

# Current Biology

## Tracking seabird migration in the tropical Indian Ocean reveals basin-scale conservation need

### Highlights

- Non-breeding seabirds dispersed widely across tropical Indian Ocean
- Divergent habitat use and itinerancy preclude localized aggregations
- Diffuse richness  $>3.9$  M km<sup>2</sup>, contrary to multi-species tracking in other oceans
- Indian Ocean tropical seabird conservation requires high seas perspective

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### In brief

Marine predators often aggregate in highly productive areas. In contrast, Trevail et al. found divergent habitat use and itinerancy of non-breeding seabirds in the tropical Indian Ocean caused diffuse species richness across  $>3.9$  M km<sup>2</sup>. These findings challenge marine predator distribution paradigms and highlight the need for high seas legislation.

Report

# Tracking seabird migration in the tropical Indian Ocean reveals basin-scale conservation need

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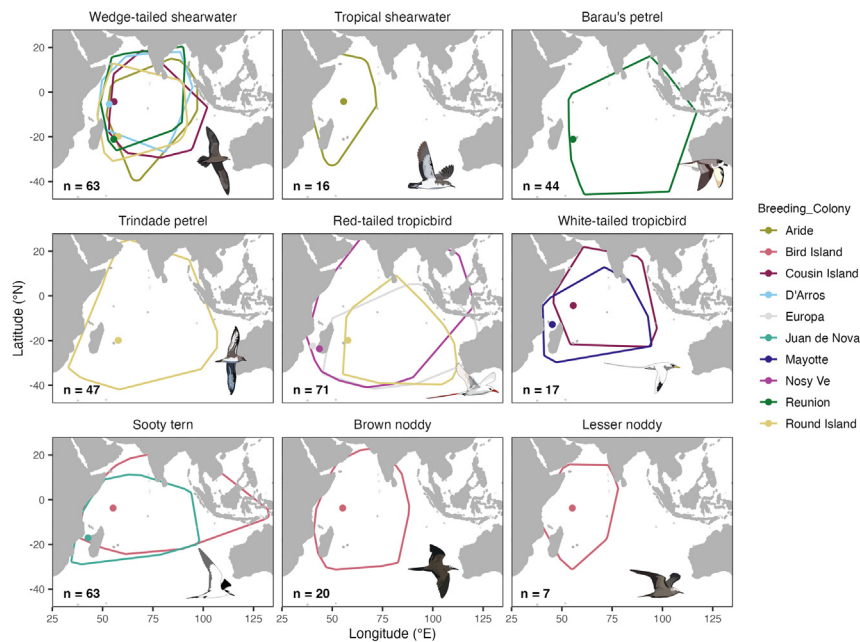
## SUMMARY

Understanding marine predator distributions is an essential component of arresting their catastrophic declines.<sup>1–4</sup> In temperate, polar, and upwelling seas, predictable oceanographic features can aggregate migratory predators, which benefit from site-based protection.<sup>5–8</sup> In more oligotrophic tropical waters, however, it is unclear whether environmental conditions create similar multi-species hotspots. We track the non-breeding movements and habitat preferences of a tropical seabird assemblage ( $n = 348$  individuals, 9 species, and 10 colonies in the western Indian Ocean), which supports globally important biodiversity.<sup>9–12</sup> We mapped species richness from tracked populations and then predicted the same diversity measure for all known Indian Ocean colonies. Most species had large non-breeding ranges, low or variable residency patterns, and specific habitat preferences. This in turn revealed that maximum species richness covered  $>3.9$  million  $\text{km}^2$ , with no focused aggregations, in stark contrast to large-scale tracking studies in all other ocean basins.<sup>5–7,13,14</sup> High species richness was captured by existing marine protected areas (MPAs) in the region; however, most occurred in the unprotected high seas beyond national jurisdictions. Seabirds experience cumulative anthropogenic impacts<sup>13</sup> and high mortality<sup>15,16</sup> during non-breeding. Therefore, our results suggest that seabird conservation in the tropical Indian Ocean requires an ocean-wide perspective, including high seas legislation.<sup>17</sup> As restoration actions improve the outlook for tropical seabirds on land<sup>18–22</sup> and environmental change reshapes the habitats that support them at sea,<sup>15,16</sup> appropriate marine conservation will be crucial for their long-term recovery and whole ecosystem restoration.

## RESULTS

Tropical marine ecosystems are in urgent need of protection to arrest catastrophic biodiversity loss.<sup>4</sup> Spatial protection of static habitats, such as reefs, seagrass beds, and mangroves, have produced conservation dividends<sup>23–25</sup> and often include core distributions of resident and breeding species.<sup>26,27</sup> However, it

is more challenging to implement a coherent strategy for mobile marine predators,<sup>1–3</sup> which play a key role in tropical ecosystem function, especially coral reef conservation.<sup>9–11</sup> Current tropical seabird communities are a fraction of historic sizes, largely due to the impacts of habitat destruction, human exploitation, invasive species,<sup>19,28–30</sup> and overfishing.<sup>31,32</sup> Land-based interventions at colonies provide hope for halting and reversing tropical



**Figure 1. Broad-scale species and colony-specific distribution of geolocator tracked western Indian Ocean seabirds**

Minimum convex polygons for each population expanded by the average precision radius of the location estimates from the state space model (90 km) used to extract pseudo-absences for habitat selection analyses. Minimum convex polygon outlines are colored by colony location. Number of individuals (across all populations) is denoted for each species.

each species spent on average ( $\pm$  SE)  $2.26 \pm 0.15$  consecutive days in a 200 km grid cell (range: 0.5–52.5; [Figure 3](#)). There was no clear spatial clustering of residency; rather, patterns were diffuse across the Indian Ocean ([Figure 3](#)).

