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REVIEW

Toward a global strategy for seabird tracking

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Abstract

Electronic tracking technologies revolutionized wildlife ecology, notably for studying the movements of elusive species such as seabirds. Those advances are key to seabird conservation, for example in guiding the design of marine protected areas for this highly threatened group. Tracking data are also boosting scientific understanding of marine ecosystem dynamics in the context of global change. To optimize future tracking efforts, we performed a global assessment of seabird tracking data. We identified and mined 689 seabird tracking studies, reporting on > 28,000 individuals of 216 species from 17 families over the last four decades. We found substantial knowledge gaps, reflecting a historical neglect of tropical seabird ecology, with biases toward species that are heavier, oceanic, and from high-latitude regions. Conservation status had little influence on seabird tracking propensity. We identified 54 threatened species for which we did not find published tracking records, and 19 with very little data. Additionally, much of the existing tracking data are not yet available to other researchers and decision-makers in online databases. We highlight priority species and regions for future tracking efforts. More broadly, we provide guidance toward an ethical, rational, and efficient global tracking program for seabirds, as a contribution to their conservation.

KEYWORDS

biogeography, biologging, biotelemetry, ecological monitoring, marine conservation, oceanography, spatial planning, threatened species

1 | INTRODUCTION

Electronic tracking technologies are revolutionizing the study of animal movements (Kays et al., 2015; Sergio et al., 2014), bolstered by mass production industries, such as cellular phones (Burger & Shaffer, 2008) and by powerful tools to store and analyze the huge amounts of data produced (López-López, 2016). By fitting miniature trackers to elusive wild animals, researchers expanded the discipline of spatial ecology to scales ranging from seconds and centimeters, to entire animal lives and the planet (Lohmann, 2018; Nathan et al., 2008). Scientific advances have been particularly spectacular in the marine environment, where animal tracking opened up new worlds of knowledge

(Block et al., 2011; Bonfil et al., 2005). Many such technologies have been pioneered by seabird researchers (Grémillet et al., 2000, 2004; Jouventin & Weimerskirch, 1990; Weimerskirch & Wilson, 2000; Weimerskirch 2002 et al., 2002), and across the last two decades over a thousand seabird tracking studies were published. Those yielded unprecedented knowledge of seabird habitat choice, foraging behavior, and migration (Wakefield et al., 2013).

This novel information is playing an increasingly important role in the conservation of marine ecosystems, and of seabirds in particular. Indeed, seabird tracking is now key to the accurate definition of priority conservation areas, such as marine Important Bird and Biodiversity Areas (IBAs) (Lascelles et al., 2016), and to support the establishment and validation of area-based management tools, such as marine protected areas and fishery regulation zones (Pichegru et al., 2010; Kruger et al., 2017; Hindell et al., 2020), as well as to evaluate the effectiveness of these initiatives in supporting conservation outcomes. With seabirds being among the most threatened bird groups (BirdLife International, 2018), including by interactions with fisheries and pollution (Burger & Shaffer, 2008; Grémillet et al., 2018; Dias, Martin et al., 2019), understanding of their spatial ecology is particularly crucial to the implementation of adequate conservation measures (Carneiro et al., 2020). Tracking studies also underpin the use of seabirds as ecological sentinels of marine ecosystems in the Anthropocene (Shaffer et al., 2006; Brisson-Curadeau et al., 2017). Indeed, detailed information on their movements at sea is shedding light on the structure and dynamics of marine systems in time and space (Grémillet et al., 2008; Péron et al., 2012). Finally, conveying maps and animations of seabirds movements to decision-makers and the public is key to winning their commitment for marine conservation (Burger & Shaffer, 2008; Lescroël et al., 2016).

Tracking however comes with substantial costs, not only economic (e.g., cost of equipment and field expeditions), but also environmental (e.g., energy of travels, and materials of equipment) and ecological (e.g., on the fitness of the tagged animals), as well as ethical considerations of animal wellbeing (Burger & Shaffer, 2008). Application of the Reduce–Refine–Replace framework (Richmond, 2000) is thus essential to collectively optimize seabird tracking schemes, by strategically defining which species or populations yield highest priority for gathering new data, as well as through the sharing of the information already collected.

Previous studies have highlighted geographic biases in the tracking of seabirds, showing that some oceans have been understudied (Mott & Clarke, 2018). However, there has not yet been an analysis of how past tracking effort has been distributed across species, or across the ranges of each individual species. Identifying spatial and taxonomic gaps in tracking knowledge is key to the development of effective species management plans, especially for threatened species, and more broadly to support spatial conservation planning of marine ecosystems.

Here, we present the results of a global assessment of current seabird tracking knowledge in a conservation context, with the aim of identifying taxonomic as well as spatial gaps and thus priorities for future tracking. For this purpose, we reviewed and mined the scientific literature to determine which species had been studied with tracking technologies, using marine provinces as spatial units (Marine Regions, 2019).

Based on these analyses, we formulate specific recommendations to guide forthcoming conservation-oriented seabird tracking.

2 | MATERIALS AND METHODS

2.1 | Taxonomic and spatial entities

2.1.1 | Species

We analyzed information for all 363 extant seabird species, belonging to 18 families, listed by *BirdLife International* (BirdLife International, 2019a) (Table S1). Seabirds are defined as species for which a large proportion of the population rely on the marine environment for at least part of the year (Croxall et al., 2012). For each species, we obtained range maps from *BirdLife International* (BirdLife International & Handbook of the Birds of the World, 2018), corresponding to coarse polygons encompassing the species' known distribution.

We classified species according to three characteristics that we anticipated to have a role in explaining variation in the attention received in previous tracking studies: conservation status, body mass, and marine habitat. Each species was thus classified into a category of conservation status (critically endangered, CR; endangered, EN; vulnerable, VU; near threatened, NT; least concern, LC; data deficient, DD) following the International Union for Conservation of Nature Red List of Threatened Species (IUCN Red List) (BirdLife International, 2018; IUCN, 2019). For analysis purposes, we converted this into a numeric discrete scale (LC = 1; NT = 2; VU = 3; EN = 4; CR = 5; excluding the four data-deficient species from analyses) (Butchart et al., 2007). We obtained mean body mass of adults from Paleczny (2012) and prevailing marine habitat (coastal vs. oceanic) for each of 323 seabird species from Dias, Warwick-Evans et al. (2019), and gathered information from the scientific literature for the remaining species (Onley & Scofield, 2007; IUCN, 2019). Based on Dias, Warwick-Evans et al. (2019), species are characterized as coastal when they remain mainly within 8 km of the shoreline throughout their lifecycle, and as oceanic otherwise. "Coastal" and "oceanic" are thus pragmatic classes rather than ecological ones (e.g., depending on the width of the coastal shelf, a species classified as "coastal" in our analysis may be using variable fractions of the neritic province *sensu* Kingsford [2018], whereas a species classified by us as "oceanic" may use not only the oceanic province *sensu* Kingsford [2018] but also part of the neritic province).

