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How a Winner Can Also Be a Loser? At-Sea Vulnerability of a Critically Endangered Endemic Seabird to Climate Change

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ABSTRACT

Aim: The last decades have been marked by a global decline of many migratory species, and predictions are even more alarming when climate change is considered. We investigated the migration patterns and marine habitat selection processes of a critically endangered endemic seabird of the tropical western Indian Ocean, and projected future habitat suitability under climate-change scenarios.

Location: Indian Ocean.

Taxon: Mascarene petrel (*Pseudobulweria aterrima*).

Methods: Non-breeding distribution of the Mascarene petrel was estimated using Global Location Sensors (GLS) and key habitat selection predictors were identified using Species Distribution Models (SDM). The best-performing models were averaged to build an Ensemble model, which was projected under three Shared Socioeconomic Pathways (SSP) to assess future changes in non-breeding habitat suitability.

Results: The Mascarene petrel exhibits a remarkably wide distribution throughout the tropical Indian Ocean during its non-breeding period. We identified seven main core areas which highlights high inter-individual variability. The species selected warm (~28°C) and deep water (−4000 m and −2000 m) with low gradient of bathymetry. Our predictive models suggest that the suitable marine habitat of this species will increase in surface area by 7%–9% as a consequence of climate change.

Main Conclusions: Our projections indicate that the Mascarene petrel may experience stable or slightly improved climatic suitability in its non-breeding marine habitat, suggesting a potential ‘climate change winner’ signal at sea. However, as many migratory species, it relies on multiple habitats and accumulates threat exposure throughout its entire life cycle. The species therefore remains highly vulnerable due to strong terrestrial pressures and its restricted endemic range during breeding, supporting its characterization as a ‘global change loser’. More broadly, our results highlight the importance of assessing threats across the entire annual cycle, particularly for migratory and wide-ranging species, to avoid misestimating overall vulnerability.

1 | Introduction

The last decades have been marked by major declines in many migratory species (Shuter et al. 2011). This trend is particularly pronounced within marine ecosystems. Indeed, more than 21% of the marine migratory species (including bony fishes, cartilaginous fishes, turtles, marine mammals and seabirds) are threatened to extinction (Lascelles et al. 2014). During their extensive

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movements, they face several human-induced threats primarily associated with bycatch, pollution, habitat alteration, overfishing, hunting, energy production and climate change (Lascelles et al. 2014; Dias et al. 2019; Cooke et al. 2024). The convention on the Conservation of Migratory Species of Wild Animals (CMS) recognized the impacts of climate change as a primary threat on migratory species (CoP 8.13). Habitat alteration, partially attributed to climate change (Lee et al. 2023), has been identified as a primary factor contributing to species declines (Watson et al. 2019), with particular concern for migratory species (Cooke et al. 2024). Climate change may also lead to major food depletion which has long term consequences on individuals' capacity to migrate (Shaw 2016). Furthermore, climate change can alter the timing of migration (Cotton 2003) leading to a mismatch between breeding phenology and the peak of food resources (Grémillet and Boulinier 2009; Winkler et al. 2014).

In the realm of conservation, the assessment of species' vulnerability to anthropogenic stressors is a critical undertaking (Foden et al. 2018). This prerequisite becomes complex when examining migratory species due to their extensive movements and the numerous habitats they visit (Robinson et al. 2009). Sensitivity and exposure to anthropogenic threats can vary significantly across habitats, and vulnerability assessment is necessary throughout all stages of the life cycle (Small-Lorenz et al. 2013). Seabirds exemplify the complexity of assessing the vulnerability of migratory species. The remarkable migratory behaviour of these birds is well illustrated by some remarkable species, such as the Arctic tern (*Sterna paradisaea*), which undertakes one of the longest migrations on Earth (Egevang et al. 2010), or the wandering albatross (*Diomedea exulans*), capable of completing two circumpolar trips around Antarctica during their sabbatical period (Weimerskirch et al. 2014). Seabirds have a multipart life-cycle which includes three main habitats: (1) terrestrial breeding habitat, (2) at-sea foraging habitat during the breeding season and (3) at-sea habitat during the non-breeding season (Schreiber and Burger 2001). The vulnerability of seabirds to anthropogenic pressures is primarily assessed in their terrestrial breeding phase, which is better known compared to their marine phase. This discrepancy arises from the long-standing challenges associated with studying seabirds in the open ocean, particularly over the extended non-breeding period (Hart and Hyrenbach 2009). However, this period is crucial for seabirds, as it enables them to restore their body condition for the subsequent reproduction and to satisfy the energy requirements necessary for moulting (Schreiber and Burger 2001). Seabirds face various threats during their non-breeding period, with by-catch and climate change standing out as the primary threats at sea (Dias et al. 2019).

Advances in electronic tracking technologies have greatly enhanced our understanding of the spatial ecology of seabirds throughout their marine phase, including during their non-breeding period (Tremblay et al. 2009). However, substantial knowledge gaps remain, particularly regarding tropical and threatened seabird species (Bernard et al. 2021). This study aims to address these gaps by examining the distribution, habitat and climate change vulnerability of a Critically Endangered tropical seabird species during its non-breeding period. The Mascarene petrel (*Pseudobulweria aterrima*), endemic to Reunion Island, has a very small population size (~100 breeding pairs, Virion et al. 2021), and faces significant terrestrial threats such as predation by cats and rats and light-induced mortality (Chevillon et al. 2022; Juhasz et al. 2022; Teixeira et al. 2024). However, like many seabird species, the at-sea phase of the Mascarene petrel remains poorly known, potentially leading to an incomplete assessment of its vulnerability. In this study, we analysed tracking data collected with Global Location Sensors (GLS) and implemented Species Distribution Model (SDM) to determine (1) the Mascarene petrel's year-round distribution with a focus on the non-breeding period, (2) its non-breeding marine habitat preference and (3) to predict changes in its habitat suitability due to climate change. In the light of these results, we will discuss the vulnerability of the Mascarene petrel throughout its life cycle.