### Diversity distributions

Species richness was high across large areas of the region. This pattern was prevalent

when considering observed richness from tracking data ([Figure 2B](#)) and predictions from both tracked colonies ([Figure 2C](#)) and non-tracked colonies ([Figure 2D](#)) and was consistent over the calendar year ([Figure S3](#)). Observed species richness was highly correlated with the number of tracked individuals (Pearson's correlation coefficient:  $r_{2472} = 0.86$ ,  $p < 0.01$ ). When considering predictions from tracked colonies only, species richness was highest where most populations' distributions overlap ([Figure 2C](#)). Predictions extended to all regional colonies further emphasized homogeneous species richness across the tropical Indian Ocean ([Figure 2D](#)). All nine species were predicted to occur in 113 grid cells (6.0%), totaling 3,914,595 km<sup>2</sup> and >two-thirds ( $\geq 7$  species) in 477 grid cells (25.4%), totaling 16,524,436 km<sup>2</sup>. There was some spatial clustering of species during the year in the central Indian Ocean and east of Seychelles; however, richness was predicted to be high ( $\geq 7$  species) across 6 to 10 million km<sup>2</sup> from November to September and >3 million km<sup>2</sup> during October when only seven species were tracked ([Figure S3](#)).

seabird population declines.<sup>18–22</sup> Nevertheless, threats at sea are more challenging to resolve. This is particularly the case during non-breeding, which can represent >50% of the annual cycle and is when migratory species may cross ocean basins and international boundaries, potentially being exposed to anthropogenic impacts on the high seas<sup>7,33,34</sup> and risking high mortality rates.<sup>15,16</sup> It is imperative, therefore, that we gain better knowledge of the migratory range of tropical seabirds<sup>35–39</sup> and factors driving their at-sea distributions.<sup>31,40</sup>

At higher latitudes marine predator aggregations have targeted effort towards area- and habitat-specific protection,<sup>5–8</sup> but there is limited evidence that this is relevant to migratory species in the tropics.<sup>26</sup> We tracked tropical seabird movements during non-breeding to ascertain species-specific habitat preferences, identify areas of high species richness, and quantify overlap with the current marine protected area (MPA) network. We also use habitat preferences of tracked birds to predict their distribution from all known tropical Indian Ocean colonies (i.e., including those for which tracking data are unavailable) based on marine habitat suitability. Together with calculations of spatiotemporal residency, our research provides a comprehensive understanding of a tropical seabird assemblage's non-breeding distribution based on at-sea behavior, habitat use, and colony locations.

### At-sea distributions

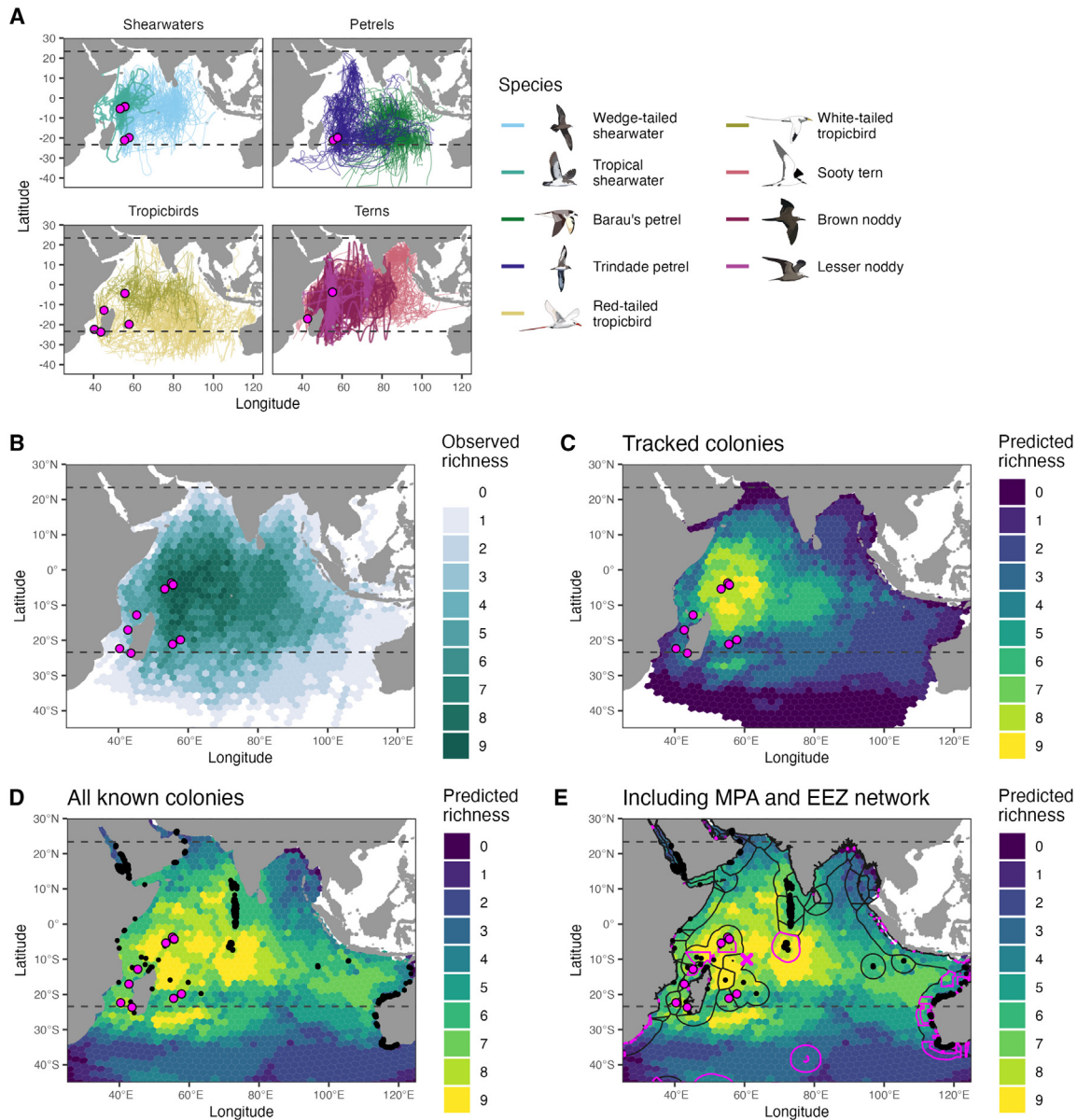
We tracked non-breeding seabirds that represent the regional assemblage of oceanic migratory species, comprising 348 individuals from nine species across ten western Indian Ocean colonies between 2008 and 2015 ([Figure 1](#) and [Table S1](#)). Their at-sea distributions covered large areas ([Figure 1](#)), and individual tracks were widely dispersed, overlapping within and among species ([Figure 2A](#)). Despite occupying broadly similar areas ([Figure 1](#)), species differed in their response to ten environmental variables ([Table S2](#) and [Figure S1](#)), both in direction and magnitude of habitat preferences ([Figure S2](#)). Tracked individuals from

For wedge-tailed shearwaters, *Ardenna pacifica*, red-tailed tropicbirds, *Phaethon rubricauda*, and sooty terns, *Onychoprion fuscatus*, habitat selection model area under the receiver operator characteristic curve (AUC) values were  $< 0.7$ , indicating weaker predictive power based on environmental variables ([Table S3](#)). When we excluded these species from predictions, results were consistent with those presented here. Predictive power of each environmental variable differed among species, although distance to the colony and sea-surface temperature were consistently important ([Figure S2](#)).