2.1.2 | Longhurst provinces

To distinguish marine areas used by seabirds around the world, we used Longhurst biogeochemical provinces as spatial units (Figure S1), mapped as 54 polygons (Marine Regions, 2019) delimited according to physical discontinuities, climatic and oceanographic characteristics, fauna, and flora (Longhurst, 1995).

We classified provinces according to three characteristics that we anticipated to have a role in explaining geographic variation in tracking intensity: distance to equator (absolute value of the *Y*-coordinates of the centroid); adjacency to the coast (a binary variable defining whether or not adjacent to a continent); and average Gross Domestic Product (GDP) per capita of the corresponding countries. The latter was obtained by averaging the GDP per capita (World Bank, 2019) of countries whose Exclusive Economic Zones (EEZ) (Marine Regions, 2019) intersect the corresponding Longhurst province. In calculating GDP per country, overseas territories were grouped according to sovereign countries (e.g., New Caledonia with France). Antarctica has no GDP, but for analytical purposes, we considered it to correspond to the average of the 29 countries that are "consultative parties" to the Antarctic Treaty (i.e., those that have research activities there).

2.2 | Review of tracking data per species

2.2.1 | Publications

For each of the 363 analyzed species, we reviewed systematically the extent to which its spatial distribution has been investigated through tracking studies. To obtain a list of candidate studies per species, we searched the Web of Science database (http://apps.webofknowledge.com) using as search terms: ("*Latin name*" or "*English name**") AND (GLS or GPS or PTT] or VHF or ARGOS or *biologging* or *track**) in the paper title, abstract, and keywords. Papers were selected through the Web of Science between early February and mid-May 2019. This initial list was in some cases augmented by few other relevant publications cited in the original studies.

Given our aim of evaluating the oceanic coverage of the tracking data, we retained only those studies in which tracking locations for a particular species were illustrated in figures (plotting of the tracks, minimum convex polygons, or kernel distributions). Sometimes the same tracking data were presented in multiple studies; in these cases, and to avoid duplication, we focused on the study presenting the original dataset.

For each selected study, data were extracted and entered into a database. The unit of record was a unique combination of species/study site/year/device/season/age of the birds equipped (multiple records were sometimes extracted from a single study). For each record, we extracted the following information:

1. Species: family, scientific name, and English name (IUCN, 2019).
2. Study site (where the birds were equipped with electronic devices): name and geographical coordinates.
3. Year in which the birds were equipped.
4. Number of individual birds tracked.
5. Type of tracking device: VHF; Argos tags, also called PTT; GPS; and GLS. Few articles report the use of electronic direction recorders (compass system) or the coupling of two types of electronic devices, GPS/VHF or GPS/PTT.
6. Season covered by the tracking data: breeding season; inter-breeding period; or both.
7. Age class of the equipped individuals: juveniles (first year from fledging); immatures (older than juveniles but not breeding); or adults (breeding).
8. Spatial distribution of tracking data, coded as presence/absence of the equipped individuals in each Longhurst province. This information was extracted visually from the figure displaying the data.

2.2.2 | Seabird Tracking Database and Movebank

We listed all species for which there were tracking records in the *Seabird Tracking Database* (BirdLife International, 2019b) and *Movebank* (Wikelski & Kays, 2019), considering only those data that were visible online (by the end of February 2019). These databases may include invisible datasets, or available to others after a data request and the establishment of a collaboration. Nonetheless, we focused on the visible data as signaling a willingness by researchers to allow others to build from their data.

2.3 | Data analyses

Data processing and analyses were performed in R version 3.4.4. Spatial analyses were performed using the "sf" package (Pebsma, 2018) and spatial mapping were printed using the "sp" package (Bivand et al., 2013) and QGIS 2.12.3 (QGIS Development Team, 2019).

2.3.1 | Temporal patterns

In order to visualize biases in taxonomy, age class, and seasons among the tracking studies, we plotted temporal trends in published studies according to family, type of tracking device, as well as the distribution of age classes of individuals tracked, and the seasons monitored.

For each record, we calculated the delay between data collection and publication by subtracting the year of data collection from the year of publication. We then obtained the median delay across all records.

2.3.2 | Characteristics of species explaining variation in tracking intensity

For each species, we calculated two indices of tracking intensity based on the information retrieved from the review of publications:

- Tracking effort, defined as the number of individuals tracked per species.
- Tracking coverage, corresponding to the proportion of marine provinces with tracking data within a species' range, calculated as the ratio between the areas of Longhurst provinces where the species has been tracked (based on the publication records) and the areas of provinces where the species is present (obtained by intersecting the species' distribution according to *BirdLife International* [BirdLife International & Handbook of the Birds of the World, 2018] with the Longhurst provinces).

We predicted that tracking intensity would be positively related with body mass, given past technical limitations in the miniaturization of tracking devices; their tendency to use oceanic ecosystems, given that for coastal species other methods of at-sea field study (e.g., coastal or boat surveys) are also available; and their risk of extinction, under the assumption that much tracking effort has a conservation focus. To test these predictions, we modeled the effect of species characteristics on tracking intensity using two independent models: one having tracking effort as the response variable, another for tracking coverage. In both models, we included three species characteristics as explanatory variables: logarithm of the mean body mass; habitat (coastal *versus* oceanic); and conservation status (from 1 for LC to 5 for CR). Given that we found no tracking studies for 178 species, we used models that enabled us to disentangle the effect of these three covariates on (1) the occurrence of tracking (i.e., whether the species was tracked at least once), using a binomial process; and (2) tracking intensity (effort or coverage) whenever the species was tracked at least once. For tracking effort (corresponding to count data), this was done with a Hurdle model from the "pscl" R package (Zeileis & Jackman, 2008), in which we assumed that the nonzero data follow a negative binomial distribution (Zuur et al., 2009). For tracking coverage (corresponding to proportion data), we used a model that combines a binomial process to explain the occurrence of tracking with a beta distribution to explain tracking coverage in monitored species, using the *gamlss* function from the eponymous R package (Rigby & Stasinopoulos, 2005). In this latter model, we assumed a beta-inflated distribution and modelled the *nu* (probability at 0) and *mu* (mean) parameters as functions of species characteristics while leaving the *sigma* (dispersion parameter) and *tau* (probability at 1) parameters as constants.

