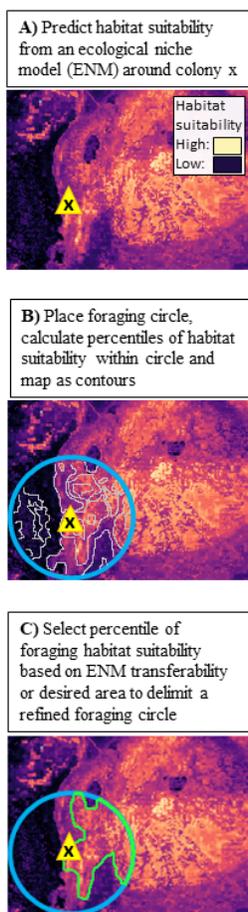Table 2 Oceanographic data sourced for modelling.

Covariate (units)	Temporal resolution	Spatial resolution	Data source (provider)
Log chlorophyll-a concentration (mg C m^{-3})	Monthly mean 2000-2019	4.4 km	MODIS-Terra (https://oceancolor.gsfc.nasa.gov)
Sea surface temperature (°C)	Monthly mean 2000-2019	4.4 km	MODIS-Terra (https://oceancolor.gsfc.nasa.gov)
Front persistence (probability of front at pixel 0-1)	Monthly mean 2006-2016	5.5 km	SST-CCI v2.1 daily SST (https://climate.esa.int/; Miller 2009)
Mean front strength (°C pixel^{-1})	Monthly mean 2006-2016	5.5 km	SST-CCI v2.1 daily SST (https://climate.esa.int/; Miller 2009)
Seasonal chlorophyll-a concentration variability (mg m^{-3})	Std Dev. across 12 months (2000-2019)	4.4 km	MODIS-Terra (https://oceancolor.gsfc.nasa.gov)
Seasonal sea surface temperature variability (°C)	Std Dev. across 12 months (2000-2019)	4.4 km	MODIS-Terra (https://oceancolor.gsfc.nasa.gov)
Seasonal front persistence variability ([?] monthly front probability 0-1)	Std Dev. across 12 months (2006-2016)	5.5 km	SST-CCI v2.1 daily SST (https://climate.esa.int/; Miller 2009)
Seasonal mean front strength variability (°C pixel^{-1})	Std Dev. across 12 months (2006-2016)	5.5 km	SST-CCI v2.1 daily SST (https://climate.esa.int/; Miller 2009)
Bathymetry (m)	Static	0.46 km	GEBCO (www.gebco.net)
Seabed slope angle (°)	Static	0.46 km	Derived from GEBCO (www.gebco.net)

We used random forests to model seabird foraging niches, parameterising each model with the 10 oceanographic variables shown in Table 2. Random forests are robust to both challenges present in spatial data (e.g. autocorrelation) and in hierarchically structured data (e.g. global trends but local variation) (Evans et al. 2011, Doherty et al. 2016). We used two approaches for each modelled species: 1) a multi-colony model, where datasets from multiple colonies were combined in a single model; and 2) colony-specific models, where each colony was modelled separately. The multi-colony model was designed to learn from the foraging niches of each colony and generalise a global foraging niche to predict foraging habitat suitability. Colony-specific models were designed to test the ability of local foraging niche to predict local foraging habitat suitability, investigate local adaptation across species ranges, and to make accurate models with GBR tracking where available (Fig. 2).

To assess model predictive performance, we used the threshold-independent measure, area under the receiver operating characteristic curve (AUC; Fielding & Bell 1997). AUC values of 0.5 are equivalent to random prediction, 0.6-0.7 indicate poor performance, 0.7-0.8 moderate performance, and >0.8 indicate good performance. We validated models by assessing performance (AUC) when predicting to different colonies, which we use as our measure of model transferability. For multi-colony models, we used leave-group-out cross validation: iterating through n colonies, we trained the model on n -1 colonies and predicted to the remaining colony. For colony-specific models we predicted to all other colonies. For both model types, we calculated global transferability (mean predictive performance across all other colonies). To assess internal model performance (colony-specific models predicting to their training colony) we performed internal spatial cross validation. We used the 4-fold clock method, where each dataset was split spatially into quarters (by k-means clustering of data coordinates), and models iteratively trained on three quarters of the data with predictive performance assessed on the remaining quarter (Guillaumot et al. 2019).

For both multi-colony and colony-specific random forest models, hyperparameters were tuned to optimise predictive performance between colonies. Model parameters, mtry (number of environmental covariates randomly chosen per node: limits tree strength and correlation) and minimum node size (number of datapoints per tree node: limits tree depth and thus model complexity) were tuned across values 2, 3, 4, 5, 6 and 5, 10, 20, 50, respectively. Models were firstly tuned for optimal predictive performance on GBR test data (for available species), and secondarily to generalise across all other colonies. When assessing model predictive performance locally, the same hyperparameters were tuned to optimise predictive performance on the training colony during internal spatial cross validation. Random forest models were constructed using the *ranger* (0.11.2) R package (Wright & Ziegler 2017) and tuned using the *caret* (6.0-82) R package (Kuhn 2008).

To investigate local adaptation in each modelled species we first described inter-colony transferability by summing the two colony-specific model AUC values of each colony pair ($\text{AUC}_{\text{colonyA - colonyB}}$ + $\text{AUC}_{\text{colonyB - colonyA}}$), before entering pairwise colony sums into a distance matrix. We then tested whether geographically closer colonies were more transferable by correlating the inter-colony transferability matrix with a matrix of pairwise colony geographical distance, and whether colonies with more similar oceanographic habitat were more transferable by correlating the colony transferability matrix with a matrix of pairwise colony oceanographic distance (matrix of Euclidean distances between colonies from mean oceanographic variable values within their accessible habitat). We tested significance of correlations with Mantel tests. To help visualise groups of colonies that were transferable to each other we performed hierarchical clustering (using the average method) on the inter-colony transferability matrix.

A) Predict habitat suitability from an ecological niche model (ENM) around colony x

B) Place foraging circle, calculate percentiles of habitat suitability within circle and map as contours

C) Select percentile of foraging habitat suitability based on ENM transferability or desired area to delimit a refined foraging circle

Term	Definition
Modelled species	Modelling units in this study, representing either individual species or groups of species.
Known foraging area	The foraging area(s) identified in each tracking dataset using the 50% UD from kernel analyses.
Colony-specific model	A random forest ENM predicting habitat suitability trained on the foraging niche of a single colony.
Multi-colony model	A random forest ENM predicting habitat suitability trained on multiple colonies to generalise a 'global' foraging niche.
Transferability Local transferability Inter-colony transferability Global transferability	The ability of a random forest ENM to predict suitable habitat outside the training region, as measured by AUC. We differentiate between: • local transferability, the ability of colony-specific models to predict their own foraging niche via clock spatial cross validation or multi-colony global foraging niche to predict that of an individual colony (via leave group out cross validation); • inter-colony transferability, the ability of colony-specific models to predict the foraging niche of another colony; • global transferability, the average ability of models to predict foraging niche at multiple other colonies.
Colony foraging radius **Colony foraging circle**	The maximum distance from the colony of origin observed in a breeding seabird population. Termed 'radius' when referring to the distance and 'circle' when mapped.
Global foraging radius **Global foraging circle**	Mean-maximum distance from colony: the average of colony-specific maximum distances from multiple colonies. Termed 'radius' when referring to the distance and 'circle' when mapped.
Refinement Transferability-supported refinement Area-limited refinement	Reducing the area of a foraging circle by excluding areas of unsuitable habitat to produce a refined foraging circle. The amount of unsuitable habitat excluded (percentile selected) can be: • transferability-supported, which uses ENM transferability to balance refined foraging circle size with refinement confidence; • area-limited, where refined foraging circle size is specified by the user.
Refinement confidence	Probability that a refined foraging circle includes known foraging areas (50% UD).
Refined foraging circle	Remaining area of a foraging circle after unsuitable habitat has been excluded. Refined foraging circles are attributed with refinement confidence, and can be seen as candidate MPAs for their respective seabird colony.