Predictions extended to all regional colonies further emphasized homogeneous species richness across the tropical Indian Ocean ([Figure 2D](#)). All nine species were predicted to occur in 113 grid cells (6.0%), totaling 3,914,595 km<sup>2</sup> and >two-thirds ( $\geq 7$  species) in 477 grid cells (25.4%), totaling 16,524,436 km<sup>2</sup>. There was some spatial clustering of species during the year in the central Indian Ocean and east of Seychelles; however, richness was predicted to be high ( $\geq 7$  species) across 6 to 10 million km<sup>2</sup> from November to September and >3 million km<sup>2</sup> during October when only seven species were tracked ([Figure S3](#)).

### Potential value of Indian Ocean MPAs

Of the five largest MPAs in the eastern Indian Ocean, two were visited by two-thirds of species tracked (Amirantes to Fortune Bank Area of Outstanding Natural Beauty (AONB) & Chagos Archipelago MPA; [Table 1](#)). Based on predictions from all colonies, the five MPAs were predicted to support  $\geq 7$  species, although



**Figure 2. Year-round non-breeding distribution of tracked tropical seabirds in the Indian Ocean**

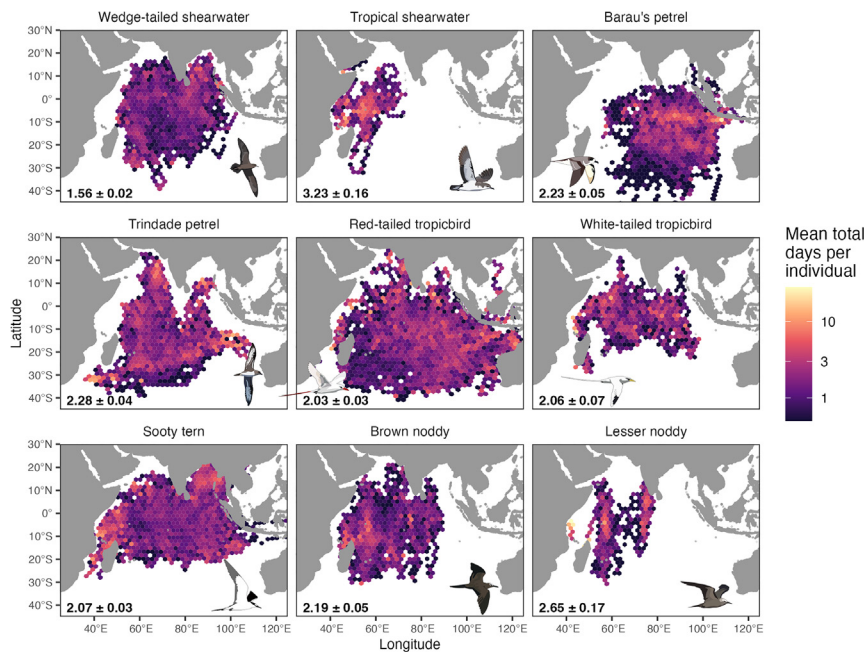
Distributions shown as (A) filtered geolocator tracks from 348 individuals of nine species (inserts aggregated by family) from ten colonies (pink circles) in the western Indian Ocean, showing species' known breeding range across the Indian Ocean (solid black circles); (B) observed species richness across a 200km tessellated grid; (C) predicted species richness based on habitat selection from tracked colonies; (D) predicted species richness based on habitat selection and considering distance of each grid cell to breeding colonies across species entire Indian Ocean range (solid black circles); and (E) overlay with location of all exclusive economic zones (EEZs; black outlines), the current network of marine protected areas (MPA) (orange outlines), and the Saya de Malha bank (orange asterisk) proposed by the High Seas Alliance as a pelagic MPA under the United Nations BBNJ Agreement. Tropics of Cancer (23.4°N) and Capricorn (23.4°S) are shown in gray dashed lines.

See also [Figures S2](#), [S3](#), and [Table S3](#).

with only small percentages of maximum richness areas (nine species; 12.4% total across all five MPAs; [Table 1](#)). Individual seabirds of each species spent, on average, between  $2.3 \pm 0.7$  and  $3.6 \pm 2.7$  days per year within an MPA ([Table 1](#)).

Habitat selection models including the Chagos Archipelago MPA revealed both attraction and avoidance of the fully protected area; given all environmental variables, three species

had a higher probability of presence outside of the MPA (parameter estimates as odds ratios  $\pm$  SE, equivalent to likelihood of observation outside an MPA compared to inside, where 1 = no selection, values  $> 1$ : MPA avoidance,  $< 1$ : MPA selection; tropical shearwater  $2.24 \pm 0.22$ , Trindade petrel  $1.51 \pm 0.03$ , and brown noddy  $1.15 \pm 0.02$ ), Barau's petrels showed no significant difference ( $0.99 \pm 0.02$ ), and the remaining five species had a



**Figure 3. Residency patterns for nine species of migratory western Indian Ocean seabirds**

Residency is expressed as cumulative days spent in a 200 km grid cell per year, presented on a log-transformed color scale. Mean ( $\pm$  SE) residency per grid cell is denoted in the bottom left corner for each species. These geolocator tracked birds tended to be more itinerant than resident.

to productive and spatiotemporally predictable frontal and upwelling zones along coastlines<sup>5,13</sup> and around seamounts.<sup>7</sup> By contrast, pelagic waters in the tropics tend to be oligotrophic,<sup>44</sup> and prey is considered less predictable than in shelf seas,<sup>45,46</sup> possibly driving the patterns observed here (Figure 2). Widespread migratory seabird diversity across the Indian Ocean could arise either because high productivity areas do not offer sufficient food to support dense multi-species aggregations, tropical seabird migration

higher probability of presence inside the MPA (lesser noddy  $0.35 \pm 0.01$ , wedge-tailed shearwater  $0.60 \pm 0.01$ , white-tailed tropicbird  $0.70 \pm 0.01$ , red-tailed tropicbird  $0.70 \pm 0.01$ , and sooty tern  $0.71 \pm 0.01$ ). When all MPAs in the region, regardless of current designation status, were considered as fully protected, the five largest MPAs still were predicted to be visited by six to nine species (Table 1).

#### Use of exclusive economic zones and high seas

40.7% of the 113 Indian Ocean grid cells that predicted maximum species richness fell within exclusive economic zones (EEZs) (Figure 2E), comprising a total area of 1,593,552 km<sup>2</sup>. The remaining 59.3% (2,321,043 km<sup>2</sup>) are in high seas.