In addition, we visually analyzed the distribution of seabird species according to their body mass, contrasting tracked versus non-tracked species as well as species tracked according to different types of devices.

2.3.3 | Characteristics of provinces explaining spatial variation in tracking intensity

For each Longhurst province, we characterized tracking intensity using two variables obtained from the review of published studies:

- Tracking effort, defined as the sum of the number of individuals tracked (across all species) per province.
- Percentage of species tracked, relative to the overall number of species present in the province (obtained from distribution maps).

We predicted that tracking intensity is positively related with distance to the Equator, given past evidence of a focus of tracking on temperate and polar regions, and a concurrent neglect of tropical regions (Mott & Clack, 2018); non-coastal province, because tracking methods were originally designed to study inaccessible areas; and higher economic capacity of the nearby countries, given the high costs of tracking (Mott & Clack, 2018). To test these predictions, we fitted generalized linear models with either tracking effort or percentage of species tracked per province as response variables, and adjacency to the coast, distance to the Equator, and GDP per capita as covariates. For the tracking effort per province (corresponding to count data), we built a generalized linear model assuming a negative binomial distribution using the "MASS" package (Venables & Ripley, 2002). For the percentage of species tracked, we obtained a linear model assuming a Gaussian distribution.

We mapped tracking effort and the percentage of species tracked per province, considering all types of devices together, as well as separately for two main types of devices: GPS, GPS/VHF or GPS/PTT (with higher accuracy, mainly used for studying foraging movements around breeding sites); and GLS, VHF, or PTT (with lower accuracy, mainly used for studying year-round movement).

2.3.4 | Gaps in tracking data

We identified gap species as those for which no tracking data were found in the published literature, and among these specifically threatened gap species. For threatened species, we also highlighted near-gaps, that is, species with very little data. For this purpose, we plotted species according to both indices of tracking intensity, and defined near-gaps with both low tracking coverage (i.e., < 50% of their range tracked) and low tracking effort (<100 individuals tracked). We repeated these analyses by separating between high accuracy (GPS, GPS/VHF, GPS/PTT) and low accuracy devices (GLS, VHF, or PTT).

In order to visualize spatial gaps in tracking coverage, we then mapped across Longhurst regions the richness in gap species, threatened gap species, and threatened near-gap species.

2.3.5 | Species coverage in publications versus online databases

To analyze the accessibility of seabird tracking data in specialized online databases, we contrasted the percentage of species in each family covered by publications with that in the two most widely used repositories of seabird tracking data: the *Seabird Tracking Database*, and *Movebank*.

3 | RESULTS

3.1 | Sample sizes and temporal patterns

Out of 1057 scientific publications analyzed, we retained 689 that contained original seabird tracking data (see Supporting Information References). These were published between 1986 and 2019 and relate to over 28,000 individuals, who were equipped with tracking devices between 1984 and 2018. The annual number of tracking studies increased strongly over time (Figure 1): from two studies in 1984, to 201 in 2011. The subsequent (2012–2017) decline is likely an artifact due to the delay between data collection and publication, linked to quality control and data analysis. Indeed, among the records analyzed there was a median of 4 years delay between collection and publication (Figure S2).

The number of published studies varied markedly across seabird families (Figure 1, Table S2). Sulidae (gannets and boobies) and Diomedeidae (albatrosses) were the dominant groups in the 1980s and 1990s, overtaken by Sphenicisdae (penguins) and Laridae (gulls) in the 2000s. Together with Alcidae (auks and allies) and Procellariidae (petrels), these six families represent 86% of all tracking studies published across the study period, while the other 11 families account for the remaining 14% (Figure 1).

Sixty-five percent of seabird tracking records concerned breeding individuals, with 29% focused on inter-breeding individuals (the remaining 7% concerned both seasons). The great majority of records concerned adult individuals (91%). GPS were the tracking devices most commonly deployed (40%), followed by PTT (29%), GLS (23%), VHF (6%), and others (GPS/PTT, GPS/VHF, compass, and dead reckoning; 2%). Devices have been used heterogeneously across seabird families (Figure S3–S5).

3.2 | Characteristics of species explaining variation in tracking intensity

We found that among the 363 species of seabirds analyzed, 185 had been tracked at least once. The probability that a species was tracked increased significantly with log-scaled body mass (Table S3, Figure S6). GLS and VHF devices have been used to track smaller species than GPS and PTT (Figure S7). The probability of being tracked was higher for oceanic than for coastal species, whereas conservation status had no significant effect (Table S3).

Among species that were tracked at least once, both tracking effort and tracking coverage increased with body mass. Tracking coverage was greater for oceanic than for coastal species, with a low effect of habitat on tracking effort. Conservation status did not have a significant effect on tracking coverage, but it was positively related with tracking effort (Table S3).