Fig. 2 Schematic of analytical framework and study glossary. Steps A-C show how a refined foraging circle (green) can be predicted for a seabird colony (yellow triangle). If tracking data originates from the colony then this is used to train a colony-specific model to predict habitat suitability and to inform a colony foraging circle; if not, habitat suitability is predicted by a multi-colony model and a global foraging circle is applied. Methods of refinement apply to both colony foraging circles and global foraging circles.

A framework integrating the foraging radius approach with ecological niche models

We integrated models of seabird foraging niche with the foraging radius approach by excluding predicted unsuitable foraging habitat within foraging radius circles to produce "refined foraging circles". Taking a precautionary approach to minimise erroneously excluding good foraging habitat from within foraging circles, we specified that the area of unsuitable foraging habitat excluded within circles was dependent upon ENM transferability, which we term "transferability-supported refinement". This allowed greater foraging circle refinement with more transferable models. The first step of our framework is to predict foraging habitat suitability and clip it to within the foraging circle of a colony of interest, limiting the foraging habitat available to the population. This allows us to derive percentiles of habitat suitability within the foraging circle which are mapped as contours. The second step scales ENM transferability values onto the percentiles of predicted foraging habitat suitability, delineating a refined foraging circle from habitat suitability values equal or above to the selected percentile. We scale transferability to percentiles ((AUC-0.5)/(0.9-0.5))*(0.9-0), such that AUC [?] 0.5 (prediction no better than random) takes the 0th percentile of foraging habitat suitability values, thus defaulting to the unrefined foraging circle. Higher AUC values take higher percentiles up until AUC [?] 0.9, which is set to an upper limit of the 90th percentile (a threshold proposed for translating seabird ENM predictions into marine Important Bird Areas by Dias et al. (2019b), thus allowing models with excellent transferability (AUC [?] 0.9) to delineate refined foraging circles with the top 10% of foraging habitat suitability values.

Transferability-supported refinement simply offers a suggested percentile of habitat suitability with which to refine foraging circles, but planners may wish to select a different percentile to create a smaller or larger refined foraging circle. We term this "area-limited refinement" and anticipate that it may be necessary to use when transferability-supported refinement produces refined foraging circles that are still considered too large for area-based management.

Framework validation and attributing refinement confidence

To validate our framework, we simulated increasing foraging circle refinement at each colony in our global tracking dataset to estimate "refinement confidence": the probability of known foraging areas (50% UDs) being included in refined foraging circles. The results allowed us to estimate how well unrefined global foraging circles capture known foraging areas and model the rate this inclusion declines when refining for different transferability ENMs. For each modelled species and colony (Table 1), we predicted foraging habitat suitability using the corresponding multi-colony model, trained on all colonies except the colony being predicted to. We predicted models to each colony using the same oceanographic variables and same month used in model training, assessed transferability using the multi-colony leave group out cross validation AUC value, and mapped foraging habitat suitability predictions onto a raster with two km cell size. At each colony, we refined the global foraging circle using the percentile selected by the model transferability AUC value, and also simulated refinement increasing from the 0th percentile (unrefined foraging circle) to the 90th percentile at five percentile intervals. Refined foraging circle polygons were obtained by binarizing foraging habitat suitability rasters with the specified percentile value, and tidied with R package *smoothr* (0.1.1) (Strimas-Mackey 2021) to remove small 'crumbs' and holes in polygons. In each iteration, we calculated the percentage of known foraging areas tracked from the colony that were included in the refined foraging circle. We fitted logistic regression models with percentage of known foraging area inclusion as the response variable and foraging habitat suitability percentile and its interaction with model transferability as explanatory

variables, allowing the slope to vary within a species-colony random effect. Logistic regression models were fitted for each modelled species separately, and all combined, using R package *lme4* (1.1-21) (Bates et al. 2015); random effects were dropped from TERN and SOTE regression models due to too few colonies.

The intercept and slopes of logistic regression models allowed refinement confidence to be predicted given model transferability and the percentile of habitat suitability selected for refined foraging circle delineation. This firstly allowed us to validate whether the AUC-percentile scaling was appropriate, under transferability-supported refinement we would expect to see high refinement confidence for all refined foraging circles, regardless of transferability (poor models refine a little, excellent models refine a lot; all retain known foraging areas). Secondly, logistic regression model coefficients allowed us to explore the trade-off between refined foraging circle size and refinement confidence as coefficients predict refinement confidence for any given size of refined foraging circle. When refining a foraging circle for species x at untracked colony y, its' size can be suggested from transferability-supported refinement (using the multi-colony global transferability value) or specified by area-limited refinement. Having the associated refinement confidence predicted from logistic regression model coefficients for refined foraging circles of different sizes allowed us to judge the amount of refinement most appropriate during our Great Barrier Reef case study.

Foraging circle refinement on the Great Barrier Reef

To demonstrate the application of our framework, we refine foraging circles for the breeding seabird community of the Great Barrier Reef. From these we identify three networks of candidate MPAs (unrefined foraging circles, transferability-supported refined foraging circles, and area-limited refined foraging circles) to demonstrate the trade-off between total area and refinement confidence. For species without tracking data on the GBR, we predicted habitat suitability using multi-colony models. The remaining species had tracking data from one or two breeding sites on the GBR (Fig. 1). For these species, habitat suitability was predicted by colony-specific models to corresponding tracked colonies and neighbouring colonies within the same designated breeding site (see supporting information), and multi-colony models to the remaining area. We predicted models upon annual averages of monthly dynamic oceanographic variables, as the modelled species breed year-round across the GBR (but most show seasonal breeding peaks), with the exception of wedge-tailed shearwaters for which oceanographic variables were averaged over their distinct breeding season (December-April). Predictions were mapped across the GBR and Coral Sea using a raster with two km cell size. We placed foraging circles around breeding sites from significant seabird areas on the GBR. Significant seabird areas were either designated as internationally-recognised Key Biodiversity Areas (KBAs) or possessed regionally significant breeding populations of one or more species (see supporting information). For the seabird species listed at each breeding site we applied the corresponding global foraging circle, unless the breeding site was part of a significant seabird area with a tracked colony, in which case the colony foraging circle was applied.

