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## Toward a global strategy for seabird tracking

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1 I. Title page

2 Towards a global strategy for seabird tracking

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38        II.     Abstract page

39                ***Abstract***

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

55

56

### 57 III. Main Text

#### 58 **1) Introduction**

59 Electronic tracking technologies are revolutionizing the study of animal movements (Sergio et al.  
60 2014; Kays et al. 2015), bolstered by mass production industries, such as cellular phones (Burger  
61 & Shaffer 2008) and by powerful tools to store and analyze the huge amounts of data produced  
62 (López-López 2016). By fitting miniature trackers to elusive wild animals, researchers expanded  
63 the discipline of spatial ecology to scales ranging from seconds and centimeters, to entire animal  
64 lives and the planet (Nathan et al. 2008; Lohmann 2018). Scientific advances have been particularly  
65 spectacular in the marine environment, where animal tracking opened up new worlds of knowledge  
66 (Bonfil et al. 2005; Block et al. 2011). Many such technologies have been pioneered by seabird  
67 researchers (Jouventin & Weimerskirch 1990; Grémillet et al. 2000, 2004; Weimerskirch & Wilson  
68 2000; Weimerskirch 2002), and across the last two decades over a thousand seabird tracking  
69 studies were published. Those yielded unprecedented knowledge of seabird habitat choice,  
70 foraging behavior and migration (Wakefield et al. 2013).

71 This novel information is playing an increasingly important role in the conservation of marine  
72 ecosystems, and of seabirds in particular. Indeed, seabird tracking is now key to the accurate  
73 definition of priority conservation areas, such as marine Important Bird and Biodiversity Areas  
74 (IBAs) (Lascelles et al. 2016), and to support the establishment and validation of area-based  
75 management tools, such as marine protected areas and fishery regulation zones (Pichegru et al.  
76 2010; Kruger et al. 2017; Hindell et al. 2020), as well as to evaluate the effectiveness of these  
77 initiatives in supporting conservation outcomes. With seabirds being among the most threatened  
78 bird groups (BirdLife International 2018), including by interactions with fisheries and pollution  
79 (Burger & Shaffer 2008; Grémillet et al. 2018; Dias et al. 2019b), understanding of their spatial  
80 ecology is particularly crucial to the implementation of adequate conservation measures (Carneiro  
81 et al. 2020). Tracking studies also underpin the use of seabirds as ecological sentinels of marine  
82 ecosystems in the Anthropocene (Shaffer et al. 2006; Brisson-Curadeau et al. 2017). Indeed,  
83 detailed information on their movements at sea is shedding light on the structure and dynamics of  
84 marine systems in time and space (Grémillet et al. 2008; Péron et al. 2012). Finally, conveying  
85 maps and animations of seabirds movements to decision makers and the public is key to winning  
86 their commitment for marine conservation (Burger & Shaffer 2008; Lescroël et al. 2016).

87 Tracking however comes with substantial costs, not only economic (e.g., cost of equipment and  
88 field expeditions), but also environmental (e.g., energy of travels, and materials of equipment) and

89 ecological (e.g., on the fitness of the tagged animals), as well as ethical considerations of animal  
90 wellbeing (Burger & Shaffer 2008). Application of the Reduce-Refine-Replace framework  
91 (Richmond 2000) is thus essential to collectively optimize seabird tracking schemes, by  
92 strategically defining which species or populations yield highest priority for gathering new data, as  
93 well as through the sharing of the information already collected.

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

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

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

## 107 **2) Materials and Methods**

### 108 **Taxonomic and spatial entities**

#### 109 *Species*

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

116 We classified species according to three characteristics that we anticipated to have a role in  
117 explaining variation in the attention received in previous tracking studies: conservation status, body  
118 mass and marine habitat. Each species was thus classified into a category of conservation status

