1 **Biological traits of seabirds predict extinction risk and vulnerability**

2 **to anthropogenic threats**

3 **RUNNING TITLE:** Traits predict seabird extinction risk

4 **ABSTRACT**

5 **Aim**

6 Seabirds are heavily threatened by anthropogenic activities and their conservation status is

7 deteriorating rapidly. Yet, these pressures are unlikely to uniformly impact all species. It remains

8 an open question if seabirds with similar ecological roles are responding similarly to human

9 pressures. Here we aim to: 1) test whether threatened vs non-threatened seabirds are separated in

10 trait space; 2) quantify the similarity of species' roles (redundancy) per IUCN Red List Category;

11 and 3) identify traits that render species vulnerable to anthropogenic threats.

12 **Location**

13 Global

14 **Time period**

15 Contemporary

16 **Major taxa studied**

17 Seabirds

18 **Methods**

19 We compile and impute eight traits that relate to species' vulnerabilities and ecosystem

20 functioning across 341 seabird species. Using these traits, we build a mixed-data PCA of species'

21 trait space. We quantify trait redundancy using the unique trait combinations (UTCs) approach.

22 Finally, we employ a SIMPER analysis to identify which traits explain the greatest difference

23 between threat groups.

24 **Results**

25 We find seabirds segregate in trait space based on threat status, indicating anthropogenic impacts

26 are selectively removing large, long-lived, pelagic surface feeders with narrow habitat breadths.

27 We further find that threatened species have higher trait redundancy, while non-threatened

28 species have relatively limited redundancy. Finally, we find that species with narrow habitat

29 breadths, fast reproductive speeds, and varied diets are more likely to be threatened by habitat-

30   modifying processes (e.g., pollution and natural system modifications); whereas pelagic

31   specialists with slow reproductive speeds and varied diets are vulnerable to threats that directly

32   impact survival and fecundity (e.g., invasive species and biological resource use) and climate

33   change. Species with no threats are non-pelagic specialists with invertebrate diets and fast

34   reproductive speeds.

35   **Main conclusions**

36   Our results suggest both threatened and non-threatened species contribute unique ecological

37   strategies. Consequently, conserving both threat groups, but with contrasting approaches may

38   avoid potential changes in ecosystem functioning and stability.

39

40   **Keywords**

41   anthropogenic threats, extinction risk, threatened, IUCN, redundancy, seabirds, traits,

42   vulnerability

43   **INTRODUCTION**

44   Humans are driving rapid changes in the world's physical, chemical and biological makeup

45   (Jenkins, 2003). Habitat transformation, species exploitation, climate change, pollution, and

46   invasive species have the largest relative global impact (IPBES, 2019). These pressures are

47   cumulative and have spread to all ecosystems, from the upper atmosphere to the deep sea

48   (Bowler et al., 2020; Geldmann, Joppa, & Burgess, 2014; Halpern et al., 2008; Venter et al.,

49   2016; Woolmer et al., 2008; Worm & Paine, 2016). Consequently, an estimated one million

50   animal and plant species are now threatened with extinction (IPBES, 2019), populations of

51   vulnerable taxa are declining, and biological diversity within assemblages is changing through

52   time due to species replacement and changes in abundance (Dornelas et al., 2014).

53

54   Biodiversity acts to stabilise ecosystem functioning under environmental fluctuations across

55   temporal and spatial scales (Tilman, Isbell, & Cowles, 2014). For example, the insurance

56   hypothesis (redundancy) suggests biodiversity provides long-term insurance to buffer

57   ecosystems against declines in their functioning, as a greater number of species ensures that

58   some species will maintain functioning even if others fail (Yachi & Loreau, 1999). Yet, the loss

59   and restructuring of biodiversity, through processes such as non-random species loss, can reduce

60   the resilience of ecosystem functions and services (Cardinale et al., 2012; Chapin et al., 2000;

61   Mace, Norris, & Fitter, 2012).

62

63   Species traits are useful tools to understand species' extinction risk, vulnerability to threats, and

64   ecological roles (Peñaranda & Simonetti, 2015). Traits are attributes or characteristics of

65   organisms measured at the individual level (Gallagher et al., 2020; Violle et al., 2007).

66   Extinctions under human pressures are not random, but relate to a number of species' traits such

67   as body size, habitat specialisation, and slow life history (Duffy, 2003; Gross & Cardinale, 2005;

68   Davidson et al., 2009; Rao & Larsen, 2010; Peñaranda & Simonetti, 2015; Cooke, Eigenbrod, et

69   al., 2019). Therefore, threats are likely to impact species with ecologically similar traits, while

70   species with ecologically flexible traits (e.g. generalist foraging strategies and large habitat

71   breadths) may have greater protection against extinction (Cooke, Eigenbrod, et al., 2019).