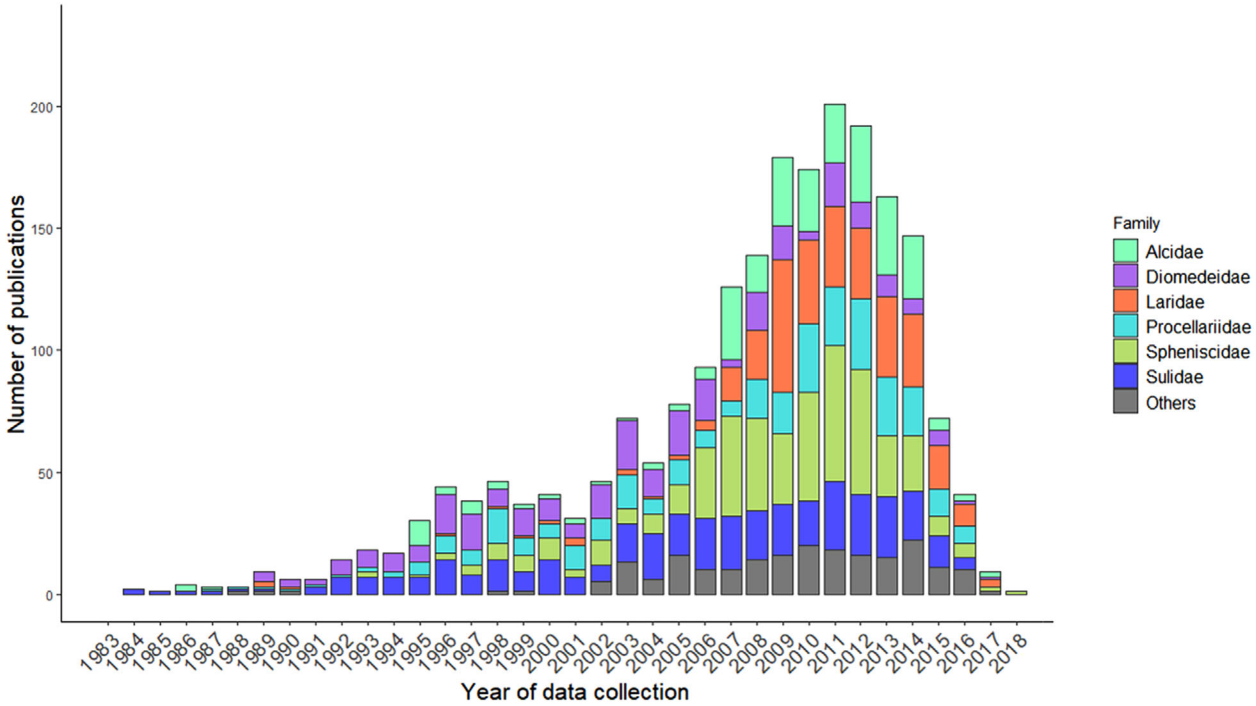

FIGURE 1 Total annual number of seabird tracking studies across 1984–2018. Seabird families are color-coded. Tracking studies with datasets covering multiple years are represented in all corresponding columns. Studies covering multiple families appear more than once in any given year (these are rare, 0.6%)

3.3 | Characteristics of provinces explaining spatial variation in tracking intensity

Tracking effort varied substantially across marine provinces, being concentrated in European, Southern Ocean, and Arctic waters, and away from the tropical Pacific and Indian Oceans (Figure 2a). Overall, we found a statistically significant, positive effect of distance to the Equator (i.e., the intertropical zone had less effort than the Polar regions) and no significant effect of adjacency to the coast and of GDP per capita (Table S4).

Broadly similar results were obtained regarding spatial variation in the percentage of species tracked, with efforts concentrated in the Southern Ocean (> 60% of species tracked) and away from the tropical Pacific and Indian Ocean (< 20%; Figure 2b).We found again a positive relationship between distance to the Equator and percentage of species tracked per province, as well as no significant effect of adjacency to the coast nor of GDP per capita (Table S4).

Different spatial patterns are obtained when contrasting high accuracy (GPS) versus low accuracy devices (GLS, VHF, PTT) in terms of both tracking effort (Figure S8) and the percentage of species tracked (Figure S9). Overall, high accuracy data are mainly concentrated around north-eastern Europe and the Southern Ocean, whereas low accuracy data are more widely distributed, even if focused mainly in polar oceans.

3.4 | Gaps in tracking data

We were unable to find published tracking studies for 178 gap species (49% of all species; Table S2), of which 54 are threatened (48% of all threatened species), Threatened gap species include two that are likely to be extinct (classified as Critically Endangered—Possibly Extinct; Butchart et al., 2006), 12 Critically Endangered, 13 Endangered, and 27 Vulnerable (Figure 3b and Table S2).

Among the 59 threatened species for which we found published tracking records, there was wide variation in tracking intensity (Figure 3a, Fig. S10). A weak correlation between tracking effort and coverage ($R^2 = 0.15$) means that some had a high number of individuals tracked but a lower proportion of their at-sea range tracked, whereas the reverse was true for others. We found 19 threatened near-gap species, that is, combining low coverage (<50% of their range tracked) and low effort (<100 individuals tracked (Figure 3a). Many more threatened species (50; 44%) have been tracked using low accuracy devices (GLS, VHF, PTT), covering higher numbers of individuals, than