2 | Methods

2.1 | Fieldwork

Fieldwork was conducted at Reunion Island (21.1° S; 55.5° E) in the southwestern Indian Ocean (Figure 1), which is the unique breeding ground of the Mascarene petrel. GLS (Mk4083, Biotrack-Ltd., Wareham, UK) were attached to metal rings using cable ties. The total mass of the equipment was approximately 2 g, representing less than 1% of the mean adult body mass (280.07 ± 35.04 g, $n = 79$ individuals), which is below the generally accepted threshold of 3% for flying birds (Phillips et al. 2003). Forty GLS were deployed on breeding adults from two breeding colonies (Rivières des Remparts and Rond des Chevrons, see Juhasz et al. 2022 for a detailed description of these colonies) during two successive breeding periods: 20 loggers from October 2017 to February 2018 and 20 from October 2018 to March 2019. Thirty GLS were recovered between August 2018 and October 2020 (recovery rate 75%). We managed to download data from 23 of these recovered tags (7 were damaged). Fifteen devices provided data on the at-sea distribution in 2018 (13 from Rivières des Remparts and 2 from Rond des Chevrons), and eight devices provided data in 2019 (5 from Rivières des Remparts and 3 from Rond des Chevrons). Overall, nineteen individuals have been successfully tracked, including four birds tracked during two consecutive years. Blood samples of all tagged birds were collected for molecular sexing and for a genomic study of the species (Teixeira et al. 2024).

2.2 | Distribution Estimation

GLS loggers continuously record light intensity associated with elapsed time, enabling the estimation of two locations per day with a spatial accuracy of 186 km (Phillips et al. 2004). Location estimation was performed using the threshold method (Hill 1994) applied with the 'GeoLight' R package (Lisovski and Hahn 2012). We removed unrealistic locations in terrestrial areas and within 10 days around the equinoxes when latitude cannot be estimated. Additionally, locations yielding unrealistic flight speeds (> 35 km.h-1 sustained over a 48 h period) were excluded (Phillips et al. 2006). The date of the beginning of the non-breeding period (initiation of the post-breeding migration) was determined by identifying a rapid increase in distance from the colony. Kernel density distributions were calculated using the 'adehabitat' R package (Calenge 2006). We defined the 50% kernel as the core area of distribution during the non-breeding period (Phillips et al. 2006).

2.3 | Species Data Preparation

Presence data were defined as locations within 50% non-breeding kernels to reduce the influence of migratory locations, occasional exploratory movements and help limit the impact of GLS location uncertainty. This approach prioritises core-use areas and may not fully capture occasional use of peripheral habitats. We randomly generated pseudo-absence points outside 50% kernels and within an area where Mascarene petrels are likely to migrate. This area was delineated by coastlines in the north, west and east of the Indian Ocean and by the northern branch of the subtropical convergence in the south, defined by the annual average position of the 18°C isotherm (Lutjeharms and Valentine 1988). This thermal front is regarded as the natural southern limit of most tropical seabird species in the Indian Ocean (Le Corre et al. 2012). To maintain a balanced dataset, we generated an equal number of pseudo-absence locations and presence locations per week. To account for the uncertainties associated with the random selection of pseudo-absences, we repeated the process 20 times and used these 20 pseudo-absence data sets to run subsequent species distribution modelling.

2.4 | Environmental Predictors

Ten potential environmental predictors were selected to model the distribution of the Mascarene petrel (Table 1), based on existing knowledge on the drivers of seabird distribution (Tremblay et al. 2009). Bathymetry (BATHY) was obtained from the NOAA (National Oceanic and Atmospheric Administration) website (see Appendix S1 in Supporting

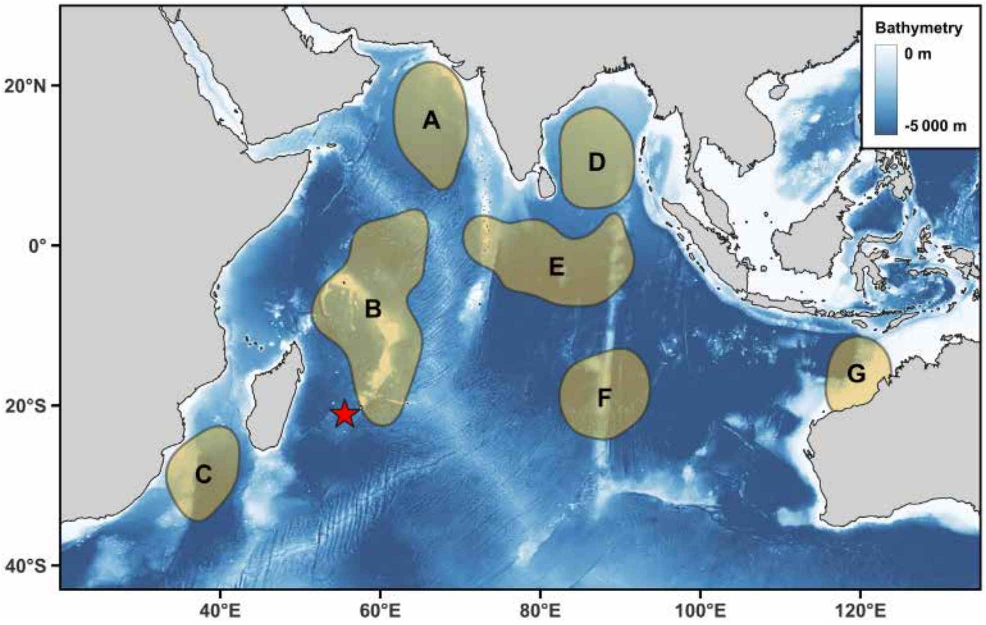

FIGURE 1 | Density distributions of Mascarene petrels (*N* = 19 birds and 23 tracks) from Reunion Island (red star) during 2 years (2018 and 2019). Density contours encompass core areas (50% kernel). Non-breeding locations were concentrated in seven core areas: Arabian sea (A), Mascarene Plateau (B), southwest of Madagascar (C), Bay of Bengal (D), south of Sri Lanka (E), 90° East Ridge (F), northwest of Australia (G).