72   Elucidating patterns and drivers of species' extinction risk will likely provide the opportunity to

73   develop more informed and effective conservation strategies (Ripple et al., 2017). Furthermore,

74   selecting meaningful and interpretable traits can help understand species' vulnerabilities and

75   their contribution to ecosystem functions (Table 1). For example, a species' diet captures

76   regulation of trophic-dynamics and nutrient storage functions, and its sensitivity to changes at

77   lower trophic levels (Tavares, Moura, Acevedo-Trejos, & Merico, 2019). Combinations of traits

78   can summarise a species' ecological role (Brum et al., 2017), and species can be grouped based

79   on ecologically similar strategies (Cooke, Eigenbrod, et al., 2019).

80

81   Seabirds are the most threatened group of birds and their conservation status is deteriorating

82   rapidly (Croxall et al., 2012; Paleczny, Hammill, Karpouzi, & Pauly, 2015). Seabirds are well

83   adapted for life in the marine environment owing to their life history and ecological strategies

84   including long life span, low fecundity and specialised foraging strategies e.g., diving for prey

85   underwater. These traits likely evolved to optimise adult survival because delivering food to

86   offspring from the open ocean requires large effort (Velarde, Anderson, & Ezcurra, 2019). Thus,

87   breeding failure in years of limited food availability has a smaller negative impact on overall

88   fitness (Velarde et al., 2019). However, seabirds require isolated terrestrial landmasses to breed,

89   and open oceans to feed, which exposes them to multiple and repeated anthropogenic threats in

90   both the terrestrial and marine environment. These threats include those that directly affect

91   survival and fecundity (e.g., invasive species, bycatch), threats that modify or destroy habitat

92   (e.g., land use, energy production) and global change threats (e.g., climate change) (Croxall et

93   al., 2012; De Palma et al., 2015; Dias et al., 2019; Rodríguez et al., 2019).

94

95   Seabirds are an exceptionally well-studied faunal group both on land during the breeding season

96   and at sea through use of technologies such as biologging (e.g., Paleczny et al., 2015; Richards,

97   Padget, Guilford, & Bates, 2019). Thus, comprehensive biological detail on seabird life history,

98   behaviour and ecology is available for trait-based studies. However, few studies have used traits

99   to investigate the macroecological patterns of seabird threat risks (Zhou, Jiao, & Browder, 2019).

100   It remains an open question how ecological strategies of seabirds expose them to specific

101   anthropogenic threats, and what consequence this has for ecosystem functioning.

102

103   Here we compiled and imputed eight traits across 341 seabird species to test whether species are

104   separated in trait space due to their extinction risk. We hypothesised that threatened species will

105   occupy distinct regions of trait space because extinction risk is non-random, and because a

106   species' traits can determine how well it is able to withstand the threats to which it is exposed

107   (Cardillo et al., 2004; Cooke, Eigenbrod, et al., 2019). Next, we quantified the redundancy of

108   species' traits per IUCN category (extinction risk). If pressures are targeting species with similar

109   ecological strategies, we expect a greater redundancy in the traits of threatened species. Finally,

110   we identify whether ecologically similar seabird species are responding similarly to human

111   pressures. We hypothesised that species threatened from climate change will exhibit habitat

112   specialisation and slow reproductive speed traits because climate change is damaging breeding

113   and foraging habitats (IUCN, 2020); species with narrow habitat breadths will be at risk from

114   habitat modifying threats because the species have fewer opportunities to shift resource use or

115   distribution in response to environmental change (Cooke, Eigenbrod, et al., 2019); species with

116   slow reproductive speeds will be affected by pressures that directly affect survival and fecundity

117   because these threats destroy breeding grounds and increase mortality (Table 1); species with no

118   threats will exhibit traits that represent ecological flexibility (e.g., generalist species with fast

119   reproductive speeds) because they can offer protection from external threats (Cooke, Eigenbrod,

120   et al., 2019).

METHODS

Trait selection and data

We compiled data from multiple databases for eight traits (Table 1) across all 341 extant species of seabirds. Here we recognise seabirds as those that feed at sea, either nearshore or offshore, but excluding marine ducks. These traits encompass the varying ecological and life history strategies of seabirds, and relate to ecosystem functioning and species' vulnerabilities. We first extracted the trait data for body mass, clutch size, habitat breadth and diet guild from a recently compiled trait database for birds (Cooke, Bates, et al., 2019). Generation length and migration status were compiled from BirdLife International (datazone.birdlife.org), and pelagic specialism and foraging guild from Wilman et al. (2014). We further compiled clutch size information for 84 species through a literature search (a list of the data sources is found in Appendix 1 & S2).