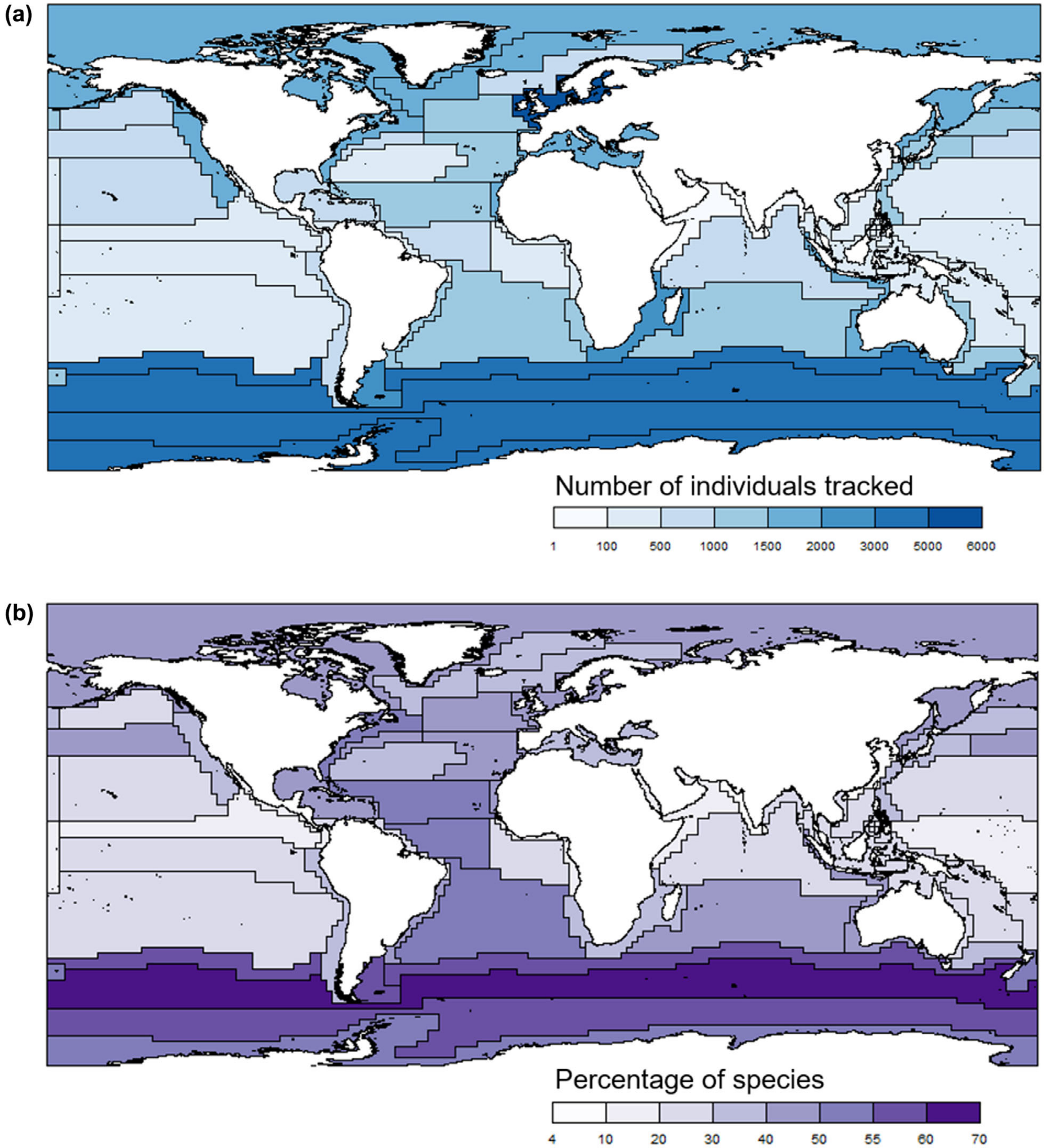

FIGURE 2 Spatial variation in tracking intensity across Longhurst provinces. (a) Tracking effort (number of individuals tracked); (b) Percentage of species in the province that were tracked

those tracked with high accuracy devices (GPS; 28 species, 25% of all threatened species; Figure S11, S12, S13).

Gap (Figure 4a), threatened gap species (Figure 4b) and threatened near-gap species (Figure 4c) are mainly present in the southern Pacific and Subantarctic Ocean and in coastal Southeast Asia and Oceania. They are almost absent from the Atlantic or Indian Oceans, or from the Antarctic coastline as well as from the Arctic Ocean for near-gap threatened species.

3.5 | Species coverage in publications versus online databases

Across all data sources, coverage of species per family was highly variable, ranging from families with tracking data for all species in at least one source (e.g., Diomedeidae, albatrosses, $n = 22$) to families with no data at all (Oceanitidae, Austral storm petrels, $n = 9$, and Podicipedidae, grebes, $n = 4$). There was also much variation across data