119 (Critically Endangered, CR; Endangered, EN; Vulnerable, VU; Near Threatened, NT; Least  
120 Concern, LC; Data Deficient, DD) following the International Union for Conservation of Nature Red  
121 List of Threatened Species (IUCN Red List) (BirdLife International 2018; IUCN 2019). For analysis  
122 purposes, we converted this into a numeric discrete scale (LC=1; NT=2; VU=3; EN=4; CR=5;  
123 excluding the four data-deficient species from analyses) (Butchart et al. 2007). We obtained mean  
124 body mass of adults from Paleczny (2012) and prevailing marine habitat (coastal vs. oceanic) for  
125 each of 323 seabird species from Dias et al. (2019b), and gathered information from the scientific  
126 literature for the remaining species (Onley & Scofield 2007; IUCN 2019). Based on Dias et al.  
127 (2019b), species are characterized as coastal when they remain mainly within 8 km of the shoreline  
128 throughout their lifecycle, and as oceanic otherwise. "Coastal" and "oceanic" are thus pragmatic  
129 classes rather than ecological ones (e.g., depending on the width of the coastal shelf, a species  
130 classified as "coastal" in our analysis may be using variable fractions of the neritic province *sensu*  
131 Kingsford [2018]; whereas a species classified by us as "oceanic" may use not only the oceanic  
132 province *sensu* Kingsford [2018] but also part of the neritic province).

### 133 *Longhurst provinces*

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

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

## 148 **Review of tracking data per species**

### 149 *Publications*

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

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

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

- 166 1. Species: family, scientific name, English name (IUCN 2019).
- 167 2. Study site (where the birds were equipped with electronic devices): name, geographical  
168 coordinates.
- 169 3. Year in which the birds were equipped.
- 170 4. Number of individual birds tracked.
- 171 5. Type of tracking device: VHF (*Very High Frequency*); Argos tags, also called PTT (*Platform*  
172 *Terminal Transmitter*); GPS (*Global Positioning System*); and GLS (*Global Location*  
173 *Sensor*). Few articles report the use of electronic direction recorders (compass system) or  
174 the coupling of two types of electronic devices, GPS/VHF or GPS/PTT.
- 175 6. Season covered by the tracking data: breeding season; inter-breeding period; or both.
- 176 7. Age class of the equipped individuals: juveniles (first year from fledging); immatures (older  
177 than juveniles but not breeding); or adults (breeding).
- 178 8. Spatial distribution of tracking data, coded as presence/absence of the equipped  
179 individuals in each Longhurst province. This information was extracted visually from the  
180 figure displaying the data.

181 *Seabird Tracking Database and Movebank*

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

## 188 **Data analyses**

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

### 192 *Temporal patterns*

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

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

### 199 *Characteristics of species explaining variation in tracking intensity*

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

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

209 We predicted that tracking intensity would be positively related with: body mass, given past  
210 technical limitations in the miniaturization of tracking devices; their tendency to use oceanic

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

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

### 233 *Characteristics of provinces explaining spatial variation in tracking intensity*

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

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

240 We predicted that tracking intensity is positively related with: distance to the Equator, given past  
241 evidence of a focus of tracking on temperate and polar regions, and a concurrent neglect of tropical  
242 regions (Mott & Clack 2018); non-coastal province, because tracking methods were originally  
243 designed to study inaccessible areas; and higher economic capacity of the nearby countries, given

244 the high costs of tracking (Mott & Clack 2018). To test these predictions, we fitted generalized linear  
245 models with either tracking effort or percentage of species tracked per province as response  
246 variables, and adjacency to the coast, distance to the Equator, and GDP per capita as covariates.  
247 For the tracking effort per province (corresponding to count data), we built a generalized linear  
248 model assuming a negative binomial distribution using the “MASS” package (Venables & Ripley  
249 2002). For the percentage of species tracked, we obtained a linear model assuming a Gaussian  
250 distribution.

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

### 255 *Gaps in tracking data*

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

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

### 265 *Species coverage in publications versus online databases*

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

## 269 **3) Results**

### 270 **Sample sizes and temporal patterns**

271 Out of 1057 scientific publications analyzed, we retained 689 which contained original seabird  
272 tracking data (see SI References). These were published between 1986-2019 and relate to over  
273 28,000 individuals which were equipped with tracking devices between 1984-2018. The annual  
274 number of tracking studies increased strongly over time (Fig. 1): from two studies in 1984, to 201

275 in 2011. The subsequent (2012-2017) decline is likely an artefact due to the delay between data  
276 collection and publication, linked to quality control and data analysis. Indeed, among the records  
277 analyzed there was a median of 4 years delay between collection and publication (Fig. S2).

278 The number of published studies varied markedly across seabird families (Fig. 1, Table S2).  
279 Sulidae (gannets and boobies) and Diomedeidae (albatrosses) were the dominant groups in the  
280 1980s and 1990s, overtaken by Spheniscidae (penguins) and Laridae (gulls) in the 2000s. Together  
281 with Alcidae (auks and allies) and Procellariidae (petrels), these six families represent 86% of all  
282 tracking studies published across the study period, while the other eleven families account for the  
283 remaining 14% (Fig. 1).