Following our framework, we conducted transferability-supported refinement of global foraging circles using multi-colony model inter-colony transferability values and colony foraging circles using colony-specific model local transferability values. To investigate the effect of further refinement, we conducted area-limited refinement on any refined foraging circle produced by transferability-supported refinement that was over 100,000 km^2, until all refined foraging circles fell below 100,000 km^2(representing a maximum layer size in a hypothetical conservation planning exercise). The refinement confidence in colony-specific models was obtained using the inclusion of known foraging areas (50% UD) from tracked GBR breeding sites within refined foraging circles while the refinement confidence in multi-colony models was determined using the logistic regression model coefficients from our global framework validation exercise. To compare differences between different refinement approaches, we created three networks of candidate MPAs from unrefined foraging circles, transferability-supported foraging circle refinement, and area-limited foraging circle refinement (<100,000 km^2). We summarised differences between networks by comparing the total foraging area required for the GBR breeding community, dissolving overlapping refined foraging circles shared by multiple breeding sites, and by comparing refinement confidence under each approach. Finally, we selected the most appropriate

refinement approach for each species and merged results to create the most suitable network of candidate MPAs for seabirds on the GBR.

Results

Foraging niche transferability

Multi-colony models were not able to successfully generalise the foraging niche of modelled species across all colonies, showing generally poor global transferability (mean AUC: 0.56, range 0.4-0.82; Table 3). However, leave-group-out cross validation showed that multi-colony models could predict suitable foraging habitat at some individual colonies (Fig 3).

Exploration of inter-colony transferability revealed that colony-specific models were transferable to one, or sometimes several, other colonies, but not all colonies (Fig. 3). For many modelled species this issue manifested as clustering in colony transferability: groups of colonies that could predict to one another, but poorly to other groups of colonies (Fig. 3-J), and partially explains low global transferability of colony-specific models (Table 3). Inter-colony transferability was not explained by geographical distance or oceanographic similarity between colonies (19 of 20 Mantel tests p > 0.05; supporting information). However, with the exception of noddies, all multi-colony models had slightly better global transferability than the colony-specific model average (Table 3), indicating multi-colony models generalised information from disparate colony clusters, boosting transferability.
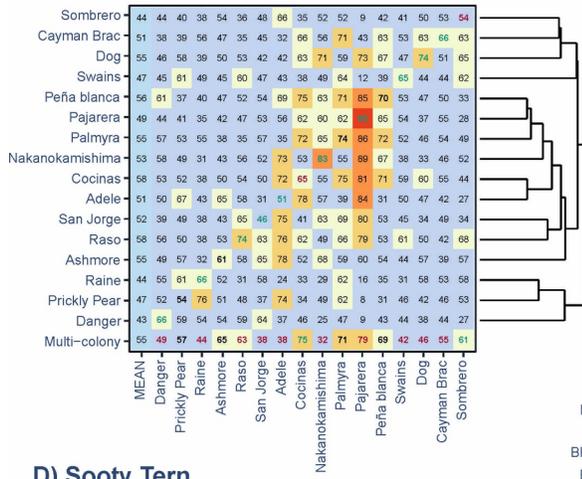
We found that multi-colony models frequently (species mean: 41%; Table 3) matched or outperformed colony-specific models at local prediction (multi-colony leave-group-out cross validation vs colony-specific spatial cross validation; multi-colony row values vs diagonal values in Fig. 3). This finding indicates that the global foraging niche was able to predict suitable foraging habitat at approximately 40% of colonies, with comparable or better accuracy than models of the local foraging niche, although this was strongly species dependent (0% for noddies, 66% for frigatebirds and terns; Table 3). However, all of the colony-specific models from GBR tracking were superior to their multi-colony model equivalent (brown booby from Raine Island and Swain Reefs, Fig. 3A; masked booby from Swain Reefs, Fig. 3E; wedge-tailed shearwaters from Heron Island on short trips, Fig. 3I and long trips, Fig. 3G; and noddies from Heron Island, Fig. 3C).

Despite poor overall global transferability, we observed differences between modelled species (Table 3). Booby species had similar multi-colony global transferability (AUC: 0.53-0.55) and showed clustering of inter-colony predictive performance (Fig. 3A, E, F). Brown and masked booby colony-specific models had a greater range of transferability than red-footed booby but the same overall average (AUC: 0.51). Frigatebirds and wedge-tailed shearwater short trip multi-colony models (AUC: 0.61 and 0.58, respectively) showed better global transferability than boobies, and the greatest transferability increase over the colony-specific model average. Both of these modelled species showed clustering of inter-colony predictive performance, the former demonstrating examples of good inter-species and inter-colony transferability (Fig. 3G, I). Tropicbirds and wedge-tailed shearwater long trip multi-colony models had poor global transferability, equivalent to that of boobies (AUC: 0.56 and 0.54 respectively). Sooty terns and noddies showed the poorest global transferability (AUC: 0.48 and 0.40 respectively), with the latter's multi-colony model being outperformed by the colony-specific model average. Terns showed the best global transferability between colonies (AUC: 0.82) but were limited by sample size (Fig. 3B).

Table 3 Summary of model transferability and foraging radii. Global transferability is the predictive performance of a model averaged over all colonies (MEAN column; Fig. 3). Local prediction gives the percentage of colonies where the multi-colony model matched or outperformed self-prediction by the colony-specific model. Foraging ranges are summarised across tracked colonies (for colony breakdown see supporting information), and inclusion of known foraging areas in global foraging circles are averaged across all tracked colonies.

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Modelled species (n training colonies)	Colony-specific global transferability (mean AUC ± sd)	Multi-colony model global transferability (AUC)	Local prediction (% of colonies where multi-colony AUC [?] colony-specific AUC)	Global minimum foraging radius (km)	Global maximum foraging radius (km)	Global (mean-maximum) foraging radius (km ± sd)	Probability of known foraging area (±95 CI) inside global foraging circle
BRBO (16)	0.51±0.05	0.55	25%	45.3	190.3	111 ± 35	0.99 (0.98,1)
MABO (12)	0.51±0.06	0.53	8%	68.8	290.6	171 ± 65	0.99 (0.97,1)
RFBO (13)	0.51±0.02	0.54	54%	96.9	473.1	273 ± 125	0.99 (0.97,1)
FRBD (9)	0.53±0.06	0.61	66%	28.4	1081.6	556 ± 435	1 (0.98,1)
TRBD (11)	0.52±0.05	0.56	54%	344.3	801.5	531 ± 174	0.99 (0.96,1)
WTST (8)	0.53±0.06	0.58	62%	185.5	298.2	254 ± 42	0.98 (0.96,0.99)
WTLG (7)	0.52±0.03	0.54	43%	509.3	1166.2	755 ± 286	0.99 (0.93,1)
SOTE (3)	0.41±0.07	0.48	33%	198.4	895.3	535 ± 349	0.89 (0.76,0.95)
NODD (5)	0.49±0.05	0.40	0%	54.8	269.1	144 ± 78	0.98 (0.87,1)
TERN (3)	0.76±0.01	0.82	66%	38.6	159.7	109 ± 63	0.98 (0.98,0.99)