## DISCUSSION

Seabirds breeding in the western Indian Ocean migrated widely across the tropical Indian Ocean (Figure 1) with diffuse patterns of diversity and predicted maximum species richness across an area >3.9 million km<sup>2</sup> and over two-thirds of species richness ( $\geq 7$  species) across >16 million km<sup>2</sup> (Figure 2). These distributions appear to be a consequence of large winter ranges (Figure 1), species-specific habitat preferences (Figure S2), and rather low or variable residency (Figure 3). Our findings are in stark contrast with multi-species marine predator aggregations in all other ocean basins,<sup>5–7,13,14</sup> with important implications for seabird conservation and marine spatial management, as globally habitats that support predator aggregations have been successfully targeted for spatial protection.<sup>43</sup>

#### At-sea distributions

Multi-species marine predator tracking has consistently described diversity hotspots across all the world's other oceans—Atlantic,<sup>5,7</sup> Arctic,<sup>14</sup> Southern,<sup>6</sup> and Pacific,<sup>13</sup> linked

strategies differ from temperate counterparts, or a combination of both.

We used habitat selection models to predict species richness from all regional colonies because it enabled us to identify environmental drivers of assemblage distributions and is resilient to uncertain and fluctuating population estimates. Species richness was high around tracked colonies (Figures 2B and 2C), and distance to colony was an important habitat selection predictor (Figure S2) most likely because space use around colonies is inherent to dispersive central-place movements during inbound and outbound migrations. This emphasizes the importance of considering regional-scale predictions from all known colonies to understand assemblage distribution (Figure 2D). Areas of high abundance and species richness are vital for conservation,<sup>7</sup> but many areas, such as the tropical Indian Ocean, have incomplete information on seabird population estimates. It would be valuable to determine whether species-specific hotspots exist by incorporating population estimates where colony sizes are well understood (for example, within the western Indian Ocean). Nevertheless, given the diverse range of inter-individual variation in migratory strategies (Figure 3), it is unclear whether such aggregations would emerge in the tropical Indian Ocean.

Although the Indian Ocean is largely oligotrophic, seasonal phytoplankton blooms occur in neritic and pelagic waters<sup>44</sup> supporting large numbers of tuna, billfishes, turtles, and whales.<sup>9,47,48</sup> Many tropical seabirds forage facultatively with sub-surface predators including tuna and dolphins, which drive prey towards the surface,<sup>49,50</sup> but we found no evidence of particularly high seabird diversity or residency in these areas (Figure 1). Some species may avoid highly productive areas to reduce competition<sup>36,51,52</sup> or because poorer water clarity may reduce foraging success.<sup>52,53</sup> Niche segregation would explain species-specific habitat selection and in turn preclude species aggregations in the Indian Ocean.

**Table 1. Observed species richness, predicted species richness, and residency of western Indian Ocean seabirds within the five largest marine protected areas (MPA) in the region (>15,000 km<sup>2</sup>)**

| MPA   | Area (km <sup>2</sup> ) | Designation status   | Max observed species richness within MPA | Max predicted species richness within MPA (from prediction across Indian Ocean range) | % of hexagons with highest predicted species richness (9 species) within MPA | Predicted species richness under current management and if fully protected (± SE among grid cells) | Mean number of total days per individual & year, per species, spent within MPA (± SE) |
|---|-------------------------|--|--|---|--|--|---|
| Chagos Archipelago MPA  | 640,000.00              | Fully protected (No extractive or destructive activities are allowed, all impacts minimized)                           | 6  | 9   | 9.7  | Current:<br>8.4 ± 0.15<br>Fully protected:<br>8.4 ± 0.15   | 2.3 ± 0.7   |
| <b>Amirantes (Marine) to Fortune Bank (Marine) Area of Outstanding Natural Beauty, Seychelles</b> | 217,588.62              | Designated and Unimplemented (Legally designated as a protected area, but not implemented with effective restrictions) | 6  | 8   | 0  | Current:<br>8.0 ± 0.0<br>Fully protected:<br>8.0 ± 0.0   | 3.0 ± 0.9   |
| <b>Aldabra Group (Marine) National Park, Seychelles</b>   | 201,235.80              | Designated and Unimplemented   | 5  | 9   | 2.7  | Current:<br>7.8 ± 0.4<br>Fully protected:<br>8.3 ± 0.3   | 3.1 ± 1.7   |
| <b>Mayotte Marine Nature Park</b>   | 68,381.00               | Less Protected (marine protection in place but allows some resource extraction)  | 1  | 7   | 0  | Current:<br>7.0 ± NA<br>Fully protected:<br>6.0 ± NA   | 3.6 ± 2.7   |
| <b>Glorieuses Marine Nature Park</b>  | 43,000.00               | Less Protected   | 2  | 7   | 0  | Current:<br>7.0 ± NA<br>Fully protected:<br>8.0 ± NA   | 3.2 ± 1.5   |

Predicted richness was taken from models excluding the MPA network, i.e., under current spatial management in the region. MPA areas are from the World Database on Protected Areas (WDPA).<sup>41</sup> Definitions of MPA designation are taken from the MPA Atlas.<sup>42</sup> See also [Table S3](#).

Residency patterns suggest that non-breeding seabirds in the Indian Ocean do not spend long periods in a single area with marked inter-individual variation (Figure 3). However, Barau's petrels, *Pterodroma baraui*, and sooty terns, *Onychoprion fuscatus*, both occupy distinct wintering areas, although they tend to be very large (e.g., Barau's petrel core wintering area ranges from 1.4 to 3 million km<sup>2</sup>).<sup>36,51</sup> Moreover, while sooty terns exhibit individual migratory site and route fidelity,<sup>36</sup> some other species are highly dispersive,<sup>31,36,38</sup> which, together with generally low residency, is consistent with low predictability of suitable foraging habitat.<sup>45</sup> More work is required to understand how the tropical environment influences migration strategies, such as individual routes and site fidelity across years,<sup>54,55</sup> both of which can have important implications for the evolution of seabird life history strategies.<sup>56,57</sup>

### Conservation implications

The current MPA network in the western Indian Ocean comprises three very large MPAs (>100,000 km<sup>2</sup>) and two smaller MPAs (>40,000 km<sup>2</sup>), all within EEZs around seabird breeding populations. Existing MPA designation did not account for seabird foraging areas, e.g., see Koldewey et al.<sup>58</sup> Nevertheless, at least eight species were predicted to occur within these MPAs, where they spent slightly more time compared to outside them (average < 4 days vs. 3 days, respectively). As well as itinerancy, 88% of maximum species richness area occurred outside MPAs, suggesting that prevailing area-specific methods of marine protection<sup>43,59</sup> are a poor fit for these species during non-breeding. We also note, however, that the low degree of migratory connectivity (i.e., the weak linkage between breeding and non-breeding distributions) in the Indian Ocean may in part mitigate risk.<sup>60</sup>

MPAs (if properly protected) may benefit both locally breeding seabirds and itinerant non-breeders via reduced extractive and destructive activities, including fishing of potential prey and sub-surface predators that offer facultative foraging opportunities. Tropical seabirds do not appear to suffer greatly from bycatch (although some may be caught intentionally for food) and do not tend to compete directly with fisheries, which typically target large fish such as tuna and billfish.<sup>31,32</sup> Even if all Indian Ocean MPAs were included in predictive models as “fully protected,” the current MPA network is not sufficient to capture the full extent of maximum species richness areas (3,914,595 km<sup>2</sup>).