284 Sixty-five percent of seabird tracking records concerned breeding individuals, with 29% focused on  
285 inter-breeding individuals (the remaining 7% concerned both seasons). The great majority of  
286 records concerned adult individuals (91%). GPS were the tracking devices most commonly  
287 deployed (40%), followed by PTT (29%), GLS (23%), VHF (6%) and others (GPS/PTT, GPS/VHF,  
288 compass and dead reckoning; 2%). Devices have been used heterogeneously across seabird  
289 families (Fig. S3, S4, S5).

### 290 **Characteristics of species explaining variation in tracking intensity**

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

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

### 300 **Characteristics of provinces explaining spatial variation in tracking intensity**

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

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

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

### 316 **Gaps in tracking data**

317 We were unable to find published tracking studies for 178 gap species (49% of all species; Table  
318 S2), of which 54 are threatened (48% of all threatened species), Threatened gap species include  
319 two that are likely to be extinct (classified as Critically Endangered -Possibly Extinct; Butchart et al.  
320 2006), 12 Critically Endangered, 13 Endangered and 27 Vulnerable (Fig 3B and Table S2).

321 Among the 59 threatened species for which we found published tracking records, there was wide  
322 variation in tracking intensity (Fig. 3A, Fig. S10). A weak correlation between tracking effort and  
323 coverage ( $R^2= 0.15$ ) means that some had a high number of individuals tracked but a lower  
324 proportion of their at-sea range tracked, whereas the reverse was true for others. We found 19  
325 threatened near-gap species, i.e., combining low coverage (<50% of their range tracked) and low  
326 effort (<100 individuals tracked (Fig. 3A). Many more threatened species (50; 44%) have been  
327 tracked using low accuracy devices (GLS, VHF, PTT), covering higher numbers of individuals, than  
328 those tracked with high accuracy devices (GPS; 28 species, 25% of all threatened species; Fig.  
329 S11, S12, S13).

330 Gap (Fig. 4A), threatened gap species (Fig. 4B) and threatened near-gap species (Fig. 4C) are  
331 mainly present in the southern Pacific and Subantarctic Ocean and in coastal Southeast Asia and  
332 Oceania. They are almost absent from the Atlantic or Indian Oceans, or from the Antarctic coastline  
333 as well as from the Arctic Ocean for near-gap threatened species.

### 334 **Species coverage in publications versus online databases**

335 Across all data sources, coverage of species per family was highly variable, ranging from families  
336 with tracking data for all species in at least one source (e.g. Diomedidae, albatrosses, n=22) to

337 families with no data at all (Oceanitidae, Austral storm petrels, n=9 and Podicipedidae, grebes,  
338 n=4). There was also much variation across data sources (Fig. 5, Table S1 and S2). Some of the  
339 species covered were represented in published studies but not in one or both of the online  
340 databases (*Movebank* and *Seabird Tracking Database*), indicating that a part of existing data was  
341 not already shared through online databases. Indeed, there were 54 species that were present in  
342 published studies but not in either of the online databases. In addition, there were discrepancies  
343 between online databases, with 115 species in *Seabird Tracking Database*, whereas only 87  
344 species were represented in *Movebank*. There were nonetheless a few families for which the total  
345 number of species covered was higher than what we found in publications, indicating that data in  
346 online databases was not a mere subset of those in published studies. For example, for Anatidae  
347 (ducks and geese) more species were covered by *Movebank* (n=12 species) than by published  
348 studies (n=9), whereas for Diomedidae (albatrosses), the *Seabird Tracking Database* covered all  
349 species (n=22), which was more than those we found in publications (n=20). This reflects the  
350 different geographic emphasis of the two online databases, with *Movebank* focusing for now on  
351 North American species, and the *Seabird Tracking Database* mainly focusing on the southern  
352 oceans. Taking into account the species for which tracking data exist in online databases (162  
353 species) and in publications (185 species), 147 species seemed to have no existing tracking data.

#### 354 **4) Discussion**

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

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

370 than coastal species. With GLS devices smaller than GPS and PTT (Fig. S14), the former have  
371 been used to track lighter species (Fig. S7).