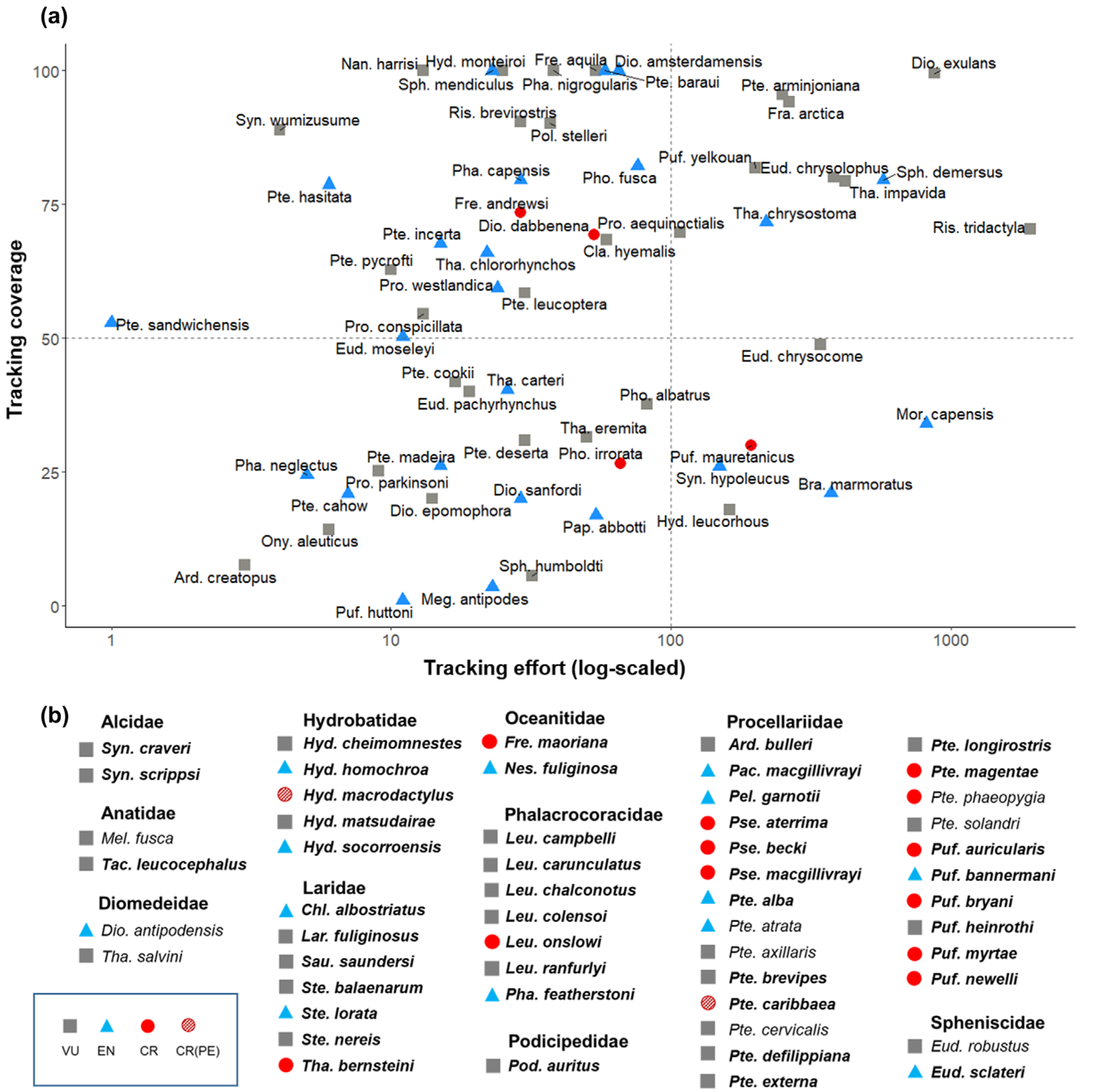

FIGURE 3 Tracking intensity of threatened species: (a) Relationship between tracking effort (number of individuals tracked per species) and tracking coverage (percentage of the species' at-sea range covered by tracking data), for threatened seabird species for which tracking data were found in the literature (n = 59). (b) List of threatened species for which no tracking data were found in the literature (n = 54). For species not in bold (n = 9) we found tracking data in online databases (*Seabird Tracking Database* or *Movebank*). The genera abbreviations for Alcidae are as follows: Bra, *Brachyramphus*; Fra, *Fratercula*; Syn, *Synthliboramphus*. For Anatidae: Cla, *Clangula*; Mel, *Melanitta*; Pol, *Polysticta*; Tac, *Tachyeres*. For Diomedeidae: Dio, *Diomedeida*; Pho, *Phoebetria*; Tha, *Thalassarche*; For Fregatidae: Fre, *Fregata*. For Hydrobatidae: Hyd, *Hydrobates*. For Laridae: Chl, *Chlidonias*; Lar, *Larus*; Ony, *Onychoprion*; Ris, *Rissa*; Sau, *Saundersilarus*; Ste, *Sternula*; Tha, *Thalasseus*. For Phalacrocoracidae: Leu, *Leucocarbo*; Nan, *Nannopterum*; Pha, *Phalacrocorax*. For *Podicipedidae*: Pod, *Podiceps*. For Procellariidae: Ard, *Ardenna*; Pac, *Pachyptila*; Pel, *Pelecanoides*; Pro, *Procellaria*; Pse, *Pseudobulweria*; Pte, *Pterodroma*; Puf, *Puffinus*. For Spheniscidae: Eud, *Eudyptes*; Med, *Megadyptes*; Sph, *Spheniscus*. For Sulidae: Mor, *Morus*; Pap, *Papasula*

sources (Figure 5, Table S1 and S2). Some of the species covered were represented in published studies but not in one or both of the online databases (*Movebank* and *Seabird Tracking Database*), indicating that a part of existing data was not already shared through online databases. Indeed, there were 54 species that were present in published studies but not in either of the online databases. In addition, there were discrepancies between online databases, with 115 species in *Seabird Tracking Database*, whereas only 87 species were represented in *Movebank*.

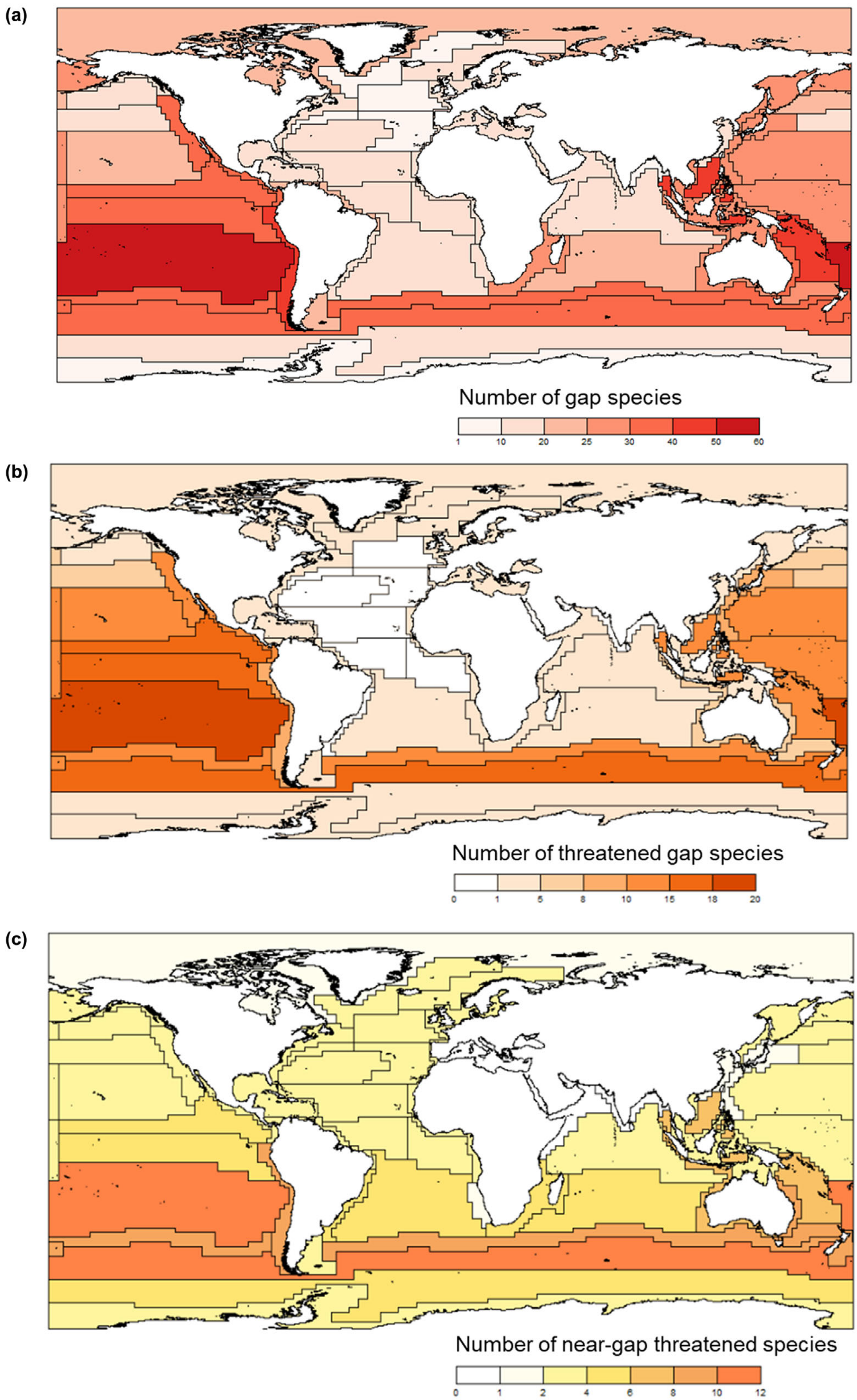

FIGURE 4 Spatial gaps in tracking data, mapped across Longhurst provinces. (a) Number of gap species, that is those for which no tracking data were found in the reviewed literature ($n = 178$). (b) Number of threatened gap species ($n = 54$). (c) Number of threatened near-gap species, that is, with both little tracking effort (< 100 individuals) and little tracking coverage (<50% of range covered) ($n = 19$)”