Anthropogenic impact is increasing in the high seas,<sup>61</sup> beyond national jurisdiction, where tropical seabirds face threats from fisheries, shipping, and pollution.<sup>31</sup> While the importance of these areas for albatross and large petrels has been established,<sup>34</sup> our study highlights their importance for high diversity across three seabird orders (i.e., Procellariiformes, Phaethontiformes, and Charadriiformes; Figure 2). The adoption of the forthcoming United Nations Convention on the Law of the Sea on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction (known as the BBNJ Agreement) provides a crucial framework for area-based management on the high seas.<sup>17,62</sup> The High Seas Alliance has identified the Saya de Mahla bank in the Indian Ocean, to the north-east of Madagascar, as a priority high seas MPA,<sup>63,64</sup> which could offer value in an area of high seabird richness (Figure 2E). Dynamic MPAs, where spatial boundaries move to track key

environments, have also been proposed for effective high sea conservation<sup>65</sup>; however, divergent habitat drivers (Figure S2) suggest this would be ineffective for non-breeding seabirds in the Indian Ocean. Therefore, we suggest that future interventions focus on international protection and sustainable resource extraction supported by the BBNJ Agreement<sup>17,34,66</sup> such as fisheries employing basin-scale stock assessments, international catch limit agreements, robust enforcement to reduce overexploitation, and societal changes to improve compliance.<sup>67,68</sup>

### Limitations

We used tracking data from the comparatively well-studied western Indian Ocean to predict species richness from all seabird colonies in the tropical Indian Ocean. Understanding whether habitat selection is similar for eastern Indian Ocean colonies (Figure 2A) would therefore be valuable.<sup>69</sup> Moreover, our predictions of species richness are limited to nine tracked species, representing about one-third of breeding seabirds in the region, and exclude the widely dispersed Sulidae (boobies, comprising four species) and Fregatidae (frigatebirds, comprising three species). Nevertheless, Sulids appear to be non-migratory in the tropics,<sup>27</sup> and frigatebirds migrate to island stopovers<sup>70</sup> such that spatial protection around breeding colonies may provide effective year-round conservation. Because we omit higher-latitude species, we most likely underestimate the total species richness in the Southern Ocean, off the western coast of Australia and inside respective MPAs. Further environmental covariates may also be important, such as those related to rainfall and visibility.<sup>71,72</sup>

### Conclusions

Our results suggest migratory seabird diversity is spread over a huge area of the tropical Indian Ocean, mostly in the high seas. This appears to be a consequence of species-specific habitat requirements, large wintering areas, and low migratory connectivity. These results highlight the biodiversity importance of the high seas and that at-sea safeguarding of seabirds requires a larger scale approach than area-specific protection, such as those recommended in temperate and polar seas. Restoring and maintaining tropical seabird communities is essential for surrounding ecosystems because of their positive impacts on nutrient cycling and coral reef health.<sup>11,73</sup> As terrestrial restoration improves breeding habitat conditions and environmental change reshapes marine conditions, large-scale high seas protection requires different scales of thinking<sup>74</sup> and societal changes to ensure seabirds have suitable at-sea environments into the future.

### STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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### SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2023.10.060>.

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### AUTHOR CONTRIBUTIONS

A.T., S.V., M.N., and R.F. designed the study and wrote the manuscript. Geo-location data were collected and analyzed to resolve migration locations for this manuscript from (1) wedge-tailed shearwaters on (a) Aride by G.R., V.B., L.C., and P.A.; (b) Cousin by M.L.C. and N.S.; (c) D'Arros by M.L.C.; (d) Reunion by M.L.C.; (e) Round Island by M.L.C.; (2) Tropical shearwater on Aride by G.R., V.B., L.C., and P.A.; (3) Barau's petrel on Reunion by M.L.C. and P.P.; (4) Trindade petrel on Round Island by M.N. and K.N.; (5) Red-tailed tropicbird on (a) Europa by A.J., M.L.C., and P.P.; (b) Nosy Ve by A.J., M.L.C., and V.P.; (c) Round Island by M.L.C. and P.P.; (6) White-tailed tropicbird on (a) Cousin by M.L.C. and N.S.; (b) Mayotte by M.L.C.; (7) Sooty tern on (a) Bird Island by A.J. and C.F.; (b) Juan de Nova by M.L.C. and S.O.; (8) Brown noddy on Bird Island by C.L., A.J., C.F., and M.L.C.; and (9) Lesser noddy on Bird Island by C.L., A.J., C.F., and M.L.C.. A.T., R.F. and J.S. analyzed location and environmental data to construct habitat suitability models. All authors contributed critically to the drafts.

### DECLARATION OF INTERESTS

The authors declare no competing interests.

### INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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## STAR★METHODS