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

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

402 Nonetheless, our results show that despite a high concentration of tracking effort in some regions  
403 (in particular northern European waters and the Subantarctic region; Fig. 2A), no single province

404 in the world has tracking records for all of the seabird species that occur there (the maximum being  
405 70% of species; Fig. 2B), even less so when considering high accuracy (GPS) data (maximum 23%  
406 of species; Fig. S9A). This shows that knowledge on the movements of seabirds remains  
407 incomplete even in the best-sampled regions.

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

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

431

## 432 **5) Conclusions and recommendations**

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

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

455 Second, the seabird tracking community, in partnership with the industry and supported by research  
456 funding agencies, should build an international fund aiming at designing the next generation of  
457 electronic tags. These will be sufficiently small to track even the smallest species (López-López  
458 2016) through life history stages (Hazen et al. 2012), across a wide range of environmental  
459 conditions, and to overcome tag loss during molting (Kooyman et al. 2015). Notably, the time is  
460 now ripe for building a bird band which fully contains a tracking device, instead of attaching tags  
461 (such as GLS) onto metal or plastic bands. Also, it is urgent to work on alternative ways to provide  
462 energy to electronic tags while birds are at sea, for instance through chemical reactions with  
463 seawater (Kim et al. 2016). This is essential for studying juveniles and immatures, which are difficult  
464 to track once they leave their natal breeding site, often for several years. Those developments are  
465 particularly relevant for polar areas where solar-powered tags are useless in winter.

466

467 Third, we encourage researchers and their institutions to invest in solutions to enable the rapid and  
468 effective sharing and archiving of tracking data in online databases, while respecting the need for  
469 adequate recognition of data collectors (Rabesandratana 2018). Such solutions involve not only

470 technical support to the time consuming process of data treatment and archiving, but also fostering  
471 a scientific culture in which data collection and sharing are adequately valued and rewarded, both  
472 by the other researchers (through collaborative opportunities and resulting publications) and by  
473 institutions (taken into account in the evaluation of researchers and consequent career  
474 progression). More broadly, the value of tracking data should be measured not only through its  
475 translation into scientific publications but also when it serves as basis to conservation and  
476 management. Online databases allow researchers and decision-makers to easily find all available  
477 spatial information for a given species or focal region and use it as a base for identifying regions  
478 that are of high biodiversity value (Hindell et al. 2020), providing recommendations on policy and  
479 management (Lascelles et al. 2016), to predict and monitor ecological changes (Ropert-Coudert et  
480 al. 2020).