Foraging and diet guild describe the most dominant foraging strategy and diet of the species. Wilman et al. (2014) assigned species a score from 0 to 100% for each foraging and diet guild based on their relative usage of a given category. Using these scores, species were classified into four foraging guild categories (*diver*, *surface*, *ground,* and *generalist* foragers) and three diet guild categories (*omnivore*, *invertebrate,* and *vertebrate & scavenger* diets). Each was assigned to a guild based on the predominant foraging strategy or diet (score > 50%). Species with category scores ≤ 50% were classified as generalists for the foraging guild trait and omnivores for the diet guild trait. Body mass was measured in grams and was the median across multiple databases. Habitat breadth is the number of habitats listed as suitable by the International Union for Conservation of Nature (IUCN, iucnredlist.org). Generation length describes the mean age in years at which a species produces offspring. Clutch size is the number of eggs per clutch (the central tendency was recorded as the mean or mode). Migration status describes whether a species undertakes full migration (regular or seasonal cyclical movements beyond the breeding range, with predictable timing and destinations) or not. Pelagic specialism describes whether foraging is predominantly pelagic. To improve normality of the data, continuous traits, except clutch size, were $\log_{10}$ transformed.

Multiple imputation

All traits had more than 80% coverage for our list of 341 seabird species, and body mass and habitat breadth had complete species coverage (Table 1). To achieve complete species trait coverage, we imputed missing data for clutch size (4 species), generation length (1 species), diet guild (60 species), foraging guild (60 species), pelagic specialism (60 species) and migration status (3 species). The imputation approach has the advantage of increasing the sample size and consequently the statistical power of any analysis whilst reducing bias and error (Kim, Blomberg, & Pandolfi, 2018; Penone et al., 2014; Taugourdeau, Villerd, Plantureux, Huguenin-Elie, & Amiaud, 2014).

We estimated missing values using random forest regression trees, a non-parametric imputation method, based on the ecological and phylogenetic relationships between species (Breiman, 2001; Stekhoven & Bühlmann, 2012). This method has high predictive accuracy and the capacity to deal with complexity in relationships including non-linearities and interactions (Cutler et al., 2007). To perform the random forest multiple imputations, we used the *missForest* function from package "missForest" (Stekhoven & Bühlmann, 2012). We imputed missing values based on the ecological (the trait data) and phylogenetic (the first 10 phylogenetic eigenvectors, detailed below) relationships between species. We generated 1,000 trees - a cautiously large number to increase predictive accuracy and prevent overfitting (Stekhoven & Bühlmann, 2012). We set the number of variables randomly sampled at each split (mtry) as the square-root of the number variables included (10 phylogenetic eigenvectors, 8 traits; mtry = 4); a useful compromise between imputation error and computation time (Stekhoven & Bühlmann, 2012). We used a maximum of 20 iterations (maxiter = 20), to ensure the imputations finished due to the stopping criterion and not due to the limit of iterations (the imputed datasets generally finished after 4 – 10 iterations).

Due to the stochastic nature of the regression tree imputation approach, the estimated values will differ slightly each time. To capture this imputation uncertainty and to converge on a reliable result, we repeated the process 15 times, resulting in 15 trait datasets, which is suggested to be sufficient (González-Suárez, Zanchetta Ferreira, & Grilo, 2018; van Buuren & Groothuis-

179   Oudshoorn, 2011). We took the mean values for continuous traits and modal values for

180   categorical traits across the 15 datasets for subsequent analyses.

181

182   Phylogenetic data can improve the estimation of missing trait values in the imputation process

183   (Kim et al., 2018; Swenson, 2014), because closely related species tend to be more similar to

184   each other (Pagel, 1999) and many traits display high degrees of phylogenetic signal (Blomberg,

185   Garland, & Ives, 2003). Phylogenetic information was summarised by eigenvectors extracted

186   from a principal coordinate analysis, representing the variation in the phylogenetic distances

187   among species (Jose Alexandre F. Diniz-Filho et al., 2012; José Alexandre Felizola Diniz-Filho,

188   Rangel, Santos, & Bini, 2012). Bird phylogenetic distance data (Prum et al., 2015) were

189   decomposed into a set of orthogonal phylogenetic eigenvectors using the *Phylo2DirectedGraph*

190   and *PEM.build* functions from the "MPSEM" package (Guenard & Legendre, 2018). Here, we

191   used the first 10 phylogenetic eigenvectors, which have previously been shown to minimise

192   imputation error (Penone et al., 2014). These phylogenetic eigenvectors summarise major

193   phylogenetic differences between species (Diniz-Filho et al., 2012) and captured 61% of the

194   variation in the phylogenetic distances among seabirds. Still, these eigenvectors do not include

195   fine-scale differences between species (Diniz-Filho et al., 2012), however the inclusion of many

196   phylogenetic eigenvectors would dilute the ecological information contained in the traits, and

197   could lead to excessive noise (Diniz-Filho et al., 2012; Peres-Neto & Legendre, 2010). Thus,

198   including the first 10 phylogenetic eigenvectors reduces imputation error and ensures a balance

199   between including detailed phylogenetic information and diluting the information contained in

200   the other traits.