### KEY RESOURCES TABLE

| REAGENT or RESOURCE                               | SOURCE   | IDENTIFIER  |
|---|--|---|
| <b>Experimental models: Organisms/strains</b>     |  |   |
| Wedge-tailed shearwater; <i>Ardenna pacifica</i>  | Aride Island, Seychelles; 4.2 S 55.7 E           | N/A   |
| Wedge-tailed shearwater; <i>Ardenna pacifica</i>  | Cousin Island, Seychelles; 4.3 S 55.7 E          | N/A   |
| Wedge-tailed shearwater; <i>Ardenna pacifica</i>  | D'Arros Island, Seychelles; 5.4 S 53.3 E         | N/A   |
| Wedge-tailed shearwater; <i>Ardenna pacifica</i>  | Reunion; 21.1S 55.5E                             | N/A   |
| Wedge-tailed shearwater; <i>Ardenna pacifica</i>  | Round Island, Mauritius; 19.9 S 57.8 E           | N/A   |
| Tropical shearwater; <i>Puffinus bailloni</i>     | Aride Island, Seychelles; 4.2 S 55.7 E           | N/A   |
| Barau's petrels; <i>Pterodroma barau</i>          | Reunion; 21.1S 55.5E                             | N/A   |
| Trindade petrel; <i>Pterodroma arminjoniana</i>   | Round Island, Mauritius; 19.9 S 57.8 E           | N/A   |
| Red-tailed tropicbird; <i>Phaethon rubricauda</i> | Europa Island; 22.4 S 40.4 E                     | N/A   |
| Red-tailed tropicbird; <i>Phaethon rubricauda</i> | Nosy Ve, Madagascar; 23.7 S 43.6 E               | N/A   |
| Red-tailed tropicbird; <i>Phaethon rubricauda</i> | Round Island, Mauritius; 19.9 S 57.8 E           | N/A   |
| White-tailed tropicbird; <i>Phaethon lepturus</i> | Cousin Island, Seychelles; 4.3 S 55.7 E          | N/A   |
| White-tailed tropicbird; <i>Phaethon lepturus</i> | Mayotte; 12.8S 45.3E                             | N/A   |
| Sooty tern; <i>Onychoprion fuscatus</i>           | Bird Island, Seychelles; 3.72 S 55.2 E           | N/A   |
| Sooty tern; <i>Onychoprion fuscatus</i>           | Juan de Nova; 17.1 S 42.7 E                      | N/A   |
| Brown noddy; <i>Anous stolidus</i>                | Bird Island, Seychelles; 3.72 S 55.2 E           | N/A   |
| Lesser noddy; <i>Anous tenuirostris</i>           | Bird Island, Seychelles; 3.72 S 55.2 E           | N/A   |
| <b>Deposited data</b>                             |  |   |
| Species distribution ranges                       | This study; BirdLife International <sup>75</sup> | <a href="http://datazone.birdlife.org/home">http://datazone.birdlife.org/home</a>   |
| <b>Software and algorithms</b>                    |  |   |
| R software  | N/A  | <a href="https://cran.r-project.org/">https://cran.r-project.org/</a>   |
| R package <i>GeoLight</i>                         | Lisovski and Hahn <sup>76</sup>                  | <a href="https://cran.r-project.org/src/contrib/Archive/GeoLight/">https://cran.r-project.org/src/contrib/Archive/GeoLight/</a>                             |
| R package <i>TripEstimation</i>                   | Summer et al. <sup>77</sup>                      | <a href="https://cran.r-project.org/web/packages/tripEstimation/index.html">https://cran.r-project.org/web/packages/tripEstimation/index.html</a>           |
| R package <i>foieGras</i>                         | Jonsen et al. <sup>78</sup>                      | <a href="https://cran.r-project.org/src/contrib/Archive/foieGras/">https://cran.r-project.org/src/contrib/Archive/foieGras/</a>                             |
| R package <i>biomod2</i>                          | Thuiller et al. <sup>79</sup>                    | <a href="https://cran.r-project.org/web/packages/biomod2/index.html">https://cran.r-project.org/web/packages/biomod2/index.html</a>                         |
| R package <i>mgcv</i>                             | Raymond et al. <sup>80</sup>                     | <a href="https://cran.r-project.org/web/packages/mgcv/index.html">https://cran.r-project.org/web/packages/mgcv/index.html</a>                               |
| Custom code for statistical analyses              | This study                                       | <a href="https://github.com/AliceTrevail/Indian_Ocean_seabird_distributions.git">https://github.com/AliceTrevail/Indian_Ocean_seabird_distributions.git</a> |

## RESOURCE AVAILABILITY

### Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Alice Trevail ([a.trevail@exeter.ac.uk](mailto:a.trevail@exeter.ac.uk)).

### Materials availability

This study did not generate new unique reagents.

### Data and code availability

- Tracking data availability is noted in original publications (Table S1). Breeding colony location data across the Indian Ocean are available from the BirdLife International Datazone. Co-author updates to colony locations within the Western Indian Ocean are available via GitHub: ([https://github.com/AliceTrevail/Indian\\_Ocean\\_seabird\\_distributions.git](https://github.com/AliceTrevail/Indian_Ocean_seabird_distributions.git)).

- Code to run habitat selection models, richness, and residency calculations are available via GitHub: ([https://github.com/AliceTrevail/Indian\\_Ocean\\_seabird\\_distributions.git](https://github.com/AliceTrevail/Indian_Ocean_seabird_distributions.git)).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

## EXPERIMENTAL MODELS AND SUBJECT DETAILS

### Seabird tracking data

We collated geolocation data for 9 seabird species from 10 colonies across the tropical Western Indian Ocean, from coastal East Africa to 70°E and latitudes 10°N to 30°S, between 2008 and 2018<sup>31</sup>: wedge-tailed shearwater, *Ardenna pacifica* (63 individuals, 5 populations, 5 years, 11 distinct months); tropical shearwater, *Puffinus bailloni* (16 individuals, 1 population, 3 years, year-round); Barau's petrel, *Pterodroma baraui* (44 individuals, 1 population, 4 years, 6 distinct months); Trindade petrel, *Pterodroma arminjoniana* (47 individuals, 1 population, 3 years, year-round); red-tailed tropicbird, *Phaethon rubricauda* (71 individuals, 3 populations, 6 years, year-round); white-tailed tropicbird, *Phaethon lepturus* (17 individuals, 2 populations, 3 years, year-round); sooty tern, *Onychoprion fuscatus* (17 individuals, 2 populations, 3 years, year-round); brown noddy, *Anous stolidus* (20 individuals, 1 population, 4 years, year-round); and lesser noddy, *Anous tenuirostris* (7 individuals, 1 population, 2 years, year-round). Light-level geolocators (global location sensor loggers; hereafter GLS) were attached to a leg ring (metal or plastic). Devices weighed less than 3% of bird body mass. Full tracking methods are available in [Table S1](#) and original publications.<sup>31,36,51,81–83</sup>

## METHOD DETAILS

### Seabird tracking data processing

Locations were estimated from GLS light data using the R packages *GeoLight*<sup>76</sup> or *TripEstimation*.<sup>77</sup> Data analyses, detailed below, follow an analytical framework presented in the [Figure S4](#). We first removed locations from 10 days each side of the equinox (i.e., 20 days total; 10<sup>th</sup> March – 30<sup>th</sup> March & 12<sup>th</sup> September – 2<sup>nd</sup> October) when equitable global day lengths render unreliable light-based location estimates.<sup>84</sup> Individual tracks were then divided into “bursts” where gaps in the data exceeded 15 days to avoid over-interpolation, and bursts with fewer than 20 locations were removed.<sup>85</sup>