481

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

491

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

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509

510       **7) References**

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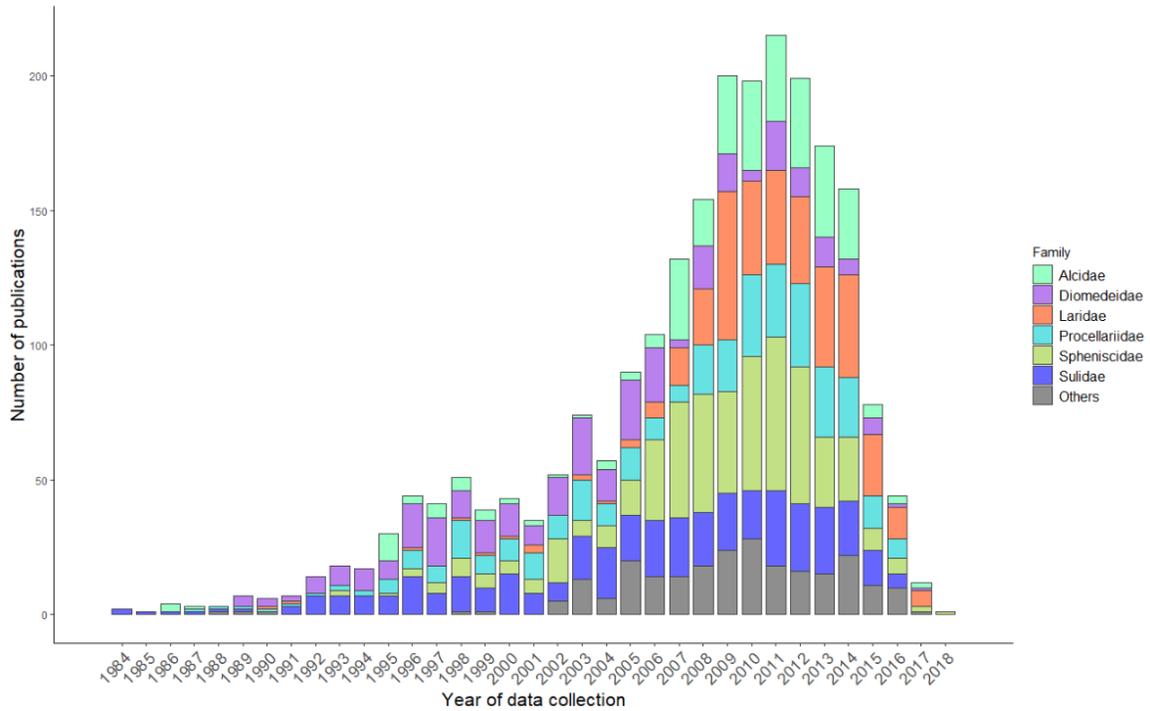
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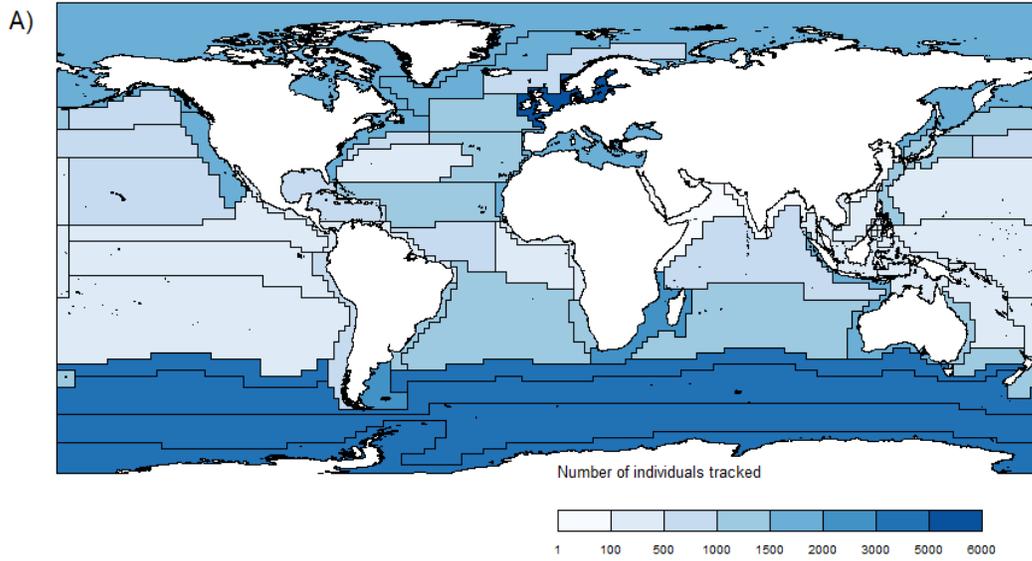
724 **Figures**

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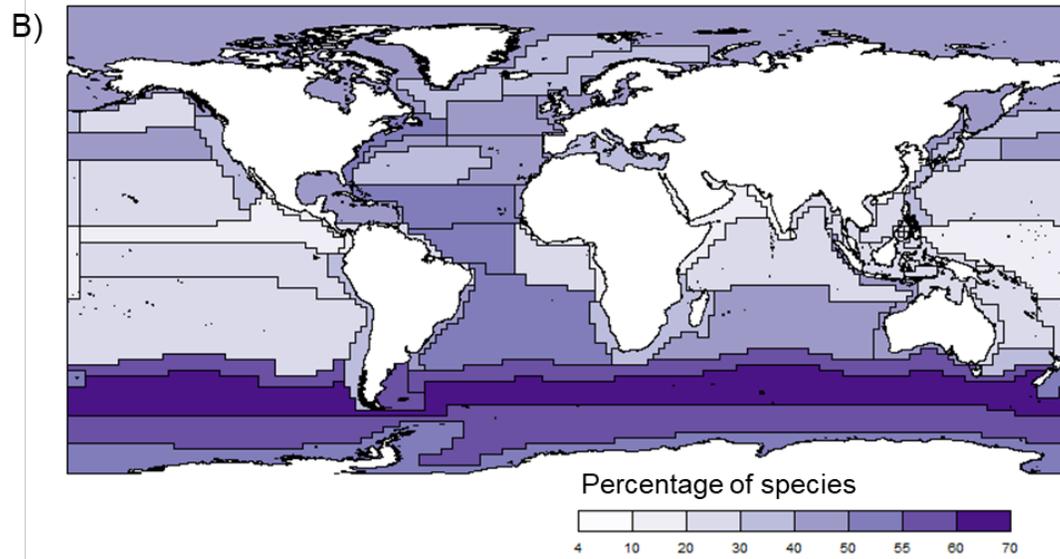