A) Brown Booby

	MEAN	Danger	Prickly Pear	Raine	Ashmore	Raso	San Jorge	Adele	Cocinas	Nakanokamishima	Palmyra	Pajarera	Peña blanca	Swains	Dog	Cayman Brac	Sombrero
Sombrero	44	44	40	38	54	36	48	66	35	52	52	9	42	41	50	53	54
Cayman Brac	51	38	39	56	47	35	45	32	66	56	71	43	63	53	63	66	63
Dog	55	46	58	39	50	53	42	42	63	71	59	73	67	47	74	51	65
Swains	47	45	61	49	45	60	47	43	38	49	64	12	39	65	44	44	62
Peña blanca	56	61	37	40	47	52	54	69	75	63	71	85	70	53	49	50	33
Pajarera	49	44	41	35	42	47	53	56	62	60	62		65	54	37	55	28
Palmyra	55	57	53	55	38	35	57	35	72	65	74	86	72	52	46	54	49
Nakanokamishima	53	58	49	31	43	56	52	73	63	83	55	89	67	38	33	46	52
Cocinas	58	53	52	38	50	54	50	72	65	55	75	81	71	59	60	55	44
Adele	51	50	67	43	65	63	31	51	78	57	39	84	31	50	47	42	27
San Jorge	52	39	49	38	43	65	46	75	41	63	69	80	53	45	34	49	34
Raso	58	56	50	38	53	74	63	76	62	49	66	79	53	61	50	42	68
Ashmore	55	49	57	32	61	58	65	78	52	68	59	60	54	44	57	39	57
Raine	44	55	61	66	52	31	58	24	33	29	62	16	35	31	58	53	58
Prickly Pear	47	52	54	76	51	48	37	74	34	49	62	8	31	46	42	46	53
Danger	43	66	59	54	54	59	64	37	46	25	47	9	43	44	38	44	27
Multi-colony	55	49	57	44	65	63	38	75	32	71	79	69	42	46	55	61	

B) Terns

	MEAN	CRTE Troubridge	CATE Senegal	ROTE Senegal
ROTE Senegal	78	65	91	66
CATE Senegal	75	58	82	92
CRTE Troubridge	76	75	75	76
Multi-colony	82	62		

C) Noddies

	MEAN	BRNO Dry Tortugas	BRNO Lancelin	BRNO St Helena	BLNO Heron	LENO Pelsaert
LENO Pelsaert	53	38	45	46	85	70
BLNO Heron	42	30	45	46	66	48
BRNO St Helena	46	43	46	49	46	49
BRNO Lancelin	55	74	74	45	64	37
BRNO Dry Tortugas	49	86	59	50	34	54
Multi-colony	40	35	47	45	34	40

D) Sooty Tern

	MEAN	Rat	Dog	Seychelles
Seychelles	46	48	44	65
Dog	44	34	63	54
Rat	32	54	39	26
Multi-colony	48	56	44	45

E) Masked Booby

	MEAN	Muertos	Palmyra	Swains	Clarion	Dog	Phillip	Ashmore	Tern	Adele	St Helena	Lord Howe	Sombrero
Sombrero	55	70	48	40	32	51	76	55	50	61	56	68	79
Lord Howe	57	51	42	62	53	52	74	60	43	67	53	42	68
St Helena	54	26	46	63	52	56	60	54	51	59	65	67	59
Adele	49	51	35	40	62	50	38	54	55	90	56	64	40
Tern	48	29	38	44	55	68	57	57	74	27	47	32	71
Ashmore	55	45	32	59	50	70	65	62	74	60	53	43	51
Phillip	48	31	50	59	55	77	79	51	29	18	60	31	64
Dog	58	25	72	50	57	66	80	62	72	48	56	49	64
Clarion	58	31	43	55	56	79	86	66	70	34	53	56	62
Swains	53	27	65	64	47	67	47	58	54	47	49	52	70
Palmyra	44	53	62	53	54	54	18	41	50	41	49	49	31
Muertos	37	56	41	49	43	27	21	43	30	13	58	42	24
Multi-colony	53	22	72	40	52	64	73	57	57	34	47	60	54	68

F) Red-footed Booby

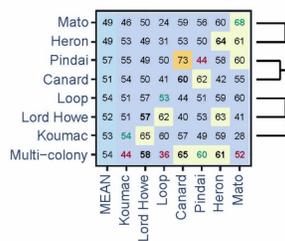|	MEAN	Chesterfield	Tern	Palmyra	Tromelin	Danger	Europa	Little Cayman	Ashmore	Genovesa	Surprise	Walpole
Walpole	50	45	41	49	61	49	52	48	43	38	72	53
Surprise	45	52	46	31	24	36	49	39	61	51	63	
Genovesa	51	60	46	58	57	42	50	50	36	50	66	45
Ashmore	50	48	44	56	40	38	52	48	76	66	57	46
Little Cayman	51	64	52	70	65	75	47	38	50	33	32	
Europa	51	42	54	76	36	55	57	52	45	49	47	
Danger	55	55	42	64	53	54	65	55	62	51	55	47
Tromelin	50	49	51	45	57	61	58	50	45	40	36	46
Palmyra	51	33	54	58	42	49	48	45	43	45	71	
Tern	52	51	55	46	66	55	55	53	49	55	41	54
Chesterfield	52	61	61	64	64	58	44	45	47	45	50	47
Multi-colony	54	46	46	75	60	61	47	54	45	57	46	57

Fig. 3 Model validation and transferability for modelled species (A-J). Matrix values describe predictive accuracy via area under the receiver operator characteristic curve (AUC); AUC values (0-1) have been multiplied by 100 to save space. Reading by row shows how well each model trained on colony-specific data predicts foraging habitat suitability at all other colonies, reading by column shows how well foraging habitat suitability at each colony is predicted by models trained with data from all other colonies. Row names denote each colony-specific model and the multi-colony model. The 'MEAN' column gives global transferability of each colony-specific model and the multi-colony model by averaging the predictive ability across all colonies in the row (excluding the self-prediction value in colony-specific models). Local prediction is compared between colony-specific model self-prediction (diagonals) and multi-colony models (bottom row) by colour of AUC value: green shows model is better than the other; red shows model is worse than the other; black shows models are comparable (AUC values within 0.05 of each other). AUC value background colour denotes performance: grey (no better than chance/very poor); yellow (poor); light orange (moderate); dark orange (good); red (excellent). Dendrograms show clustering of pairwise colony AUC values; closely clustered colonies predict one another better. Family group models (B, C & G) have species codes added to colony names: CRTE = crested tern, CATE = caspian tern, ROTE = royal tern, LENO = lesser noddy, BLNO = black noddy, BRNO = brown noddy, GRFR = great frigatebird, LEFR = lesser frigatebird, MAFR = magnificent frigatebird. All colonies in the family group model for tropicbirds (H) represent red-billed tropicbird, with the exception of the Ashmore Reef (Australia) colony, which is red-tailed tropicbird (denoted with *).

Tropical seabird foraging radii

When considering all species and colonies, foraging radii ranged from 28.4 to 1166.2 km (Table 3). By increasing foraging range, modelled species were generally ordered: terns, brown booby, noddies, masked booby, wedge-tailed shearwater short trip, red-footed booby, tropicbirds, sooty tern, frigatebirds, wedge-tailed shearwater long trip. We found that the global foraging circle for each species contained a high percentage (89-100%) of known foraging areas from each tracked colony (Table 3).

Validating foraging circle refinement

We found an average of 89% of known foraging areas were included within refined foraging circles when using transferability-supported refinement of global foraging circles around each colony from our tracking dataset (Fig. 4). Our AUC-percentile scaling was effective at limiting the exclusion of erroneously predicted foraging habitat in poorer transferability models giving 80-99% known foraging area inclusion when the 45th percentile of habitat suitability or below, was used to delimit refined foraging circles. For refined foraging circles delimited with habitat suitability above the 45th percentile, our scaling maintained known foraging area inclusion at ~80%, showing that greater foraging circle refinement was effectively offset by the more accurate prediction of foraging habitat by higher transferability models.