TABLE 1 | Description of environmental predictors used in the Mascarene petrel distribution model.

Environmental variable	Depth (m)	Variable full name	Unity
ST	0–100	Sea water Temperature integrated from 0 to 100 m deep	°C
GST	0–100	Gradient of Sea water Temperature integrated from 0 to 100 m deep	—
BATHY	—	Bathymetry	m
GBATHY	—	Gradient of bathymetry	—
SSH	Surface	Sea Surface Height	m
GSSH	Surface	Gradient of Sea Surface Height	—
CURRENT	0–100	Geostrophic sea water velocity integrated from 0 to 100 m deep	m.s-1
GCURRENT	0–100	Gradient of geostrophic sea water velocity integrated from 0 to 100 m deep	—
CHLA	0–100	Chlorophyll a concentration integrated from 0 to 100 m	mg.m-3
WIND	—	Wind speed	m.s-1

Information for details). All other environmental variables were downloaded from the Copernicus Marine Service from three products based on in situ and satellite data (see Appendix S1 for details). Seawater temperature (ST), current speed (CURRENT), and chlorophyll-a concentration (CHLA) were averaged over the first 100 m of the water column to highlight deeper structures including gyres, upwelling, eddies, or deep chlorophyll maximum, which have been shown to influence marine productivity and prey abundance (Jena et al. 2013). All variables have been aggregated at a resolution of 2 × 2 degrees to match the resolution of the Mascarene petrel locations (186 km, Phillips et al. 2004). Daily WIND variable was averaged on a weekly basis. These operations were achieved using the CDO software (Climate Data Operators, https://code.mpimet.mpg.de/projects/cdo). The variables wind speed (WIND) and CURRENT were computed using zonal and meridional components. Spatial gradients of seawater temperature (GST), sea surface height (GSSH), current (GCURRENT) and bathymetry (GBATHY) were calculated using eight neighbourhood pixels in the *terrain* function from 'raster' R package (Péron et al. 2012; Hijmans et al. 2015), applying beforehand a Gaussian filter with a 3 × 3 pixels moving window ('spatialEco' R package, Evans et al. 2021) to remove artefacts. All the environmental predictors were included in species distribution models because they exhibited weak correlations, as determined by their Variance Inflation Factor (with a threshold above 3, Shrestha 2020).

2.5 | Species Distribution Modelling

To account for uncertainties associated with the choice of a particular modelling strategy (Araújo and New 2007), we implemented eight statistical and machine learning binomial regression models: a linear model (GLM), two multiple splines regressions (GAM, MARS), three machine learning classifiers (CTA, RF and GBM), one implementation of the maximum entropy method (MAXNET) and one artificial neural network (ANN) using the 'biomod2' R package (Thuiller et al. 2020). Each algorithm was tuned separately using the BIOMOD_Tuning function (Thuiller et al. 2020). Models were calibrated using 20 pseudo-absence datasets (Barbet-Massin et al. 2012) and a 10-fold cross-validation procedure for internal validation (Kohavi 1995). In total, 1600 models were fitted (8 algorithms × 20 pseudo-absence datasets × 10 cross-validation runs). Each model was calibrated using 80% of the presence and pseudo-absence data, while the remaining 20% was reserved for external validation. Both internal and external validations were based on the True Skill Statistic (TSS) index (Allouche et al. 2006). Model evaluation metrics (TSS, sensitivity and specificity) are summarized by algorithm in Appendix S2.1 (Figure S2.1).

The top-performing individual models were retained if they achieved TSS values ≥ 0.6 under external validation (Coetzee et al. 2009). Ensemble predictions were computed as an unweighted mean of predicted presence probabilities across all retained models (Araújo and New 2007; Marmion et al. 2009). To describe uncertainty among models, we quantified the spatial standard deviation of predicted habitat suitability across retained models (Appendix S3). We then used the ensemble model to produce a map of the Mascarene petrel current habitat suitability over the Indian Ocean. We used an average of environmental predictors for the non-breeding period (February to September, when the first and last tagged individuals departed from and returned to the colonies) over the 2 years of the tracking (2018 and 2019). The importance of each environmental predictor was assessed using a permutation-based approach. Specifically, the Pearson's correlation between the model incorporating the randomized variable and the reference model (with the true variable values) was calculated, and the result was subtracted from 1. On the other hand, when these two models are correlated, the importance of the randomized variable is low.