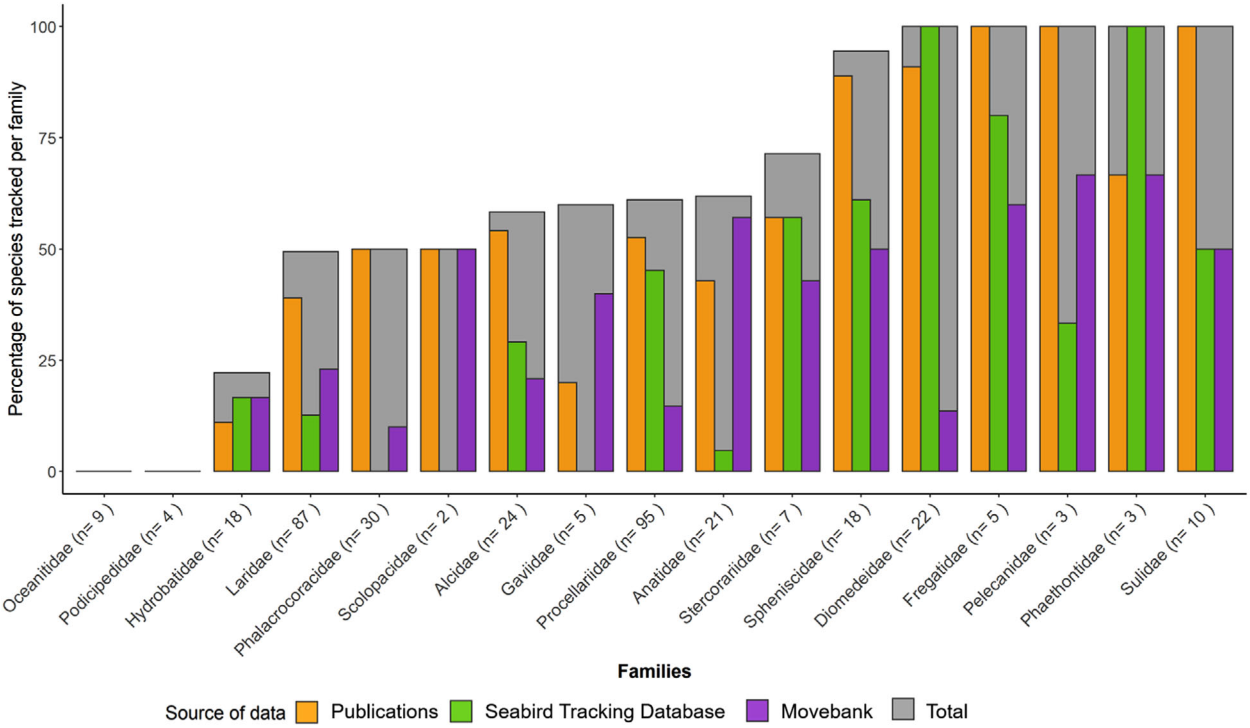

FIGURE 5 Percentage of seabird species tracked by family and by data source: publications (up to mid-May 2019), the *Seabird Tracking Database*, and *Movebank* (in February 2020)

There were nonetheless a few families for which the total number of species covered was higher than what we found in publications, indicating that data in online databases was not a mere subset of those in published studies. For example, for Anatidae (ducks and geese) more species were covered by *Movebank* (n = 12 species) than by published studies (n = 9), whereas for Diomedeidae (albatrosses), the *Seabird Tracking Database* covered all species (n = 22), which was more than those we found in publications (n = 20). This reflects the different geographic emphasis of the two online databases, with *Movebank* focusing for now on North American species, and the *Seabird Tracking Database* mainly focusing on the southern oceans. Taking into account the species for which tracking data exist in online databases (162 species) and in publications (185 species), 147 species seemed to have no existing tracking data.

4 | DISCUSSION

This world-wide assessment of seabird tracking studies demonstrates major taxonomic and geospatial biases in the global understanding of seabird spatial ecology as explored with electronic tracking tags. Given the delay between data collection and publication, as well as our own delay between reviewing the literature and publication of our results, additional data certainly exist. Nonetheless, our results underline the current absence of a coordinated framework for the tracking of the world's seabirds, and we therefore provide guidance toward a global strategy for seabird tracking.

As expected, we found that heavier seabirds such as gannets and albatrosses were more likely to be tracked, with an over-emphasis on species with a body mass above 1000 g and an underrepresentation of the smaller species that is most striking among those lighter than 320 g (Figure S6). This is due to persisting technical constraints on electronic tag miniaturization. Rapidly shrinking electronic components nonetheless reduced tag mass/size across the last two decades (Kays et al., 2015). Even though seabird researchers have taken advantage of these advances as soon as they became available (Figure S14), they have been until recently a limitation to tracking efforts. Linked to this body mass effect, oceanic seabird species were more likely to be tracked than coastal species. With GLS devices smaller than GPS and PTT (Figure S14), the former have been used to track lighter species (Figure S7).

Contrary to our expectations, we found no effect of conservation status on seabird tracking effort and a slight negative effect on tracking coverage. This could reflect the diversity of reasons underpinning the choice of species in tracking studies, with abundant species chosen to address ecology questions, whereas threatened species are tracked for conservation planning. It is also likely to reflect the fact that some threatened species are not easily accessible to researchers (e.g., because the location of their breeding sites is unknown, or their remaining populations are found in inaccessible areas) and some are so rare and vulnerable that it is too risky to handle them. In any case, we found no tracking data in the literature for about half of all species, including about half of all threatened species, with only one in four threatened species having been tracked using high accuracy devices. Furthermore, for some of the tracked species, the available data remain well below what is needed to understand their distribution and ecology, which requires both a sufficient number of tracked individuals and adequate representativeness of the tracked populations across the species' range size (Sequeira et al., 2019; Soanes et al 2013). Unfortunately, we found that among 113 threatened species only 10 had both high tracking effort (more than 100 individuals tracked) and good coverage (>50% of the range). Of these, only six had sufficient coverage through high accuracy devices (typically covering feeding movements in the breeding grounds), and only six through low accuracy devices (typically covering year-round movements), with only three having both (Figure S13), highlighting that much research is still required.

Unexpectedly, we found no significant effect of country richness (GDP per capita of the adjacent coastal countries) on the geographical distribution of tracking studies. This appears to contrast with results by a previous study that found a positive relationship between the number of papers collecting at-sea seabird data (including tracking) published by each country (as established by first author's address) and its GDP (Mott & Clarke, 2018). In practice, there is no contradiction given that our analysis looked at the spatial distribution of the tracked birds, which can extend very far from where they were equipped. Our results thus indicate that the knowledge benefits of research investment by richer nations extend much more broadly than the waters adjacent to these countries. As a different explanation, this can also reflect collaborations between researchers with access to better research funding and those in lower-income countries where the seabird breeding colonies are located. In both cases, these are welcomed news to the global conservation of seabirds.

Nonetheless, our results show that despite a high concentration of tracking effort in some regions (in particular northern European waters and the Subantarctic region; Figure 2a), no single province in the world has tracking records for all of the seabird species that occur there (the maximum being 70% of species; Figure 2b), even less so when considering high accuracy (GPS) data (maximum 23% of species; Figure S9A). This shows that knowledge on the movements of seabirds remains incomplete even in the best-sampled regions.