Simulating increasing refinement of global foraging circles around each colony from our tracking dataset demonstrated that in the absence of transferability-supported refinement, refined foraging circles delimited by less transferable models always had a lower probability of including known foraging areas than those delimited by more transferable models (Interaction between percentile of foraging habitat suitability and model transferability: $\chi^2_1 = 100.1$, p < 0.001; Fig. 4). Simulation results for individual modelled species demonstrated the same pattern but there were differences between species due to ecology and sampling effort (Table 4, visualised in supporting information). Inclusion of known foraging areas in global foraging circles set the baseline probability for inclusion prior to refinement and differed between species (e.g. high in frigatebirds, low in sooty terns – despite similar foraging ranges; Tables 3 & 4). The steepest declines in known foraging area inclusion with foraging circle refinement were seen in masked and brown boobies and tropicbirds, whereas terns retained the highest inclusion of known foraging areas under refinement because their multi-colony model had good global transferability. Improving model transferability gave the greatest boost to inclusion of known foraging areas within refined foraging circles in tropicbirds, brown booby, sooty tern and masked booby, whereas frigatebirds known foraging area inclusion was least affected by model transferability (Table 4). The noddies model did not include the interaction term with transferability as all multi-colony model predictions were below 0.5 AUC.
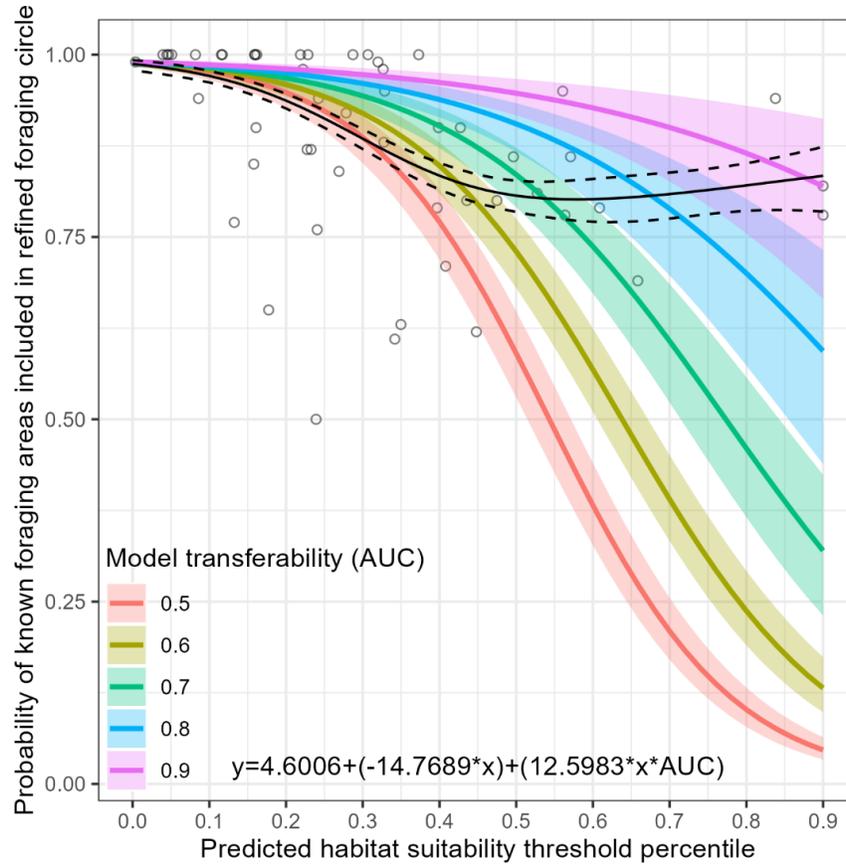
Fig. 4 Probability of known foraging area inclusion within refined foraging circles refined by multi-colony models with different transferability (AUC). Coloured lines (± 95% CI) represent the interaction between inclusion of known foraging areas in refined foraging circles, when simulating refinement over all possible percentiles of predicted foraging habitat suitability, and multi-colony model transferability (five transferability values selected for demonstration; regression equation provided to predict on log odds scale). Black rings show the known foraging area inclusion observed at tracked colonies when refined foraging circles were refined using the percentile of habitat suitability selected by transferability-supported refinement. The black line (± 95% CI) displays the trend through these rings (from a generalised additive model), showing overall high known foraging area inclusion and effective offset of greater refinement by more accurate models.

Table 4. Species-specific logistic regression model coefficients for predicting probability of known foraging area inclusion within refined foraging circles. Intercepts give the probability of known foraging area inclusion within unrefined global foraging circles. Coefficients are presented on the log odds scale and can predict probability of known foraging area inclusion for a desired percentile of habitat suitability value (p) from a multi-colony model with transferability (t) using the equation: $\exp(\beta_0+(\beta_1{*}p)+(\beta_2{*}p{*}t))/(1+\exp(\beta_0+(\beta_1{*}p)+(\beta_2{*}p{*}t)))$. For example, the probability of masked booby (MABO) known foraging areas being included in a refined foraging circle refined with the 30th percentile (0.3) of foraging habitat suitability and predicted from a poor transferability model (e.g. AUC=0.64) is: $\exp(4.39+(-15.42{*}0.3)+(13.1{*}0.3{*}0.64))/(1+\exp(4.39+(-15.42{*}0.3)+(13.1{*}0.3{*}0.64)))= 90\%$.

Species	β_0 Intercept	β_1 foraging habitat suitability percentile	β_2 interaction between foraging habitat suitability perc
BRBO	4.84±0.45	-18.83±2.02	18.44±3.28
MABO	4.39±0.54	-15.42±1.84	13.1±3.04

Species	β_0 Intercept	β_1 foraging habitat suitability percentile	β_2 interaction between foraging habitat suitability perc
RFBO	4.58±0.57	-11.58±2.21	8.23±3.84
FRBD	6.4±1.37	-11.13±2.98	4.51±3.48
TRBD	4.8±0.8	-19.96±1.88	21.4±2.71
WTST	3.97±0.43	-11.28±2.47	7.58±4.08
WTLG	4.22±0.8	-12.49±1.68	8.64±1.76
SOTE	2.09±0.47	-12.18±4.13	16.9±8.02
NODD	3.76±0.95	-9.38±1.42	NA
TERN	4.12±0.18	-9.18±0.57	7±0.65

Total foraging area of the Great Barrier Reef breeding seabird community

The total foraging area of the Great Barrier Reef breeding seabird community was estimated at 2,941,000 km^2 by global foraging circles, of which 197,000 km^2 was predicted unsuitable foraging habitat and excluded following transferability-supported refinement (Table 5). There were large differences in the total area of unsuitable habitat excluded from foraging circles between species due to radius size (Table 3), proximity of GBR colonies (overlap of foraging circles; Fig. 5a) and model transferability (Fig. 5b). We saw the greatest refinement in species with large foraging radii (e.g. wedge-tailed shearwater long trips, frigatebirds, tropicbirds) and species which had better model transferability (e.g. terns, Fig. 5b). The better local prediction of GBR colony-specific models over multi-colony models afforded locally tracked species greater transferability-supported refinement (Fig. 5). This led to greater total unsuitable habitat exclusion when locally tracked sites were well represented and transferability was higher (e.g. wedge-tailed shearwater short trips compared to brown booby and masked booby; Fig 5; Table 5). By contrast, noddies had the highest number of breeding colonies but unsuitable foraging habitat could only be excluded at one site with local tracking because their multi-colony model transferability was too poor (AUC<0.5) for foraging circle refinement. Sooty terns were the only species for which we were unable to use transferability-supported refinement for any foraging circles due to their poor multi-colony model transferability and absence of GBR tracking data. Refined foraging circles on the GBR produced through transferability-refined refinement had high refinement confidence, with a 96% average probability of including known foraging areas (Table 5). This was higher than the 89% average from our global validation exercise (Fig. 4) due to the contribution of locally tracked GBR colonies, which all had 100% inclusion of known foraging areas in refined foraging circles.