To estimate migratory movements of tracked individuals, given the spatial error inherent to GLS telemetry data, we used state space models to predict locations at 12-h intervals.<sup>86</sup> Models were implemented using the function ‘fit\_ssm’ within the R package *foieGras*.<sup>78</sup> A conservative speed filter of 30 ms<sup>-1</sup> was included to remove erroneous locations that can result in problems with model fitting.<sup>85</sup> Tracking locations were modeled with an *a priori* spatial error of 186 km.<sup>87</sup> Adapted from the analysis framework in Ropert-Coudert et al.,<sup>85</sup> models were first run as a correlated random walk for all bursts of tracking data. For bursts where the correlated random walk model failed to converge, as determined using *nlminb* convergence criteria, we used a random walk model. If both correlated random walk and random walk models failed to converge, those tracking bursts were removed from the final dataset. Finally, all model predicted tracks were visually inspected for trends still indicative of a lack of model fit (e.g., large error relative to track length). Any bursts that failed this inspection were removed from the final dataset, which ultimately comprised 80.7% of bursts derived from a correlated random walk, and the remaining 19.2% derived from a random walk. Data from all species, breeding colonies and years were retained in the final dataset. Herein, location estimates and tracks refer to interpolated locations from state space model-derived movement paths.

### Observed species richness

We mapped the at-sea distributions of seabirds using the GLS tracking data. To do so, we constructed a spatial density map of the Indian Ocean by binning location data from tracks into 200km diameter tessellated hexagons, in Lambert azimuthal equal-area projection.<sup>5</sup> For each grid cell, we summed the total number of species present as a measure of relative species richness, both throughout species' migration and by calendar month. To understand the relationship between observed species richness and seabird abundance, we calculated the percentage of tracked individuals in each grid cell, weighted by sample size per species, and calculated correlation between richness and abundance using Pearson's correlation coefficient.

### Environmental variables

Large areas of the Indian Ocean are nutrient-poor, although there are seasonally predictable phytoplankton blooms in some coastal regions, such as the Somalia current, and, to a lesser extent, in mid-ocean basins, triggered predominately by seasonal monsoons that force horizontal advection and vertical nutrient upwelling.<sup>44</sup> At finer scales, locally enhanced productivity can occur where physical oceanographic features mix, advect and/or entrain nutrients,<sup>88</sup> such as at ocean fronts,<sup>89</sup> eddies<sup>90</sup> and seamounts.<sup>91</sup> While seasonally predictable phytoplankton blooms may drive seabird breeding phenology,<sup>92</sup> our understanding of the relative influence of environmental conditions on the migration of multiple seabird species, and the potential for identification of shared habitats in the Indian Ocean, is limited.

To assess at-sea habitat suitability, we extracted several environmental variables that can affect prey availability or accessibility<sup>88</sup>; [Table S2](#) and [Figure S1](#)), bathymetry (seafloor depth, m), seafloor slope (°), sea surface temperature (SST; °C), sea surface temperature anomaly (SSTa, °C), sea surface temperature spatial gradient ( $\nabla$ SST, °C km<sup>-1</sup>), chlorophyll a concentration (mg m<sup>-3</sup>), wind

speed ( $\text{m s}^{-1}$ ), wind stress curl ( $\text{WSC } \nabla \times \tau$ ;  $\text{N m}^{-2} \text{ km}^{-1}$ ), sea surface height (SSH, m), and eddy kinetic energy (EKE;  $\text{m}^2 \text{ s}^{-2}$ ). For each tracking location, we extracted the mean value of each environment variable within the average precision radius of location estimates from the state space model (90 km).

Environmental variables used to understand seabird movement ecology vary from daily to monthly or seasonal composites.<sup>93</sup> To determine the most appropriate temporal resolution for this study, we evaluated the variability of each environmental variable.<sup>94</sup> We extracted daily, weekly, 15-day, and monthly composites of each variable (at 90 km spatial resolution) and for a subset compared both the correlation between mean values and the number of valid pixels. Where correlation between all mean values was high ( $R > 0.7$ ; i.e., low variability between temporal resolutions), we chose the shortest temporal resolution that comprised of  $> 50\%$  valid pixels within a composite. For wind stress curl, a measure of wind-driven up-/downwelling (Table S2), correlation between mean values was moderate, suggesting that wind stress curl varies more over time than other environmental variables here. We therefore chose to include the 7-day composite, which had the highest correlation with other temporal resolutions ( $R > 0.6$ ). Correlation between all environmental variables was low when averaged across the study domain (in all cases,  $-0.5 > R > 0.5$ ), but regions of strong abiotic coupling associated with oceanographic features such as the sub-tropical front, coastal currents, Seychelles-Chagos thermocline ridge and Great Whorl are detected in spatially resolved correlations (Figure S1).

## QUANTIFICATION AND STATISTICAL ANALYSIS

### Habitat selection

We used habitat selection analyses to understand species-specific environment drivers of migratory distribution. As a measure of the available environment, we selected random pseudo-absences from within the minimum convex polygon (MCP; Figure 1) of each population<sup>95</sup> expanded by the average precision radius of the location estimates from the state space model (90 km). Habitat selection was analyzed using generalized additive models (GAMs) with a binomial response variable (used habitat at tracking locations = 1, available habitat within MCPs = 0). We found GAMs had greater predictive power than random forest models, and equal to maximum entropy models, when tested with spatially blocked cross validation in *biomod2*<sup>79</sup> and GAMs in *mgcv*,<sup>80</sup> i.e., a model was trained on a proportion of the data across a spatial grid and the predictive performance on the remaining test proportion was evaluated using AUC values and True skill statistic values. Each species was modeled separately.

All environmental variables were included in all models with smoothers restricted to 4 knots to reduce over-fitting. Variables highly skewed towards zero (SST gradient, chlorophyll and eddy kinetic energy) were log transformed prior to modeling. Distance to the colony was included as a linear predictor in each model to account for high numbers of locations nearby the colony at either end of migration. Year and colony were included as factors when replication across these occurred. We did not include individual ID in any models, because including random slopes for each environmental variable (to capture individual differences in habitat selection) would have been computationally unfeasible.<sup>96</sup> Random intercepts alone do not capture differences in individual habitat selection, and were not necessary because we used the same ratio of pseudo-absences to used points for each individual.<sup>95</sup>

We determined the most appropriate number of pseudo-absences by measuring changes in predictor variables smoothers and model fit using AUC values of models with increasing pseudo-absences from 1 to 50 per used point.<sup>35,97</sup> In all cases, weights were assigned to used locations in the model according to the number of pseudo-absences to account for their relative proportions in the dataset. To assess model validity, we used AUC values and extracted model predictive power, sensitivity and specificity from a confusion matrix<sup>98</sup>; (Table S3).

To interpret habitat selection of each species, we extracted the response curves as well as variable importance as determined by spatially blocked cross validation.