2.6 | Future Projections

The projection of the future habitat suitability of the Mascarene petrel was performed using a new ensemble model calibrated with the most significant environmental variables (BATHY, GBATHY, ST, importance index > 0.100). This approach was chosen due to the limited number of projections available for some variables, which could otherwise affect the reliability of the results. We downloaded all General Circulation Models (GCM) from the sixth Coupled Model Intercomparison Project (CMIP6) available on the ESGF website for the Shared Socioeconomic Pathways (SSP) and time periods considered (see below). We obtained monthly ST projections from six GCM: CanESM5, CMCC-ESM2, IPSL-CM6A-LR, MIROC-ES2L, NorESM2-LM and UKESM1-0-LL. We then averaged ST across these six GCM for each SSP and time period. This approach provides a consensus ST predictor for projections; however, it does not provide an explicit estimate of inter-GCM uncertainty within each SSP. Nevertheless, previous work suggests that, in SDM-based projections, uncertainty related to model choice and SPP far exceeds variability among GCMs (Thuiller et al. 2019). Three SSP corresponding to variable increasing emissions scenarios were considered: low-range emissions (SSP1-2.6, corresponding to the Paris Agreement), mid-range (SSP3-7.0) and high-range (SSP5-8.5). We performed temporal projections of habitat suitability over three future 20-year periods, 2030s (an average from 2020 to 2040), 2050s (2040–2060), 2070s (2060–2080), considering only the months of Mascarene petrel non-breeding period (February to September, see Fieldwork sub-section).

To accommodate potential differences between historical GCM projections and the observed climate, we applied the 'delta change' (DC) method (Navarro-Racines et al. 2020). In order to produce future environmental variable projections that are corrected of potential inabilities of GCM to reproduce the past climate, this methodology applies differences between future and historical GCM projections to historical observations:

$$\Delta X_{tix} = Historical_{ix} - X_{tix} \tag{1}$$

$$CorrectedX_{tix} = Baseline_{x} + \Delta X_{tix} \tag{2}$$

The first equation calculates the delta (change) between the future and historical periods. $Historical_{ix}$ represents the historical data of SSP i (from 1999 to 2014) merged with the initial period of SSP i (from 2014 to 2019) for environmental variable x, to cover the same temporal period as the baseline. X_{tix} represents the projected data for the 20-year period t for SSP i and environmental variable x. The second equation calculates a corrected environmental variable $CorrectedX_{tix}$ for the 20-year period t and SSP i that were used in models for future distribution projection. $Baseline_x$ represents the observed environmental variable x, downloaded on the Copernicus platform (see Appendix S1) from 1999 to 2019 and monthly averaged.

All analyses were conducted in R 4.3.0 (R Core Team 2023) and analyses were organized using targets pipelines (Landau 2021).

3 | Results

3.1 | Non-Breeding Distribution Characterization

The Mascarene petrel departs from the colony for its post-breeding migration on 12th March ±29.2 days and remains at sea during its entire non-breeding period, which lasts 5.1 ± 0.8 months (average date of return to the colony: 14th August ±27.6 days). The species is widely distributed during its non-breeding period, with birds migrating across the entire Indian Ocean. We determined seven distinct core oceanic areas with higher location densities (Figure 1). Most birds (*c.a.* 75%, $n = 17$ tracks) visited only one of these core areas during their non-breeding period. Birds that utilized several core areas were categorized in the area in which they spent most of their time. All core areas were distributed in the tropical Indian Ocean: 4 tracks were in the Arabian Sea (A), 9 in the Mascarene plateau (B), 3 in the Bay of Bengal (D), 3 in a large area south of Sri-Lanka (E), 1 in the 90° East Ridge (F), 1 in the southwest of Madagascar (C) and 1 in the northwest of Australia (G) (Figure 1). Among the four individuals which were tracked during two consecutive years, three returned to the same non-breeding core area (two in the Mascarene plateau and one in the Arabian Sea), and one changed from the Mascarene plateau in 2018 to the southwest of Madagascar in 2019. Distribution of tracks between core areas was not related to sex (Fisher's exact test, $n = 23$, p-value $= 1$), colony (Fisher's exact test, $n = 23$, p-value $= 0.303$) or year (Fisher's exact test, $n = 23$, p-value $= 0.444$).

3.2 | Modelling of the Non-Breeding Distribution

The ensemble model demonstrated good performances during external validation with a $TSS = 0.844$. The difference between TSS obtained from internal validation ($TSS = 0.855$) and external validation was low ($\Delta = 0.011$) suggesting a low risk of overfitting. The sensitivity and specificity (true presence and true absence respectively) were well-balanced, both exceeding 90% (93.7% and 91.7% respectively), indicating accurate prediction for presences and pseudo-absences. The environmental predictors that best explained the Mascarene petrel distribution were GBATHY, BATHY and ST (Table 2). Non-breeding core areas used by the Mascarene petrel were characterized by high seawater temperatures (ST optimum around 28°C) with a gentle gradient in bathymetry (GBATHY < 0.02) and a bathymetry between −4000 and −2000 m (Figure 2). These features correspond to a very large area across the tropical and equatorial Indian Ocean, where the habitat suitability of Mascarene petrel is high (Figure 3). There is a strong correspondence in habitat suitability with the core areas identified using GLS (Figures 1 and 3), with an exception in the vicinity of the Comoro Islands (northwest of Madagascar). The habitat suitability in this region is high, although there is no core area identified there (Figure 1).

TABLE 2 | Importance of environmental predictors in the Mascarene petrel distribution model.

Variable	Variable full name	Variable importance
ST	Sea water Temperature integrated from 0 to 100 m deep	0.295
BATHY	Bathymetry	0.291
GBATHY	Gradient of bathymetry	0.103
SSH	Sea Surface Height	0.048
GST	Gradient of Sea water Temperature integrated from 0 to 100 m deep	0.039
CHLA	Chlorophyll a concentration integrated from 0 to 100 m	0.020
GSSH	Gradient of Sea Surface Height	0.010
GCURRENT	Gradient of geostrophic sea water velocity integrated from 0 to 100 m deep	0.013
WIND	Wind speed	0.012
CURRENT	Geostrophic sea water velocity integrated from 0 to 100 m deep	0.004

Note: Indexes of variables range in importance from 0 (no influence of that variable on the model) to 1 (a large influence of that variable on the model).