726

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



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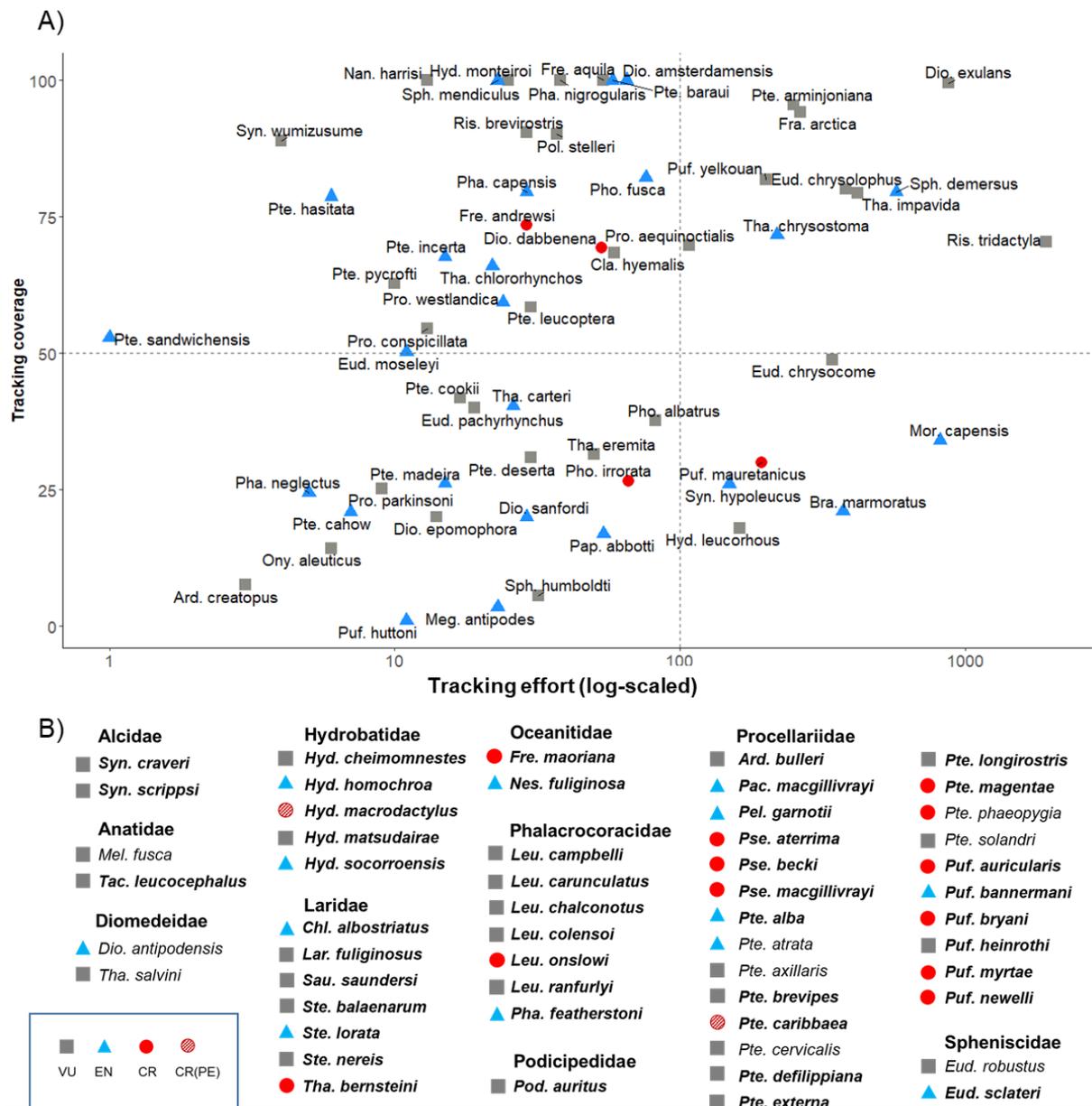


732

733 **Figure 2.** Spatial variation in tracking intensity across Longhurst provinces. A) Tracking effort

734 (number of individuals tracked); B) Percentage of species in the province that were tracked.