### Predicted species richness

We predicted migratory seabird richness both for tracked populations, and for all breeding populations of the study taxa across the Indian Ocean. Using habitat selection preferences of tracked populations to determine species richness, we were able to include colonies with no tracking data and poor information about population sizes in predictions. We did not include abundance of individuals or populations, but rather consider species richness given accessibility of habitat to breeding colonies across each species' range. Outside of the Western Indian Ocean, population estimates are incomplete, and regional efforts to restore terrestrial breeding habitats are leading to population recoveries that would continue to change the abundance landscape. Furthermore, the regional scale of our analyses (species-level modeling of 10 environmental variables) limited our ability to account for individual variance in our models, which would be key to predicting individual-level abundance from each colony. Here, by predicting spatial patterns of species richness rather than combining tracking with population data, such as has been achieved for better studied regions (e.g.,<sup>7</sup>), our approach; (i) allows us to incorporate colonies of unknown population size thereby increasing spatial scale, (ii) is robust to population changes (either declines or recoveries<sup>18</sup>) ensuring that our estimates remain relevant to future at-sea conservation; and (iii) enables us to identify at-sea environments that are best able to support numerous seabird species. This latter point is increasingly important - as environmental change shifts oceanic conditions, understanding and protecting those ecologically significant areas that support a diversity of different species will be increasingly critical.

We first calculated the mean of all environmental variables in each 200km hexagonal grid cell (described above) across the study period (2008-2018), for each month and year. For each species, we used the habitat selection model (GAMs, described above) to predict the probability of occurrence in each grid cell during each month period, given the environmental conditions.

We predicted probability of seabird occurrence for tracked colonies first, limiting predictions to within MCPs of study populations for each species. We accounted for accessibility to breeding colonies by setting values of colony distance as the mean distance of each grid cell to tracked colonies. To extend predictions of species richness to all breeding colonies within the Indian Ocean, we used current species distribution ranges from BirdLife International<sup>75</sup>; accessed April 2021, visible on the BirdLife online Data Zone: <http://datazone.birdlife.org/home> updated in the Western Indian Ocean (between 28 and 71°E and 26°S–13°N) according to authors' regional knowledge (Figures 2A and 2D). We predicted species occurrence within an estimate of the maximum at-sea range of each species, derived by buffering Indian Ocean breeding distributions by the maximum recorded distance from the colony and maximum southerly extent from the tracking data for each species. We set values of colony distance as the minimum distance of each grid cell to any breeding colony, thereby accounting for the minimum accessibility of a given grid cell to any breeding colony.

We limited predictions to months corresponding to each species' non-breeding period that we have tracking data from, only (Table S1), despite asynchronous breeding across the region by some species. This approach avoids potentially inaccurate assumptions of habitat preference outside of the tracking periods, and therefore we present a conservative estimate of species richness. To marginalize over model fixed effects, all predictions were run using parameter estimates for each colony and year in the original model, and the resulting probabilities of occurrence were averaged. We thereby account for differences in behavior between tracked colonies but make a necessary assumption that models are indicative of species behavior across their range. We then calculated the average probability of occurrence for each month, across all years of the study period. For each month, we calculated whether a species was predicted to be present or absent from optimal thresholds of occurrence from the model receiver operating characteristic (ROC) curves, thereby minimizing both false positives and false negatives. To calculate predicted species richness in each grid cell across the calendar year, we summed the total number of species predicted to be present at any time (i.e., across the species' non-breeding period), therefore following comparable methods to observed species richness.

### Residency

Individual seabirds often show high fidelity to migratory routes and/or large geographic areas.<sup>36</sup> To further understand whether movement dynamics of the Western Indian Ocean seabird assemblage can explain patterns of habitat use, i.e., whether species spend extended periods of residency during migrations in concentrated areas of the Indian Ocean, we calculated the consecutive number of days in a grid cell per individual. We use this as a proxy for residency at the same spatial scale as richness, relevant to environmental gradients and the existing MPA network. This measure is directly comparable among species and does not rely on deriving unknown and potentially species-specific behavioral states from coarse resolution data. We mapped the mean consecutive number of days per grid cell, per individual, for each species across the Indian Ocean region to visualize spatial distributions of residency.

### Potential value of Indian Ocean MPAs

To gain management and conservation insights from movement ecology of the Western Indian Ocean seabird assemblage, we consider the potential value of existing spatial marine management in the Indian Ocean. Current management in the region comprises several MPAs within territorial waters that range from designated but not yet protected, to fully protected.<sup>41</sup> For the five largest MPAs in the Western Indian Ocean (>40,000 km<sup>2</sup>; Aldabra Group (Marine) National Park, Amirantes (Marine) to Fortune Bank (Marine) Area of Outstanding Natural Beauty, Chagos Archipelago MPA, Glorieuses Marine Nature Park, and Mayotte Marine Park) we calculated the maximum observed and predicted species richness at grid cells within the MPA, indicative of habitat suitability, the percentage of grid cells with the highest predicted species richness (9 species) that fall within the MPA network, and the mean consecutive days per individual, per species, at grid cells within the MPA. A grid cell was classified as 'inside' the MPA by > 50% area. Here, we only consider the five largest MPAs in the tropical Western Indian Ocean because our study focusses on species breeding within these latitudes.

The largest MPA in the Indian Ocean, the Chagos Archipelago MPA, has been fully protected from all extractive activities since 2010,<sup>58</sup> although some illegal fishing persists.<sup>67</sup> As a measure of seabirds' use of fully protected MPAs, given their habitat preferences, we ran additional habitat selection models (as described above) including whether a location was inside or outside of the Chagos Archipelago MPA as a factor. We then tested whether the entire network of proposed, designated and implemented MPAs in the Indian Ocean would capture species richness if they were to be fully protected. To do so, we predicted species richness using habitat selection models including the Chagos Archipelago MPA. We assigned any grid cell for which > 50% of the area was within any MPA as 'inside' as a way of simulating the same level of protection as within the Chagos Archipelago MPA. Predictions were implemented with monthly environmental values and considering accessibility to all colonies in the region from the BirdLife International distribution dataset as described above. We then extracted predicted richness within the 5 largest MPAs within the Western Indian Ocean (Table 1).

MPAs both in the Indian Ocean and globally have, to date, been designated within EEZs (200NM offshore). There is increasing recognition that protection of marine species requires consideration of the high seas, outside of territorial jurisdiction.<sup>2</sup> To understand the distribution of tropical seabird species richness in the Indian Ocean between EEZs and the high seas, we quantified the percentage of grid cells with the highest predicted species richness (9 species, from models excluding MPA, therefore representative of current spatial management) that fall both within EEZs<sup>99</sup> and in international waters on the high seas).