201

202   To quantify the average error in random forest predictions across the imputed datasets (out-of-

203   bag error), we calculated the mean normalized root squared error and associated standard

204   deviation across the 15 datasets for continuous traits (clutch size = 13.3 ± 0.35 %, generation

205   length = 0.6 ± 0.02 %). For categorical data, we quantified the mean percentage of traits falsely

206   classified (diet guild = 28.6 ± 0.97 %, foraging guild = 18.0 ± 1.05 %, pelagic specialism = 11.2

207   ± 0.66 %, migration status = 18.8 ± 0.58 %). Since body mass and habitat breadth have complete

208   trait coverage, they did not require imputation. Low imputation accuracy is reflected in high out-

209   of-bag error values where diet guild had the lowest imputation accuracy with 28.6% wrongly

210   classified on average. Diet is generally difficult to predict (Gainsbury, Tallowin, & Meiri, 2018),

211   potentially due to species' high dietary plasticity (Gaglio, Cook, McInnes, Sherley, & Ryan,

212   2018) and/or the low phylogenetic conservatism of diet (Gainsbury et al., 2018). With this caveat

213   in mind, we chose dietary guild, as more coarse dietary classifications are more predictable

214   (Gainsbury et al., 2018), and we investigated the impact of the trait imputation with sensitivity

215   analyses.

216   **Sensitivity**

217   To compare whether our results and conclusions were qualitatively similar between the imputed

218   (main manuscript) and non-imputed (Appendix S3) datasets, we ran all of our analyses with and

219   without the imputed data. We further quantify the variance for continuous traits and coefficient

220   of unalikability (Redd, 2020) for categorical traits between the 15 imputed trait datasets (Fig.

221   S3.1). Finally, to compare whether our results and conclusions are impacted by using different

222   measures of clutch size for different species, we ran our analyses by excluding the modal or

223   mean clutch size separately.

224   **Species extinction risk**

225   The International Union for Conservation of Nature's (IUCN) Red List of Threatened Species

226   (iucnredlist.org) is the most comprehensive information source on the global conservation status

227   of biodiversity (IUCN, 2020). This powerful tool classifies species into nine categories of

228   extinction risk. Here we use five IUCN Red List categories to group extant species into broader

229   global risk groups. Species categorised as Critically Endangered (CR), Endangered (EN) and

230   Vulnerable (VU) were defined as *threatened*, and species classified as Near Threatened (NT) and

231   Least Concern (LC) were defined as *non-threatened*.

232

233   Two species classified as Data Deficient (*Oceanites gracilis* and *Oceanites pincoyae*), and one

234   Not Evaluated species (*Larus thayeri*) were removed from the species list leaving a total of 338

235   species for all subsequent analyses.

Principal component analysis of mixed data

236

237 To quantify the trait space shared by threatened and non-threatened seabirds, we ordinated 338

238 seabirds based on eight traits with a principle component analysis (PCA) of mixed data. We used

239 the package "PCAmixdata" and function *PCAmix* (Chavent, Kuentz, Labenne, Liquet, &

240 Saracco, 2017). PCA of mixed data takes a two-step approach through merging the standard

241 PCA with multiple correspondence analysis (MCA) (Chavent, Kuentz-Simonet, Labenne, &

242 Saracco, 2014). For continuous data, PCAmix is a standard PCA, whereas for categorical data,

243 PCAmix it is an MCA (Chavent et al., 2014). We used kernel density estimation to extract the

244 95% quantiles of the probability distribution for threatened and non-threatened via the *kde*

245 function from the package "ks" (Duong, 2020). To quantify the degree to which threat status

246 explains trait space variations among seabirds, we used the permutational MANOVA framework

247 in the *adonis* function and package "vegan" (Oksanen et al., 2018). The function partitions the

248 sums of squares of a multivariate data set using dissimilarities (Oksanen et al., 2018).

Trait-level distributions and proportions

249

250 To quantify the difference in individual traits between threatened and non-threatened seabirds,

251 we calculated Hedge's g effect size with function *hedges_g* and package 'effectsize' (Ben-

252 Shakhar, Makowski, & Lüdecke, 2020) for continuous traits, and the percent difference for

253 categorical traits. Moreover, differences in the means of threatened and non-threatened species

254 within continuous traits were compared with Mann-Whitney U tests using function *wilcox.test* (R

255 Core Team, 2018). For categorical traits, we tested for independence with a Chi-squared

256 approach using function *chisq.test* (R Core Team, 2018).

Unique trait combinations

257

258 To quantify the redundancy of species' trait combinations per IUCN Red List Category, we used

259 unique trait combinations (UTCs). Here UTC is defined as the proportion of species with trait

260 combinations that are not found in other seabird species. To compute the UTCs of the 338

261 seabirds, we broke the continuous traits into three equally spaced bins (small, medium and large)

262 between minimum and maximum values. Following this, the proportion of UTCs within each

263 IUCN Red List Category was calculated as a percentage.

Seabird Threats

264

265 We extracted the past, present, and future threats for 338 seabirds from the IUCN Red List

266 database using the function *rl_threats* and package "rredlist" (Chamberlain, 2018). These data

267 have recently been updated in a quantitative review from >900 publications (Dias et al., 2019),

268 and are classified into 12 broad types (Table 2). We reclassified the IUCN threats into five

269 general categories (Table 2): (1) *climate* – encompasses climate change and severe weather

270 threats; (2) *direct* – threats that directly affect survival and fecundity; (3) *habitat* - threats that

271 modify or destroy habitat; (4) *no threats* – species with no identified IUCN threats; and (5) *other*

272 – threats that are indirectly or not caused by humans (González-Suarez, Gomez, & Revilla,

273 2013). We excluded *other* threats (geological events) from our analyses because they are not

274 directly linked to anthropogenic activity.