This said, some regions, mainly in tropical seas, do stand out as having particularly limited tracking data, both in terms of effort (number of individuals tracked) and in taxonomic coverage of their seabird species. This is in agreement with the results by Mott and Clarke (2018). The historical neglect of tropical seabirds may be indicative not only of limited local resources, but also reflect variation in seabird ecology. Indeed, tropical seabirds have notably lower seasonality, and thus lower breeding synchrony, than those at higher latitudes (Burr et al., 2016) and this in turn affects the success of seabird researchers in tag deployment and retrieval. A complementary perspective to spatial gaps in tracking comes from the distribution of species that have received no, or very little, tracking investment. We found that these species are mainly concentrated in the southern Pacific, Subantarctic Ocean, and in coast Southeast Asia and Oceania (Figure 4). These gaps in data are particularly worrying for threatened species, for which it is most urgent to identify at-sea habitats, in order to guide future management and conservation plans (e.g., definition of Marine Protected Areas or no-take areas).

Our analysis underestimates existing knowledge. We found that for an additional 31 species there were tracking records in online databases that we could not find in publications (Figure 5, Table S1 and S2). Nonetheless, our results are evidence that very important gaps and biases remain in the global knowledge of seabird movement, both taxonomically and geographically, nearly two decades after BirdLife International's initial efforts to synthesize seabird tracking knowledge (BirdLife International, 2004). This reflects the fact that seabird tracking research has largely progressed without international coordination, mainly driven by the scientific questions of each team or the conservation concerns regarding certain species. Given the threats faced by seabirds (BirdLife International, 2018) it is crucial that such coordination improves in the future, to ensure a strategic use of the limited resources available.

5 | CONCLUSIONS AND RECOMMENDATIONS

We recommend a periodic update of this analysis as a means of monitoring progress and guiding strategic decisions regarding future investment in seabird tracking. Based on our results, we urge the seabird tracking community to embrace four main challenges.

First, to jointly work on a global seabird tracking scheme, to yield a complete picture of seabird spatial ecology, now technically possible for virtually all species given the small size of modern tracking devices (Figure S14). This will require working collaboratively to fill the major taxonomic and geographical gaps we have identified. In particular, we recommend, a coordinated ramping up of effort toward the study of tropical seabird species (Mott & Clarke, 2018), with an emphasis on the Pacific Ocean and Southern Oceans. These data will be key to inform national and international management and conservation efforts, including through the work of the South Pacific Regional Fisheries Management Organisation (SPRFMO, 2009) and of the Convention on Conservation of Antarctic Marine Living Resources (CCAMLR, 1982). Indeed, at a time when there is wide recognition for the need to expand the coverage provided by marine protected areas and other effective area-based conservation measures (e.g., Aichi target 11 to cover 10% of coastal and marine areas by 2020; SCBD, 2010), tracking data will be crucial to ensure that such expansion is strategically done to protect the areas that are most important to biodiversity. We recommend that particular attention be given to threatened species that have received none or very little tracking effort so far, where possible (i.e., when their breeding colonies are known) and provided this does not add substantial stress to the populations (particularly for those with very small known breeding populations). Indeed, an understanding of their at-sea habitats is in many cases key to effective conservation planning, alongside measures for reducing land-based threats to their breeding colonies, such as the control of invasive predators (Dias, Martin et al., 2019).

Second, the seabird tracking community, in partnership with the industry and supported by research funding agencies, should build an international fund aiming at designing the next generation of electronic tags. These will be sufficiently small to track even the smallest species (López-López, 2016) through life history stages (Hazen et al., 2012), across a wide range of environmental conditions, and to overcome tag loss during molting (Kooyman et al., 2015). Notably, the time is now ripe for building a bird band which fully contains a tracking device, instead of attaching tags (such as GLS) onto metal or plastic bands. Also, it is urgent to work on alternative ways to provide energy to electronic tags while birds are at sea, for instance through chemical reactions with seawater (Kim et al., 2016). This is essential for studying juveniles and immatures, which are difficult to track once they leave their natal breeding site, often for several years. Those developments are particularly relevant for polar areas where solar-powered tags are useless in winter.

Third, we encourage researchers and their institutions to invest in solutions to enable the rapid and effective sharing and archiving of tracking data in online databases, while respecting the need for adequate recognition of data collectors (Rabesandratana, 2018). Such solutions involve not only technical support to the time-consuming process of data treatment and archiving, but also fostering a scientific culture in which data collection and sharing are adequately valued and rewarded, both by the other researchers (through collaborative opportunities and resulting publications) and by institutions (taken into account in the evaluation of researchers and consequent career progression). More broadly, the value of tracking data should be measured not only through its translation into scientific publications but also when it serves as basis to conservation and management. Online databases allow researchers and decision-makers to easily find all available spatial information for a given species or focal region and use it as a base for identifying regions that are of high biodiversity value (Hindell et al., 2020), providing recommendations on policy and management (Lascelles et al., 2016), and to predict and monitor ecological changes (Ropert-Coudert et al., 2020).

Fourth, seabird tracking data should be systematically used and, if needed, collected (among other data sources) to establish baseline environmental conditions and evaluate potential impacts, whenever a country or company sponsored by a nation wishes to exploit the sea in areas beyond national jurisdiction. Such use should be mandatory through international agreements such as the International Seabed Authority or Regional Fisheries Management Organizations. Thereby, an investment in higher resolution (GPS) tracking data is particularly crucial to the identification of the most important areas used by seabirds at a scale fine enough to allow an understanding of and their potential interactions with at-sea threats such as fisheries, offshore hydroelectric plants, and oil spills.

Unbiased tracking of the world's seabirds is essential for understanding their ecology and of the impacts of environmental changes on their population trajectories. It is therefore key to seabird conservation in a changing world, as well as for understanding global marine ecosystem dynamics, for marine spatial planning and the design and efficiency of marine protected area networks (Lascelles et al., 2012; Young et al., 2015). This requires exploratory tracking of poorly known species, as well as repeated tracking within long-term observatories of seabirds as sentinels of the marine environment. Yet, potential impacts of tracking on seabird welfare always have to be carefully weighed against conservation benefits. In that respect, a research program only aiming at "tracking all seabirds" is simply not good enough. It has to be linked with major management efforts to push seabird conservation forward.

DATA AVAILABILITY STATEMENT

All necessary information is included in the manuscript and its annexes. The data that supports the findings of this study are available in the Supporting Information of this article.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS CONTRIBUTIONS

DG, AR, and AB designed the study. AB collected the data. AB and VC analyzed the data. AB and DG wrote the first draft of the paper. All authors contributed to the final version.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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