After transferability-supported refinement had been completed, six modelled species still contained some colonies with refined foraging circles that exceeded 100,000 km^2 (Fig. 5b). Using area-limited refinement to drop these refined foraging circles below 100,000 km^2 excluded a further 1,629,000 km^2 of predicted unsuitable foraging habitat from the community (Table 5). However, this came at a cost of reducing refinement confidence, with the average inclusion of known foraging areas in refined foraging circles dropping from 97% to 55% in these species. Sooty tern, tropicbirds and frigatebirds all required large area-limited refinement to meet the 100,000 km^2 limit, greatly reducing their refinement confidence (16-40% inclusion; Table 5). Wedge-tailed shearwater long trips required the greatest refinement to meet the area limit and highlighted the power of tracking data from the GBR; refined foraging circles delineated by the 90th percentile of habitat suitability dropped predicted inclusion of known foraging areas to 6% in multi-colony models but only to 87% in colony-specific models (Table 5). Area-limited refinement of wedge-tailed shearwater short trips and red-footed booby foraging circles to meet the 100,000 km^2 limit was achieved with minor reduction in known foraging area inclusion (77-95%). Applying the most appropriate foraging circle refinement approach to each modelled species (none for sooty tern, area-limited for wedge-tailed shearwater and red-footed booby, and transferability-supported for the remainder) created a network of refined foraging circles for the breeding seabird community of the GBR that balanced size against refinement confidence (Fig. 6).
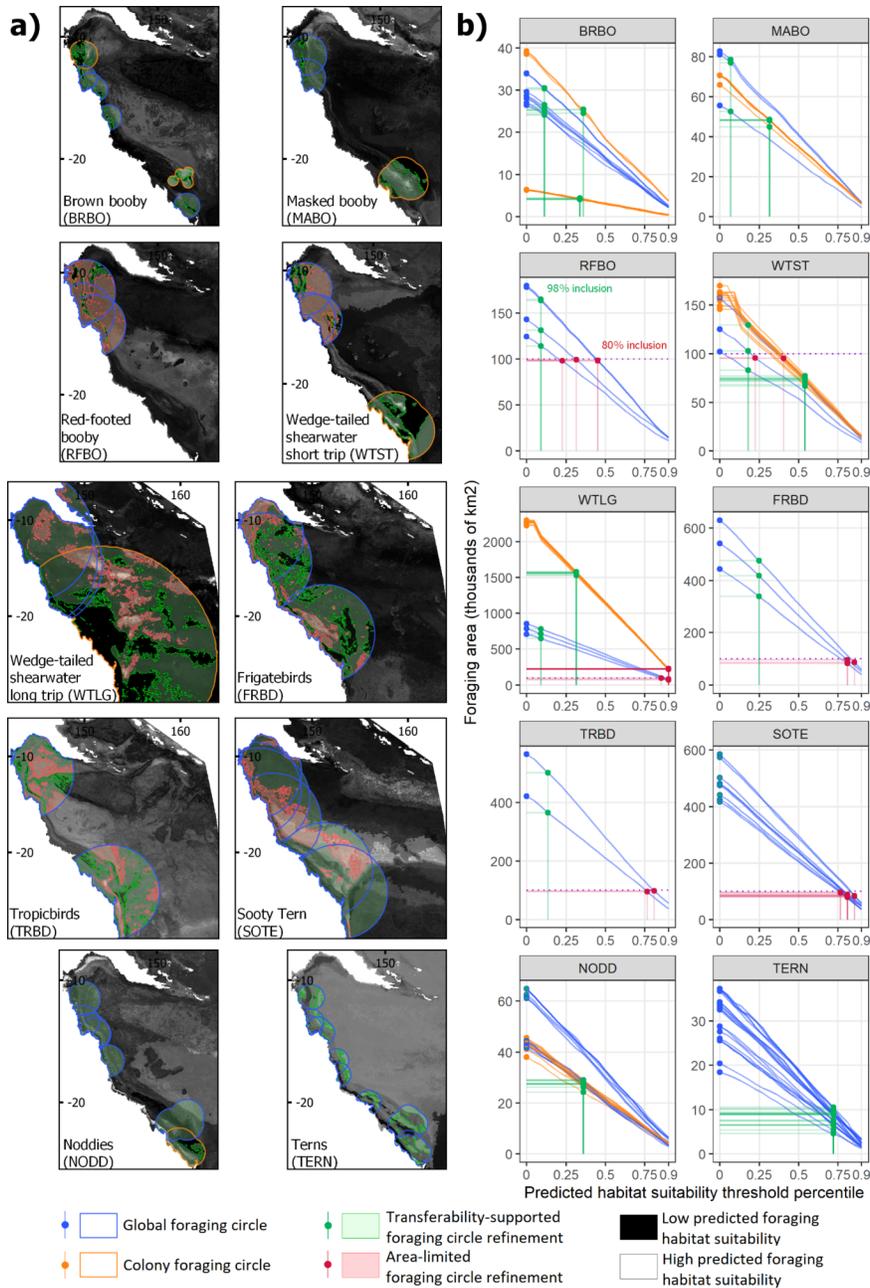
Fig. 5 Foraging circle refinement on the Great Barrier Reef, Australia. Panel a) shows foraging circles and refined foraging circles (over more suitable predicted habitat), mapped for each species using their GBR breeding sites. Panel b) plots increasing simulated foraging circle refinement at each GBR breeding site, and where the thresholds used for refined foraging circles mapped in a) lie in relation to the trade-off between size and refinement confidence. If GBR colonies have local tracking data then colony foraging circles are refined using GBR colony-specific models (yellow); otherwise global foraging circles are refined using multi-colony models (blue). Unrefined foraging circles are mapped and their areas shown at habitat suitability percentiles of 0. Refined foraging circles from transferability-supported refinement are shown in green. Refined foraging circles from area-limited refinement are shown in red for colonies that need further refinement to get below

a 100,000 km^2 limit (purple dotted line). Greater foraging circle refinement reduces the confidence that refined foraging areas include known foraging areas, as demonstrated for a red-footed booby (RFBO) colony (see supporting information for breakdown of predicted known foraging area inclusion at all GBR breeding sites).