3.3 | Non-Breeding Distribution Projections

The projection of the ensemble model across various climate change scenarios revealed a surface expansion of suitable habitat for the Mascarene petrel over time (Figure 4 and see Appendix S4). The habitat suitability variations were minimal in the low-range scenario (Figure 5). The suitable surface habitat increases by 7% between the current period and the 2060–2080 periods (Figure 4). In the case of the medium- and high-range scenarios, there was a decrease in the number of pixels with very high habitat suitability value over time, while other areas became more favourable, particularly those located south of the equator and closer to Reunion Island (Figure 5). Anyway, the suitable surface habitat increases by 9% between the current period and the 2060–2080 periods in both scenarios (Figure 4).

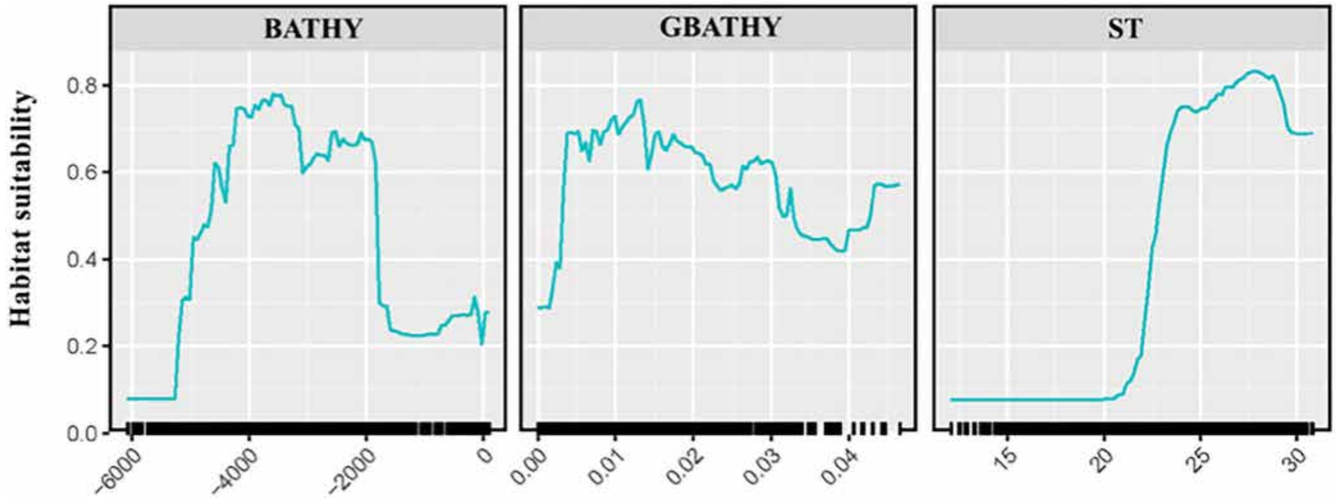

FIGURE 2 | Response curves of the Mascarene petrel distribution model for the most significant environmental predictors: Bathymetry (BATHY), gradient of bathymetry (GBATHY), seawater temperature integrated between zero and 100 m deep (ST).

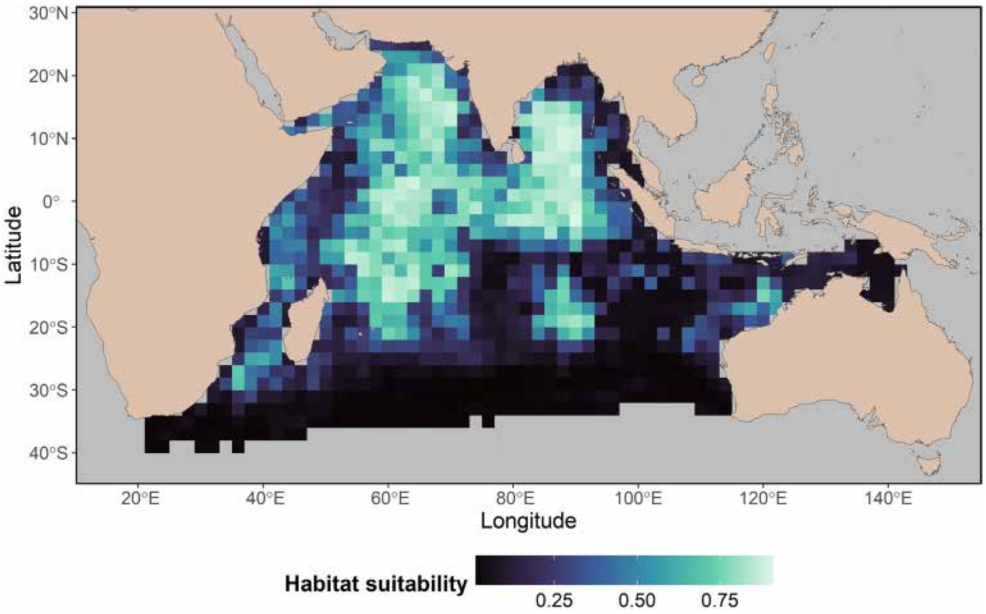

FIGURE 3 | Projection of current habitat suitability of Mascarene petrel mapped across the Indian Ocean using environmental predictors over the 2 years of tracking study (2018 and 2019).