SIMPER analysis

275

276 To identify which traits explain the greatest difference between threats, we took a similarity of

277 percentages (SIMPER) approach using the function *simper* in package "vegan" (Oksanen et al.,

278 2018). SIMPER typically identifies the species that contribute the greatest dissimilarity between

279 groups (levels) by disaggregating the Bray-Curtis similarities between inter-group samples from

280 a species-abundance matrix (Clarke & Warwick, 2001). Here, we assembled a trait-by-threat

281 matrix, where traits have 23 levels and threats have 11 levels. Trait levels were summed from the

282 four continuous traits with 3 bins each (12 levels) and four categorical traits with 11 levels

283 (Table 1), and threats are the IUCN threat categories (first 11 levels from Table 2). For each

284 threat, we calculated the proportion of species in each trait category. The reclassified IUCN

285 threats were used to isolate the traits that contribute the greatest difference between climate

286 threats, habitat threats, direct threats and no threats.

287

288 All analyses were performed in R version 3.5.0 (R Core Team, 2018).

RESULTS

Threat status segregation in multidimensional trait space

We found threatened species (n = 105) are distinct from non-threatened species (n = 233) in terms of their biological trait diversity (PERMANOVA, R^2 = 0.122, p = 0.001; Fig. 1). Together, the first two dimensions (identified herein as "Dim1" and "Dim2") of the mixed data PCA explain 41% of the total trait variation (Fig. 1). Dim1 integrates non-pelagic specialism (loading = 1.336), clutch size (loading = 0.860), invertebrate diet (loading = 0.645), omnivore diet (loading = -0.158), pelagic specialism (loading = -0.306), generation length (loading = -0.696), surface foragers (loading = -0.855), and vertebrate and scavenger diet (loading = -0.881). Species with high Dim1 scores are typically characterised as non-pelagic scavengers with fast reproductive speeds e.g., cormorants, gulls and terns. Species with low Dim1 values have slow reproductive speeds and are pelagic surface foragers with diets high in invertebrates e.g., albatrosses, petrels, shearwaters and storm-petrels. Dim2 integrates ground (loading = 1.481) and generalist (loading = 0.979) foraging strategies, full migrants (loading = 0.360), body mass (loading = -0.347), divers (loading = -0.967), and non-migrants (loading = -1.088). Species with high Dim2 are small bodied ground or generalist foragers e.g., gulls, terns, skuas and jaegers while those with low Dim2 are large bodied non-migrating divers e.g., shags, boobies and penguins.

Eight species from the Laridae family fell outside the 95% kernel contour for the threatened species. These include the Black-billed Gull (*Larus bulleri*), Lava Gull (*Larus fuliginosus*), Relict Gull (*Larus relictus*), Black-fronted Tern (*Chlidonias albostriatus*), Black-bellied Tern (*Sterna acuticauda*), Chinese Crested Tern (*Thalasseus bernsteini*), Aleutian Tern (*Onychoprion aleuticus*), and Indian Skimmer (*Rynchops albicollis*).

Individual trait differences

We found a significant difference in six traits between threatened and non-threatened species (Fig. 2; Table 3). Specifically, habitat breadths of threatened species are 2.2 times smaller [95% CI: -2.52, -1.95] than non-threatened seabirds, clutch sizes are 0.46 times smaller [95% CI: -0.69, -0.22], and generation lengths are 0.43 times longer [95% CI: 0.20, 0.67]. Compared to

11

318   non-threatened species, we found threatened species have 18.8% more pelagic specialists, 26.5%

319   more surface foragers, 5.0% fewer divers, 4.2% fewer ground foragers, 17.4% fewer generalist

320   foragers, 31.5% fewer species with invertebrate diets, 22.5% greater species with vertebrate and

321   scavenger diets, and 9.0% greater species with omnivore diets (Fig 2). There was no difference

322   in the body mass, or migration traits between threatened and non-threatened species (Table 3).

323   We found threatened species are typically surface feeders with a diet higher in fish and carrion.

324   They are mostly pelagic specialists that have narrow habitat breadths, small clutch sizes and long

325   generation times. In comparison, non-threatened species are typically generalist foragers with a

326   diet high in invertebrates. These species also typically have shorter generation lengths and larger

327   clutch sizes with a broader habitat breadth and less pelagic specialism.

328   **Trait redundancy**

329   We classified 166 different trait combinations across 338 seabirds. Of these trait combinations,

330   59% are composed of only one species (n = 98) and are defined as unique trait combinations

331   (UTCs). The proportion of UTCs decreases with increasing IUCN threat level (Fig 3).