Table 5 Summary of foraging area of the Great Barrier Reef breeding seabird community. Total foraging area is estimated from unrefined global foraging circles and refined foraging circles from transferability-supported refinement and area-limited refinement (<100,000km^2). The foraging areas generated by both refinement methods are supported by associated refinement confidence (predicted probability that refined foraging circles contain known foraging areas). All species totals represent total foraging area of all colonies, with overlapping areas dissolved. For a breakdown of results per colony see supporting information.

| Species	n breeding sites (n with tracking data)	n breeding colonies	Area of global foraging circles (km^2)	Area of
BRBO	6 (2)	19	181,000	147,000
MABO	3 (1)	10	239,000	195,000
RFBO	3	4	269,000	252,000
FRBD	3	3	1,231,000	951,000
TRBD	2	2	988,000	868,000
WTST	4 (1)	14	455,000	318,000
WTLG	4 (1)	14	2,936,000	2,265,00
SOTE	6	9	1,420,000	1,420,00
NODD	7 (1)	25	328,000	313,000
TERN	9	22	277,000	85,000
All species	11	37	2,941,000	2,744,00
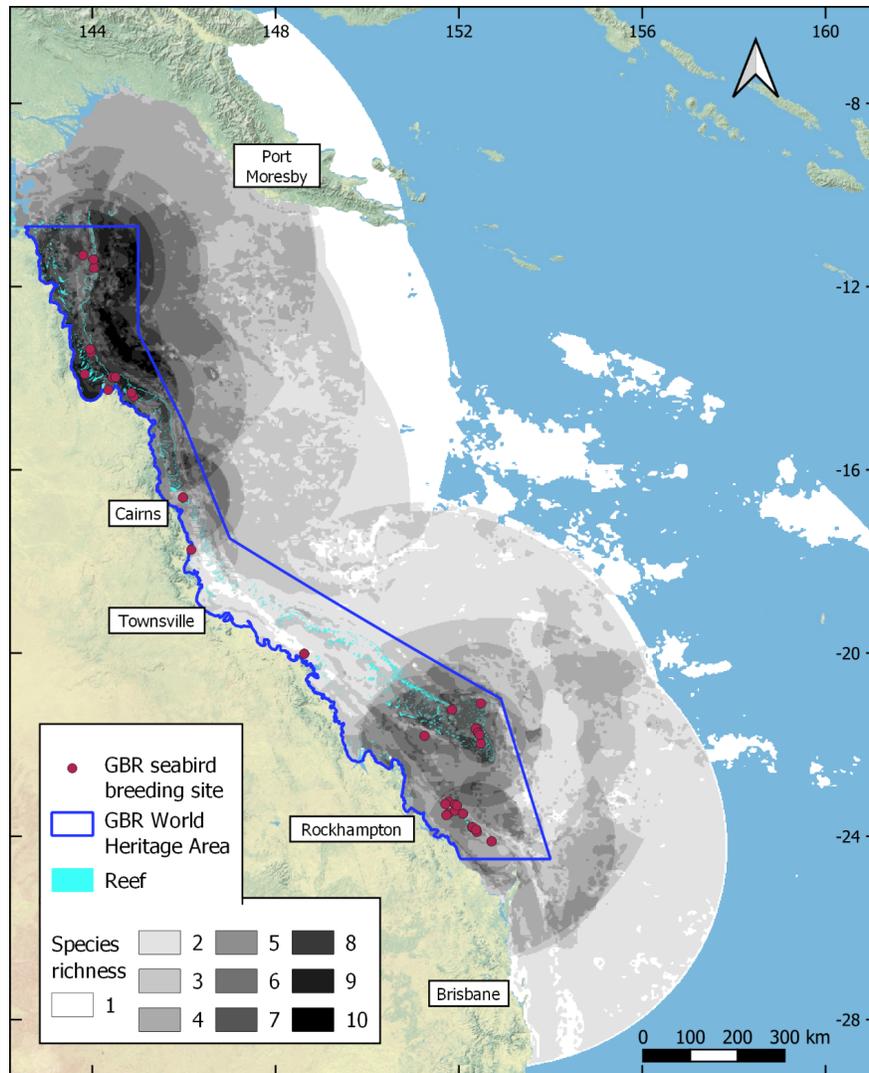
Fig. 6 Network of candidate MPAs for the breeding seabird community of the GBR, that balances size of protected area against refinement confidence (probability of including known foraging areas). Refined foraging areas are delineated for each modelled species and overlapped to show richness hotspots, see supporting information where species-specific boundaries are mapped. Breeding sites are omitted that exclusively contained seabird species we could not model (e.g. small terns, see supporting information)

Discussion

Relying on the most comprehensive tropical seabird tracking dataset to date, we investigated whether ENMs can transfer (predict) foraging niches of breeding tropical seabirds between global colonies, and whether ENMs can be combined with the foraging radius approach (Thaxter et al. 2012) to refine foraging circles around breeding colonies. We found little ability to generalise and transfer ENM predictions across all colonies for any tropical seabird species. However, we frequently observed clusters of colonies that predicted well to one another, but poorly to other colony clusters. Despite the limited ability of ENMs to predict for-

aging niche in new regions, they were able to refine foraging circles by excluding predicted areas of unsuitable foraging habitat. We found inclusion of known foraging areas was almost certain in unrefined foraging circles, and remained high when foraging circle refinement was specified by model transferability, where neither greater refinement from high transferability models nor minor refinement from poor transferability models erroneously excluded important foraging habitat. When applied to the Great Barrier Reef, this framework was able to reduce, with confidence, the area required to protect foraging resources of the breeding seabird community.

ENM transferability

Limited ENM transferability can be caused by differences in the range and/or combinations of environmental variables between training and test datasets (extrapolation); poor description of underlying processes by explanatory variables in models (misspecification); and differences in pressures (e.g. competition, predation, local marine productivity etc) between training and test populations (local adaptation) (Randin et al. 2006, M. McPherson & Jetz 2007, Torres et al. 2015, Péron et al. 2018). Extrapolation likely impacted transferability of colony-specific models, as they were more likely to encounter novel environmental values when predicting to test colonies. By contrast, training of multi-colony models across numerous colony-specific environmental ranges reduced the likelihood of extrapolation when predicting to test colonies, and could explain their slightly better global transferability compared to colony-specific models (Table 3).

Misspecification of models could have contributed to limited global transferability, as we tried to predict seabird foraging with long-term averages of oceanographic variables. Our goal here was to characterise seabird foraging associations with persistent oceanographic features in the seascape rather than ephemeral ocean phenomena, as predictive maps representative across space and time are likely to be the most pertinent for conservation scientists and managers (Guisan et al. 2013). The downside of this approach is that foraging areas selected by GPS-tracked birds do not reflect the concurrent oceanography in our models, which could miss foraging association with fine scale dynamic features (e.g. intra-seasonal upwellings), known to attract tropical seabirds (Kai et al. 2009, Miller et al. 2018). Model misspecification is supported by a general inability of colony-specific models to predict their own foraging niche (diagonal values in Fig. 3) and attributed to using long-term oceanographic variables because similar studies using high-resolution oceanographic variables produced good self-prediction (Péron et al. 2018). Future marine transferability studies should consider their study objective (Yates et al. 2018) (e.g. informing management or ecological understanding) and the dynamism of their ocean region (e.g. temperate shelf break vs pelagic frontal system) when selecting spatial and temporal scale of ocean covariates to use in ENMs.

We consider local adaptation a major cause of limited transferability in this study because multi-colony models did not provide a great improvement in transferability over the colony-specific model average. This finding suggests a limited ability of multi-colony models to generalise patterns in local adaptation of foraging niche from multiple colonies (Gilmour et al. 2018), and boost their transferability (Matthiopoulos et al. 2011). This could be explained by local adaptation causing homogenisation: when models fitted at large spatial scales average the responses of populations from contrasting habitats, and fail to capture and predict local extremes (hotspots and coldspots) (Paton & Matthiopoulos 2016). Model homogenisation likely affected all species known for local adaptation: frigatebirds (Mott et al. 2016); tropicbirds (Diop et al. 2018); wedge-tailed shearwater (Weimerskirch et al. 2020); and in particular boobies, known for their extreme foraging plasticity (Mendez et al. 2017, Gilmour et al. 2018).