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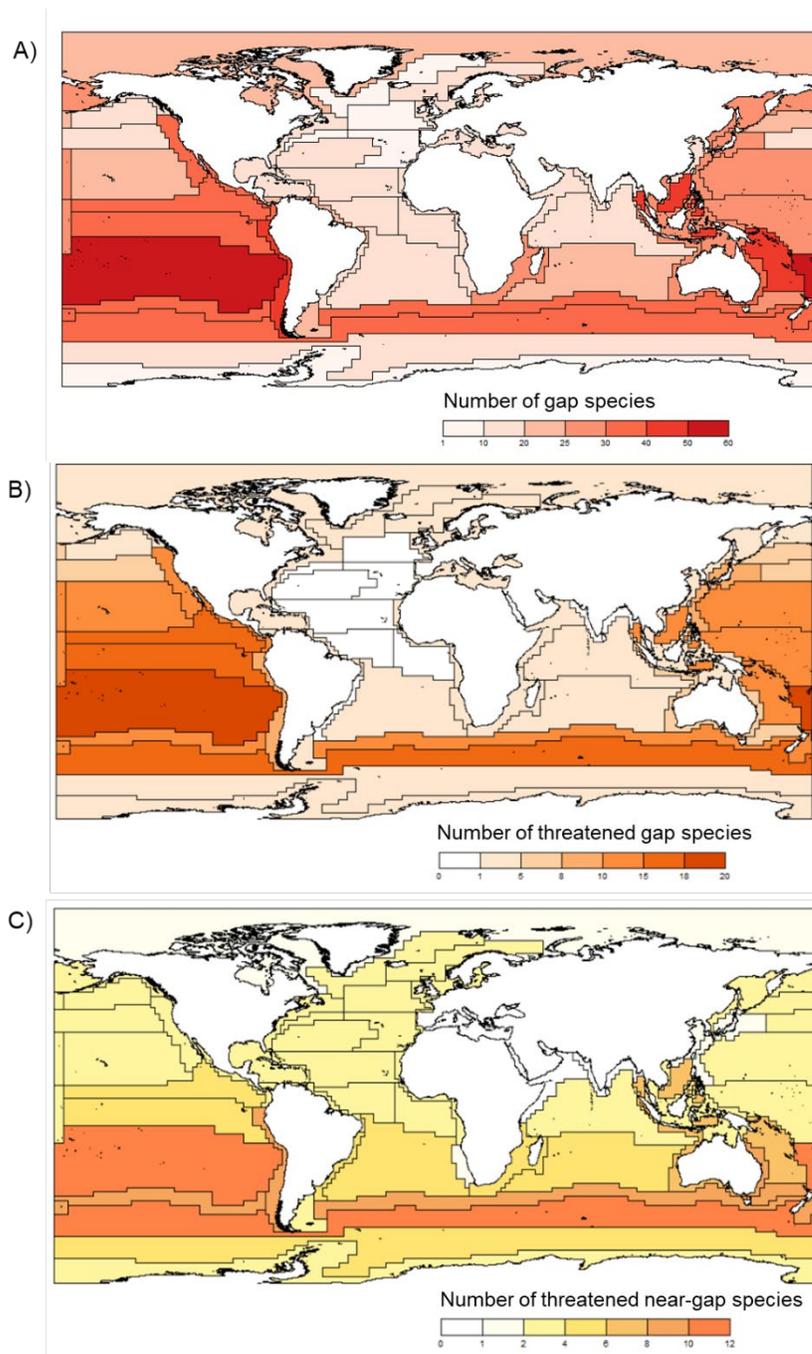


736

737 **Figure 3:** Tracking intensity of threatened species: A) Relationship between tracking effort (number  
 738 of individuals tracked per species) and tracking coverage (percentage of the species' at-sea range  
 739 covered by tracking data), for threatened seabird species for which tracking data were found in the  
 740 literature (n=59). B) List of threatened species for which no tracking data were found in the literature  
 741 (n=54). For species not in bold (n=9) we found tracking data in online databases (*Seabird Tracking*  
 742 *Database* or *Movebank*). The genera abbreviations for Alcidae are: Bra. *Brachyramphus*; Fra.  
 743 *Fratercula*; Syn. *Synthliboramphus*. For Anatidae: Cla. *Clangula*; Mel. *Melanitta*, Pol. *Polysticta*,