4 | Discussion

4.1 | Wide Non-Breeding Distribution of the Species and High Inter-Individual Variability

The Mascarene petrel exhibits a remarkable widespread distribution across the entire Indian Ocean during its non-breeding period. This extensive distribution results from a large variability among individuals. Most birds migrated to a single core area, and seven such core areas were identified. This pattern contrasts with the observations made on other seabird species in the Indian Ocean (Pinet et al. 2011; Legrand et al. 2016) or elsewhere (Tranquilla et al. 2013; Oosthuizen et al. 2022), which tend to have a more localized non-breeding distribution. Nonetheless, the same migratory strategy with high inter-individual variability was found in other species, such as southern skuas (*Stercorarius antarcticus lonnbergi*) (Delord et al. 2018), wandering albatrosses (Weimerskirch et al. 2015), Round Island petrels (*Pterodroma arminjoniana*) (Franklin et al. 2022), and sooty terns (*Onychoprion fuscatus*) (Jaeger et al. 2017). The sooty tern is the most abundant seabird in the Indian Ocean, and the high inter-individual variability in non-breeding distribution was explained as a strategy to reduce intra-specific competition (Jaeger et al. 2017). However, the Mascarene petrel has a very small population size compared to sooty terns, leading to a lower risk of intra-specific competition. Some studies suggest that the non-breeding distribution can be influenced by factors such as sex (Jaeger et al. 2014), breeding colony (Weimerskirch et al. 2015) or year (Dias et al. 2011). However, our results indicate that the Mascarene petrel is not significantly affected by these factors.

Interestingly, the seven core areas identified for the Mascarene petrel have been identified as major hotspots for other tropical seabirds during their non-breeding period. The Bay of Bengal

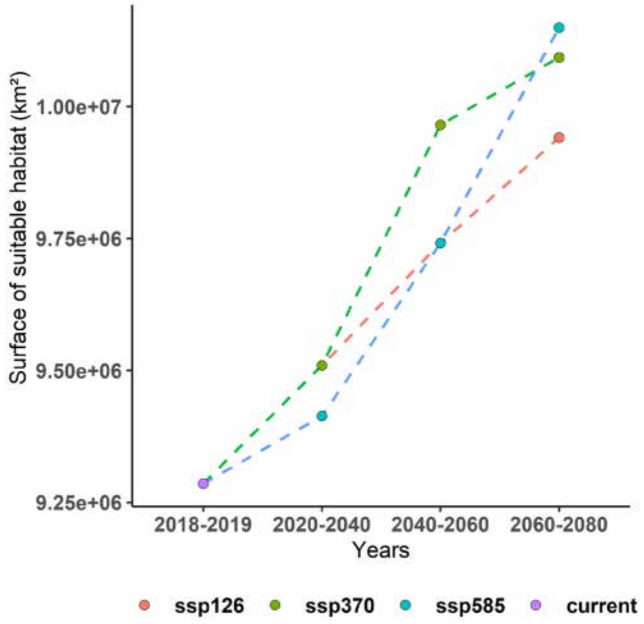

FIGURE 4 | Surface of habitat suitability for the Mascarene petrel (in km^2 and calculated with the Mollweide projection in R) across various time periods (2018–2019, 2020–2040, 2040–2060 and 2060–2080) under three different climate change scenarios (red: Low-range SSP1-2.6, green: Mid-range SSP3-7.0, and blue: High-range SSP5-8.5). Pixels are considered as suitable above 0.627 threshold corresponding to the cutoff parameter (optimizing the sensitivity and specificity) of the ensemble model calibrated with the most significant environmental variables (ST, BATHY, GBATHY).

(Figure 1, kernel D) stands out as the primary non-breeding area of sooty terns from Bird Island, Seychelles (Jaeger et al. 2017). The 90° East Ridge area (Figure 1, kernel F) coincides with the non-breeding areas of Barau's petrels (*Pterodroma baraui*) (Pinet et al. 2011, Legrand et al. 2016) and red-tailed tropicbirds (*Phaethon rubricauda*) (Le Corre et al. 2012). Additionally, some sooty terns (Jaeger et al. 2017) and Round Island petrels (Franklin et al. 2022) also migrate to this region. The Arabian Sea (Figure 1, kernel A) is the main non-breeding area of Round Island petrels (Nicoll et al. 2017; Franklin et al. 2022). The zone located south of Sri Lanka (Figure 1, kernel E) coincides with the non-breeding area of wedge-tailed shearwaters (*Ardenna pacifica*), white-tailed tropicbirds (*Phaethon lepturus*) (Catry et al. 2009; Le Corre et al. 2012), great frigatebirds (*Fregata minor*) (Weimerskirch et al. 2017) and lesser noddies (*Anous tenuirostris*) (Lebarbenchon et al. 2023). The northwest of Australia (Figure 1, kernel G) is also frequented by red-tailed tropicbirds (Jaeger et al. *unpublished data*) and Round Island petrels (Franklin et al. 2022). Lastly, the largest non-breeding area located on the Mascarene Plateau (Figure 1, kernel B) is known to host several seabird species during their breeding and non-breeding periods (Catry et al. 2009; Le Corre et al. 2012; Jaeger et al. 2017; Franklin et al. 2022; Trevail et al. 2023; Lebarbenchon et al. 2023).