332   Consequently, a greater proportion of non-threatened species (32%) contribute UTCs compared

333   to threatened species (23%). We, therefore, found greater redundancy in traits of threatened

334   species and less redundancy in traits of non-threatened species (Fig. 3).

335

336   **SIMPER**

337   Our similarity percentages analysis (SIMPER) identified the combination of reproductive speed

338   traits (generation length and clutch size), specialisation traits (pelagic specialism, diet guild,

339   habitat breadth, and foraging guild), and body mass explained >50% of the dissimilarity between

340   threat categories (Table 4). Focussing on climate change versus other types of threats first

341   reveals that the four traits (pelagic specialism, diet guild, habitat breadth, and reproductive

342   speed) explain the greatest dissimilarity between groups species threatened by either climate

343   change or direct threats. By comparison, pelagic specialism, habitat breadth, and reproductive

344   speed (as above), and also body mass explain the greatest dissimilarity between species

345   threatened by climate change or habitat threats. Comparing species threatened by climate change

346   versus no threats revealed clutch size traits in underpinning dissimilarity, in addition to diet

347   guild, pelagic specialism and body mass. Comparisons between other types of threats, such as

348   species impacted by direct versus habitat threats identified reproductive speed, pelagic

349   specialism, diet guild, and foraging guild traits as explaining the greatest dissimilarity. Between

350   direct and no threats, diet guild, habitat breadth, pelagic specialism, and foraging guild traits

351   explain the greatest dissimilarity. Finally, diet guild, habitat breath, reproductive speed, and

352   pelagic specialism traits explain the greatest dissimilarity between the habitat and no threats

353   groups.

354

355   By comparing the proportion of species per trait between each threat category (Table 4), we

356   found general patterns emerge between species' traits and their threats (Fig. 4). A greater

357   proportion of species at risk to climate change and direct threats exhibited slow reproductive

358   speeds and were pelagic specialists. For species at risk to habitat threats, a higher proportion of

359   species occupied small habitat breadths, were non-pelagic specialists, and had short generation

360   lengths. Finally, for seabird species with no threats, a greater proportion of species had fast

361   reproductive speeds, invertebrate diets and were non-pelagic specialists.

362   **Sensitivity**

363   We found that our results and conclusions are comparable between the imputed and non-imputed

364   datasets (see Appendix S3 in supporting information: Figs. S3.2 – S3.5, Tables S3.1 – S3.6).

365   Furthermore, the variance between the 15 imputed trait datasets was minimal (Fig. S3.1). Finally,

366   we found our results are not impacted by using different measures of clutch size for different

367   species (Fig. S3.5, Tables S3.5 & S3.6).

368   **DISCUSSION**

369   We revealed that threatened and non-threatened seabirds occupy different regions of trait space.

370   Specifically, threatened species share a distinct subset of similar traits that are associated with a

371   higher risk of extinction. Therefore, the loss of threatened species, such as wide-ranging

372   albatross and shearwaters, may have direct implications for ecosystem functioning such as

373   trophic regulation, nutrient transportation and community shaping (Graham et al., 2018; Tavares

374   et al., 2019). We further found non-threatened species have relatively unique ecological

375   strategies and limited redundancy. Consequently, non-threatened species could have less

376   insurance to buffer against ecosystem functioning declines should they become threatened in the

377   future (Yachi & Loreau, 1999). We must therefore conserve both threatened and non-threatened

378   species, but with contrasting approaches to avoid potential changes in ecosystem functioning and

379   stability. Both threatened and non-threatened species would benefit from routine monitoring of

380   populations and threats which will allow researchers and managers to establish baselines for

381   future comparison and data sharing (e.g. Hebert et al., 2020). Threatened species would further

382   benefit from targeted conservation interventions to protect their unique ecological strategies. For

383   example, through actions such as eliminating habitat threats through conserving important

384   breeding and foraging habitats, and reducing bycatch, and irradiating invasive species like

385   rodents and cats at breeding colonies (Jones, 2010). While implementing major management

386   actions are challenging because they take significant policy development, are often costly, take

387   time, and require international collaboration, our analyses suggest large benefits for protecting

388   the ecological roles of seabirds in nature.

389

390   We found a number of traits emerge with strong association to extinction risk and different types

391   of threats. Overall, anthropogenic pressures may be selecting against slow-lived and specialised

392   species (e.g., albatross and petrels) in favour of fast-lived and wide-ranging generalists (e.g.,

393   gulls and terns). This result agrees with the patterns of other birds and mammals (Cooke,

394   Eigenbrod, et al., 2019; Davidson et al., 2009; Peñaranda & Simonetti, 2015). However, in

395   contrast to numerous studies (Cardillo et al., 2005; Cooke, Eigenbrod, et al., 2019; Ripple et al.,

396   2017), we found no difference in the body mass of threatened and non-threatened species.