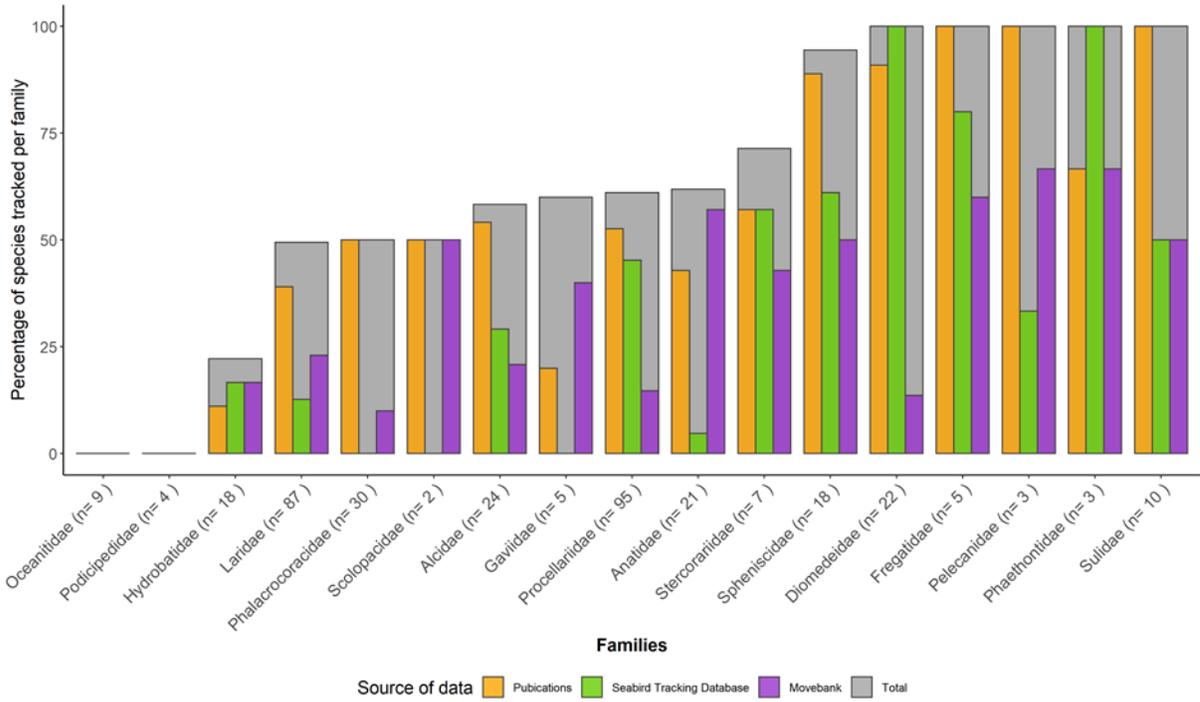
744 Tac. *Tachyeres*. For Diomedeidae: Dio. *Diomedeida*, Pho. *Phoebetria*, Tha. *Thalassarche*. For  
745 Fregatidae: Fre. *Fregata*. For Hydrobatidae: Hyd. *Hydrobates*. For Laridae: Chl. *Chlidonias*, Lar.  
746 *Larus*, Ony. *Onychoprion*, Ris. *Rissa*, Sau. *Saundersilarus*, Ste. *Sternula*, Tha. *Thalasseus*. For  
747 Phalacrocoracidae: Leu. *Leucocarbo*, Nan. *Nannopterum*, Pha. *Phalacrocorax*. For Podicipedidae:  
748 Pod. *Podiceps*. For Procellariidae: Ard. *Ardenna*, Pac. *Pachyptila*, Pel. *Pelecanoides*, Pro.  
749 *Procellaria*, Pse. *Pseudobulweria*. Pte. *Pterodroma*, Puf. *Puffinus*. For Spheniscidae: Eud.  
750 *Eudyptes*, Med. *Megadyptes*, Sph. *Spheniscus*. For Sulidae: Mor. *Morus*, Pap. *Papasula*.

751



752

753 **Figure 4.** Spatial gaps in tracking data, mapped across Longhurst provinces. A) Number of gap  
 754 species, i.e. those for which no tracking data were found in the reviewed literature (n=178). B)  
 755 Number of threatened gap species (n=54). C) Number of threatened near-gap species, i.e., with  
 756 both little tracking effort (< 100 individuals) and little tracking coverage (<50% of range covered)  
 757 (n=19)”



758

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

761

762

763 **Supplementary materials for this manuscript include the following:**

764        Figures S1 to S14

765        Tables S1 to S4

766        SI References

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