4.2 | Current and Future Mascarene Petrel Distribution

Our ensemble model had increased skills (TSS) compared to individual statistical techniques and yielded inferences considered

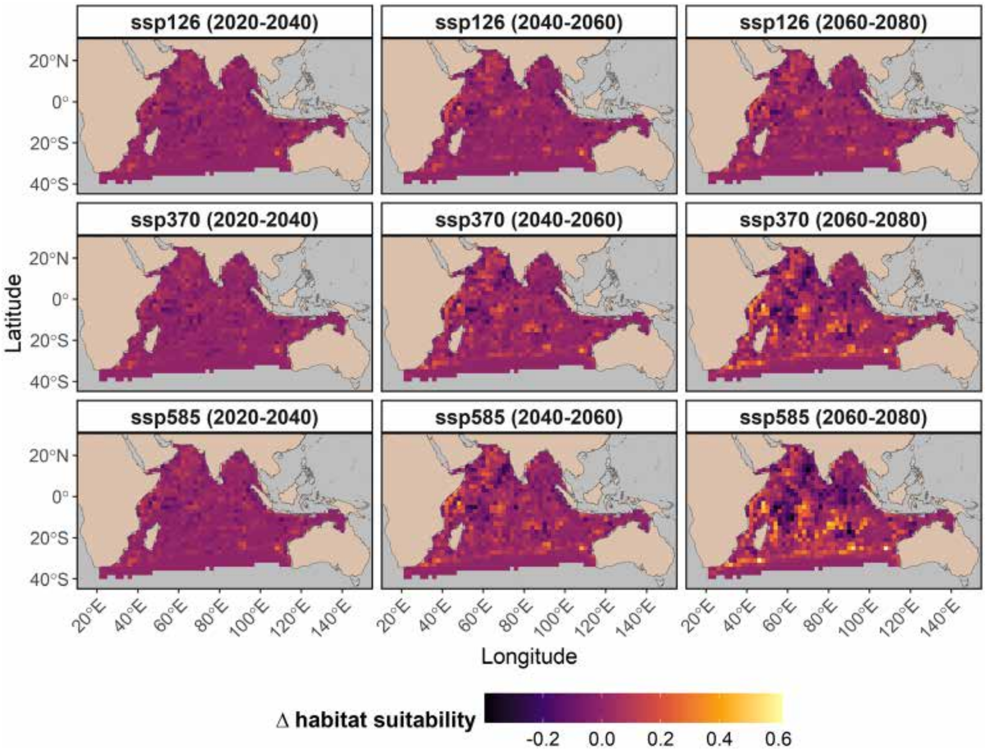

FIGURE 5 | Variation of future habitat suitability for the Mascarene petrel from −1 (area becoming less favourable) to 1 (area becoming more favourable) according to climatic change scenarios (low-range: SSP1-2.6, mid-range: SSP3-7.0, high-range: SSP5-8.5) and different time periods (2020–2040, 2040–2060 and 2060–2080).

as interpretable in comparison to similar studies (Legrand et al. 2016; Pereira et al. 2018). The current distribution of the Mascarene petrel (Figure 1) coincides with the modelled suitable areas (Figure 3), validating the accuracy of our models. An exception was observed in the northwest area of Madagascar, which was predicted as a suitable environment but did not host any core distribution areas. Yet, we did not track the entire population, and therefore there is a possibility that not all the individual variability was sampled.

We found that the most influential factors affecting the at-sea distribution of the Mascarene petrel were ST, BATHY, and GBATHY ranked in order of decreasing importance. These variables are known predictors of seabird distribution because they integrate key physical processes that affect prey fields (Tremblay et al. 2009; Trevail et al. 2023). Typically, seabirds in polar and temperate zones exhibit a preference for lower temperatures, indicating locally enhanced productivity and prey availability (Scales et al. 2014), a trend also observed for the Barau's petrel, another seabird endemic to Reunion Island (Legrand et al. 2016). In contrast, the Mascarene petrel selects areas characterized by higher temperatures (average 28°C, Figure 2). This does not necessarily imply low prey availability, as warm tropical waters can still concentrate prey through physical structuring (e.g., eddies) and through the vertical behaviour of prey communities. A preference for warm waters has also been reported in other tropical seabirds in the region, the white-tailed tropicbirds in the Seychelles, potentially reflecting species-specific foraging modes and prey types (Ensanyar-Volle et al. 2023). The associations with BATHY from −4000 to −2000 m and low GBATHY further suggest the use of open-ocean habitats rather than shelf edges, coastlines or seamounts, which are often selected by species relying on predictable topographic enhancement of productivity (Scales et al. 2014). Together, these patterns point towards a pelagic, warm-water non-breeding habitat, potentially shaped by broad-scale water-mass characteristics and mesoscale processes. Given the spatial uncertainty inherent to GLS locations, these interpretations should be viewed as hypotheses that can be refined with higher-resolution tracking and concurrent prey/oceanographic data.

The Mascarene petrel suitable habitat does not seem to be vulnerable to climate change during the non-breeding period, as its ecological niche during this period is primarily characterized by static predictors (BATHY and GBATHY). Furthermore, it selects a high temperature optimum (28°C), which could be advantageous in the Indian Ocean, as this region has warmed faster than other tropical regions since the 1950s (Han et al. 2014). Our models confirm this hypothesis by suggesting the expansion of Mascarene petrel's suitable habitat under all climate change scenarios (Figure 4). Under the Paris Agreement scenario, the expansion is relatively minimal compared to medium- and high-range scenarios. In these latter scenarios, ST increases significantly, potentially surpassing the Mascarene petrel optimum. Under such conditions, some areas may become unfavourable (depicted as black pixels in Figure 5). However, in medium- and high-range scenarios, the majority of regions that currently experienced less favourable conditions due to lower temperatures become more suitable for the species in the future (depicted as yellow pixels in Figure 5). Climate change has previously been associated with a potential reduction in the surface of suitable habitat (Legrand et al. 2016) as well as the displacement of favourable at-sea areas during the breeding period (Péron et al. 2012) or the non-breeding period (Grecian et al. 2016), away from breeding grounds. To the best of our knowledge, this study is the first to report a potential positive impact of climate change on the non-breeding at-sea habitat suitability of a seabird. This potential positive impact does not seem to be an artefact of the thermal niche truncation (Feeley and Silman 2010), as evidenced by the observed reduction in habitat suitability at higher temperature ranges (ST > 28°C, Figure 2). Additionally, the modelled Mascarene petrel thermal niche might only reflect a portion of its current or future fundamental niche (Chevalier et al. 2024). Consequently, its theoretical adaptability to climate change may be underestimated.