397   Therefore, threats are targeting all seabird sizes from the largest (Wandering Albatross,

398   *Diomedea exulans*, 7000 g) to the smallest seabird (European Storm-petrel, *Hydrobates*

399   *pelagicus*, 25 g). Potential explanations could be that major threats to seabirds are not size

400   dependent. For example, invasive species on a breeding island would consume all species' eggs,

401   and all sizes of seabirds are attracted to fishing vessels (Caut, Angulo, & Courchamp, 2008;

402   Zhou et al., 2019).

403

404   Our results support our hypothesis that species at risk to climate change threats exhibit slow

405   reproductive speeds and are pelagic specialists. We suggest that this is due to the potential

406   negative impacts of climate change on foraging and breeding habitats for seabirds that could lead

407   to reduced nutritional supply and reduced reproductive success, which would impact slow-lived

408   pelagic species more intensely (IUCN, 2020).

409

410   Moreover, traits distinguishing species at risk from direct threats were slow reproductive speed,

411   pelagic specialism, and diet guild traits, reflecting recent findings for mammals (González-

412   Suarez et al., 2013). Here, direct threats encompass invasive species and bycatch, which are the

413   top two threats facing seabirds worldwide (Dias et al., 2019), in addition to human disturbance.

414   Most species at risk to direct threats are tubenose seabirds (albatross, petrels, shearwaters).

415   Tubenoses are highly pelagic species that depend on the ocean for foraging. Therefore, tubenoses

416   often strongly overlap with fishing vessels (Clay et al., 2019) and opportunistically scavenge

417   fisheries discards. In this process, birds are caught on baited hooks and drowned, or entangled in

418   nets and collide with cables which results in high mortality. Consequently, an estimated 320,000

419   seabirds die annually in longline fleets alone (Anderson et al., 2011). Tubenose seabirds are

420   further strongly impacted by invasive species (e.g., rats and cats) and human disturbance at

421   breeding colonies (Dias et al., 2019). These seabirds lay a single egg per season; therefore, their

422   populations have a lower capacity to compensate for bycatch mortality and poor reproductive

423   success due to invasive species and human disturbance.

424

425   We found species at risk of habitat modifying threats have the smallest habitat breadths, and

426   slower reproductive speeds than species with no threats, and omnivorous diets. This finding

427   corroborates previous studies which identify that habitat specialisation increases species'

428   vulnerability and limits their capacity to adapt to environmental change (González-Suarez et al.,

429   2013; Peñaranda & Simonetti, 2015). Habitat specialisation and species' vulnerability are

430   ultimately linked due to the strong interaction between habitat breadth and resource use, where

431   species with narrow habitat breaths have a restricted extent for resource use and less

432   opportunities to shift resource use in response to environmental stressors (Cooke, Bates, et al.,

433   2019). For instance, habitat threats particularly impact coastal and wetland seabirds, such as

434   cormorants and gulls. This is likely because these habitats, which are vital for these seabirds

435   during wintering and breeding, are being modified and destroyed by activities such as land use

436   change and tourism, with limited alternative resources.

437

438   As hypothesised, we found that species with no threats exhibit traits related to ecological

439   flexibility (fast reproductive speeds, but no evidence of habitat or dietary generalism). We also

440   found that these species are typically non-pelagic specialists with invertebrate diets. We

441   therefore provided further evidence that ecological flexibility can offer protection from a range

442   of external threats (Cardillo et al., 2004; Cooke, Eigenbrod, et al., 2019). Specifically, faster

443   reproductive speeds allow species to more rapidly respond to changes in resource availability,

444   especially to the highly variable resources of marine environments (Velarde et al., 2019). If, as

445   predicted, human-driven selection pressures on birds intensify in the future (Cooke, Eigenbrod,

446   et al., 2019), then seabirds with no threats could potentially expand in number and distribution.

447   Although, by contrast, intensified human pressures could also begin to impact upon these

448   species. In response, effective monitoring of species with no current threats could identify which

449   outcome is becoming realised, and the possible management interventions required.

450

451   Identifying traits most associated with threats can lead to more informed and effective

452   conservation strategies. Species at risk to direct threats need targeted conservation interventions

453   through bycatch mitigation and invasive species eradication to protect highly pelagic species

454   with slow reproductive speeds. These initiatives are beginning to show great promise. For

455   example, implementing bird deterrents in a South African trawl fishery reduced albatross deaths

456   by 95% between 2004 to 2010 (Maree, Wanless, Fairweather, Sullivan, & Yates, 2014).

457   Furthermore, eradicating rats from breeding colonies has dramatically recovered seabird

458   populations (Veitch et al., 2019), and restored ecosystem functions such as nutrient

459   transportation to soil and plants (Jones, 2010; Wardle, Bellingham, Bonner, & Mulder, 2009;

460   Wardle, Bellingham, Fukami, & Bonner, 2012). Habitat breadth is strongly related to threat

461   status via species' capacity to adapt to changes in habitat cover. Habitat conservation therefore

462   reduces the selection pressure against species that are sensitive to habitat change. Examples of

463   marine habitat conservation measures for seabirds include designating marine protected areas to

464   conserve important seabird hotspots, movement pathways, and foraging areas (D'Aloia et al.,

465   2019; Ronconi, Lascelles, Langham, Reid, & Oro, 2012). At breeding sites, conservation

466   measures include closing colony visitation during the breeding season and establishing buffer

467   zones for land, water, and air to eliminate disturbance and nest abandonment.