We failed to explain inter-colony transferability with two factors describing local adaptation (geographic distance and oceanographic similarity; Redfern et al. 2017, Gilmour et al. 2018), suggesting colony demographic information could be an important missing factor (Paton & Matthiopoulos 2016). Breeding colony size is known to be a major driver of local adaptation in seabird foraging behaviours, where density dependent competition forces greater foraging ranges at larger colonies (Ashmole 1963, Lewis et al. 2001). Competition pressure may also come from neighbouring breeders, such that populations segregate foraging areas (Bolton et al. 2018), and from different species (Oppel et al. 2015, Mendez et al. 2017). However, including

demographic covariates within ENMs requires complex modelling (Wakefield et al. 2017), which given their interaction in driving local adaptation may extrapolate poorly beyond the training region.

We modelled seabird foraging niches excluding a distance-to-colony variable (Péron et al. 2018), which is commonly included in seabird ENMs. Distance-to-colony is often the most important explanatory variable (Oppel et al. 2017, Miller et al. 2019) in seabird ENMs but encodes local adaptation as it is driven by colony-specific demographic information (Lewis et al. 2001). It is difficult to see how ENMs dominated by distance-to-colony could accurately predict foraging areas at unknown colonies unless training and test colonies had similar demographic pressures. Furthermore, if modelling multiple colonies together, model homogenisation would cause an average distance-to-colony to be predicted, potentially yielding the same result as the foraging radius approach (predicting a colony buffer). Our results show that modelling seabird foraging niches using long-term ocean variables alone yields generally poor transferability, and further study is needed to assess whether including distance-to-colony boosts transferability and generates spatial predictions useful for informing management.

Refining foraging circles

Minimising the cost of protected areas while maximising the confidence that they appropriately serve a species (e.g. contain core habitat) is a key goal of systematic conservation planning (Margules & Pressey 2000), and the refinement of seabird foraging circles presents a good example of this challenge. We demonstrate high confidence that known foraging areas are included within presented global foraging radii estimates (Table 3). However, foraging circles from these radii are too large to implement practical conservation measures across, particularly for wider ranging seabird species (Soanes et al. 2016, McGowan et al. 2017), for which an area-based conservation approach may not be efficient or desirable (Oppel et al. 2018). Although we acknowledge that cost and area are not analogous within conservation planning, smaller protected areas for seabirds reduce likelihood of conflict with other marine users (e.g. fishers) and require lower monitoring/policing effort (work hours, fuel etc) relative to larger areas. Using predicted habitat suitability to refine foraging circles provides a way of reducing protected area size, but the confidence in predictions must be considered so that conservation efforts are not allocated to the wrong areas. Our framework accounts for confidence by making the level of foraging circle refinement dependent upon ENM transferability. As we found that inclusion of known foraging areas remained high when foraging circles were refined using transferability-supported levels, we can be confident that neither greater refinement from high transferability models nor minor refinement from poor transferability models erroneously exclude important foraging habitat.

Even minor refinement of foraging circles adds information to marine spatial planning when multiple breeding seabirds are considered together. Overlaying unrefined foraging circles from multiple species just shows increasing overlap of concentric circles towards colonies, informing planners only that areas of sea surrounding the most seabird species-rich islands are the most important. These can be improved by weighting foraging circles with their breeding populations and distributing birds over an accessibility surface (inverse colony distance) within the circle (Critchley et al. 2018), but this still lacks ecological realism. The refinement of foraging circles with ENMs integrates habitat preferences into the planning process. For GBR seabirds, this reveals that areas offshore from colonies, particularly open sea adjacent to outer reefs, are likely foraging hotspots for multiple species (Fig. 6).

Our study of foraging circle refinement presents several tools for tropical seabird conservation, whose use we advocate in a hierarchical manner based on local data availability. Firstly, we present the most comprehensive collation of tropical seabird foraging radii to date. The estimates presented for each species can be used to represent foraging ranges for any population in the world without local tracking, and the colony-specific foraging ranges presented in the supporting information form a valuable resource for users interested in specific regions. Foraging radii alone have important applications, particularly the mean-maximum foraging range, such as assessing seabird population connectivity with planned offshore energy generation projects (Woodward et al. 2019). Secondly, where a candidate seabird protected area is required for a tracked colony, our framework can be followed to generate a colony foraging circle and refine it using a colony-specific model

trained with the tracking data. Thirdly, where candidate seabird protected areas are required for untracked colonies and tracking data exist from several colonies in the same region, a global foraging circle can be estimated and refined with a multi-colony model trained on the regional tracking data. For species without any local tracking (frigatebirds, tropicbirds, red-footed booby, sooty tern and terns in our GBR study), we advise cautious application of a global multi-colony model. The generally poor transferability of global ENMs would only prescribe minor refinement of global foraging ranges, but we nonetheless advise local expert opinion or distribution data (e.g. at-sea surveys) should be used to verify that predicted 'unsuitable' habitat is indeed unsuitable. Refined foraging circles can be considered candidate MPAs for their respective seabird population. As distinct polygons they can be considered individually or overlapped, to identify multi-species foraging hotspots, in higher level marine spatial planning exercises, to ensure seabird representation in multi-taxa MPA delineation. It should be noted that our foraging circle refinement framework is ENM neutral, and users should select environmental covariates and model algorithms of their preference.

Advancing regional knowledge of seabird foraging areas

ENMs trained on GBR tracking allowed better refinement than globally trained models, demonstrating the value of local tracking data. A key recommendation from our study is collection of more seabird tracking data at regional level. If there was a representative (good coverage of species and sites) GBR database of seabird tracking information, there would be no need to apply model predictions from across the world to the GBR as we have done here. Coordination of a systematic regional seabird tracking campaign offers the most efficient solution to credibly identify known foraging areas for the GBR seabird community, as demonstrated by projects in the UK (FAME and STAR; Wakefield et al. 2017). Key breeding populations should be prioritized for tracking, but it is essential that colonies from the same species are tracked in different areas of the GBR. Our observation that foraging habitat suitable for brown boobies from Swain Reefs could not predict that of conspecifics from Raine Island (and vice versa; Fig. 6A) highlights the limits of model transferability within the same region. Furthermore, it may be necessary to investigate whether models of foraging niche are transferable between neighbouring colonies, in particular when partitioning of foraging areas between colonies is observed, as shown for wedge-tailed shearwaters breeding in New Caledonia (Weimerskirch et al. 2020). Selected colonies should be tracked during years of typical ocean conditions with a good sample of birds (>30; Soanes et al. 2013, Lascelles et al. 2016) to ensure the observed foraging niche is representative of the populations' true foraging niche. A systematic seabird tracking campaign would dramatically reduce uncertainty in where seabirds forage on the GBR, enabling better focused management actions and inclusion of seabird foraging areas in higher level planning such as zoning of MPAs within the GBR. Nonetheless, the globally-informed predictions of habitat suitability and foraging radii presented here form the best working hypotheses of where seabirds forage on the GBR, and are a valuable starting point for management and protection of seabird foraging resources.

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