The non-breeding habitat of the Mascarene petrel could therefore offer an advantage in the face of climate change, assuming the preservation of all links in the trophic chain and the absence of any ecological regime shift (Lees et al. 2006; Grémillet et al. 2008). Climate change has been shown to increase the mismatch between the availability of food resources and the timing and location expected by seabirds (Keogan et al. 2018). This match–mismatch could lead to an ecological trap, as described in several seabird species (Grémillet and Boulinier 2009), where birds may shift to lower-quality prey (Fromant et al. 2021) or become concentrated in productive areas where their prey has been affected by climate change (Grémillet and Boulinier 2009). Additionally, the Mascarene petrel faces potentially numerous other threats at sea during the non-breeding period including industrial fisheries due to overfishing, as well as maritime pollution from maritime trade. For example, significant overfishing in the Indian Ocean (Zeller et al. 2023) may result in a decrease in the density of sub-surface predators, such as tuna, which help tropical seabirds to catch their prey (Thiebot and Weimerskirch 2013).

4.3 | Challenges in Migratory Species Vulnerability Assessment

The geographic range has been identified as one of the most reliable predictors of extinction risk (Chichorro et al. 2019). The Mascarene petrel's extensive geographic range over the Indian Ocean during its non-breeding period offers more opportunities to adapt its diet or distribution in response to environmental changes compared to species with smaller ranges (Chichorro et al. 2019). Another noteworthy trait is the inter-individual variability in distribution, which appears to predispose it to adapt to changing conditions (Phillips et al. 2017). High inter-individual variability may confer an advantage as threats vary in each non-breeding area. Our results thus indicate that several traits of Mascarene petrels lead to a low sensibility to climate change and potentially to other anthropogenic threats during the non-breeding period. Combined with the low exposure to climate change suggested in this study, the vulnerability of Mascarene petrel should be considered weak during the non-breeding period.

In contrast, the Barau's petrel, another endemic petrel of Reunion Island, shows a greater vulnerability during its non-breeding period (Legrand et al. 2016). This species has a smaller non-breeding distribution with low inter-individual variability and is potentially more exposed to the impacts of climate change (Legrand et al. 2016). This might seem paradoxical as the IUCN Red List status is more favourable for the Barau's petrel (BirdLife International 2018a) than for the Mascarene petrel (BirdLife International 2018b) and they experienced similar terrestrial threats. This difference in conservation status is primarily attributed to a larger population size estimation for Barau's petrel (33,000 breeding pairs, Chevillon et al. 2022), which likely reflects variations in species demographic histories (Teixeira et al. 2024).

Our study exemplifies the challenges of assessing the vulnerability of migratory species, whose threats can vary across different habitats and life stage. To accurately evaluate their vulnerability, it is essential to consider the entire life cycle. Our projections indicate that the Mascarene petrel may experience stable or slightly improved climatic suitability in its non-breeding marine habitat, suggesting a potential ‘climate change winner’ signal at sea. In contrast, it is an island endemic with a very small population, facing severe threats at its terrestrial breeding sites. These include predation by introduced mammals, such as cats and rats which kill chicks and adults, and light-induced mortality (Chevillon et al. 2022; Juhasz et al. 2022). Taken together, these results emphasize that focusing on a single season or environment can misrepresent overall vulnerability. The Mascarene petrel may appear comparatively favoured in terms of marine climatic suitability during the non-breeding period, yet remains a ‘global change loser’ when considering its full annual cycle and the cumulative impacts of strong land-based pressures. Maintaining active conservation efforts across all habitats used by migratory species throughout their life cycle is thus crucial, as these species rely on multiple habitats, increasing their exposure to threats at different life stages.

Author Contributions

A.J., M.L.C. and P.P. conceived and designed the study, M.L.C. and P.P. performed fieldwork, L.H. performed molecular sexing, R.F., A.J., F.G. and M.S. analysed the data, R.F. and A.J. wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Current environmental variables were downloaded using E.U Copernicus Marine Service Information https://data.marine.copernicus.eu/products (see Appendix S1 for details). The bathymetry is the ETOPO 2006 product obtained from the NOAA website: https://oceanservice.noaa.gov/. Historic and future environmental variables from CMIP6 were downloaded on ESGF website: https://esgf-node.llnl.gov/projects/cmip6/. Code used to download and process environmental variables and to run habitat selection models is available on GitHub: https://github.com/r-fernandezz/. Tracking data are available on: https://data.seabirdtracking.org/dataset/2059.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Full description of environmental predictors used in the Mascarene petrel distribution model. **Appendix S2:** Mean model evaluation metrics by algorithm across all fitted models. The True Skill Statistic (TSS) index, used for both external and internal validations, ranges from 0 (poor validation) to 1 (excellent validation). Sensitivity and specificity range from 0 (weak model capacity to identify true presence or absence, respectively) to 100 (strong model capacity to identify true presence or absence, respectively). **Appendix S3:** Spatial standard deviation of predicted habitat suitability across the individual models retained for the ensemble ($TSS \geq 0.6$). **Appendix S4:** Projection of future habitat suitability of the Mascarene petrel based on climatic change scenarios (low-range: SSP1-2.6, mid-range: SSP3-7.0, high-range: SSP5-8.5) and different time periods (2020–2040, 2040–2060 and 2060–2080).