468

469   Here we used the IUCN database to identify the traits most associated with different threats.

470   While the IUCN threats database is a valuable resource, its collation via expert opinion is

471   subjective and can contain bias (Hayward, 2009). Therefore, some threats may be unreported or

472   overreported. Furthermore, rare or understudied species, for example the Critically Endangered

473   magenta petrel (*Pterodroma magenta*) with fewer than 100 mature individuals, likely have fewer

474   known threats than highly studied species such as the Atlantic puffin (*Fratercula arctica*).

475   Further studies that couple spatial patterns of extrinsic threats with intrinsic traits could offer

476   valuable insight into species vulnerabilities to anthropogenic threats, and ultimately help inform

477   effective management and conservation at local and global scales.

478

479   In conclusion, we expanded our understanding of extinction risk drivers in seabirds through a

480   trait-based approach. Our findings highlight the need to conserve both threatened and non-

481   threatened species in order to conserve the diversity of ecological strategies and associated

482   ecosystem functions. We suggest traits be coupled with spatial patterns of extrinsic threats to

483   advance conservation management strategies.

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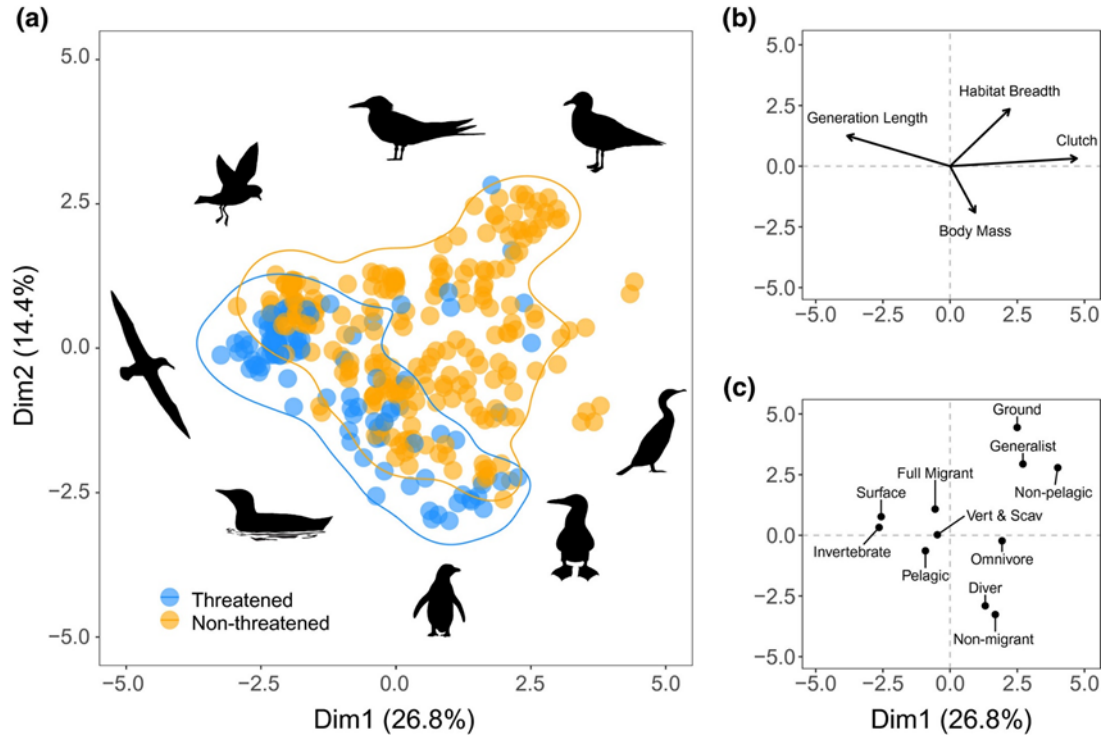697   https://doi.org/10.1098/rsbl.2012.0201

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713

714 Data Accessibility Statement

715 The raw (non-imputed) trait data and complete (imputed) trait data used for all analyses are

716 available for download on Dryad: https://doi.org/10.5061/dryad.x69p8czhd. The R code

717 summarizing the major analytical steps are available on GitHub:

718 https://github.com/CerrenRichards/seabird-extinction-risk.

Figures


Figure 1 Mixed data PCA biplot of seabird traits. a) Points are the principal component scores of each seabird (mean values across 15 imputed datasets). Contours indicate the 95% kernel quantiles for threatened (blue) and non-threatened (orange) seabird species. Silhouettes represent a selection of families aggregated at the edge of trait space. All silhouettes created by authors. Coordinates of b) continuous and c) categorical traits. Coordinates were rescaled to match the mixed data PCA.
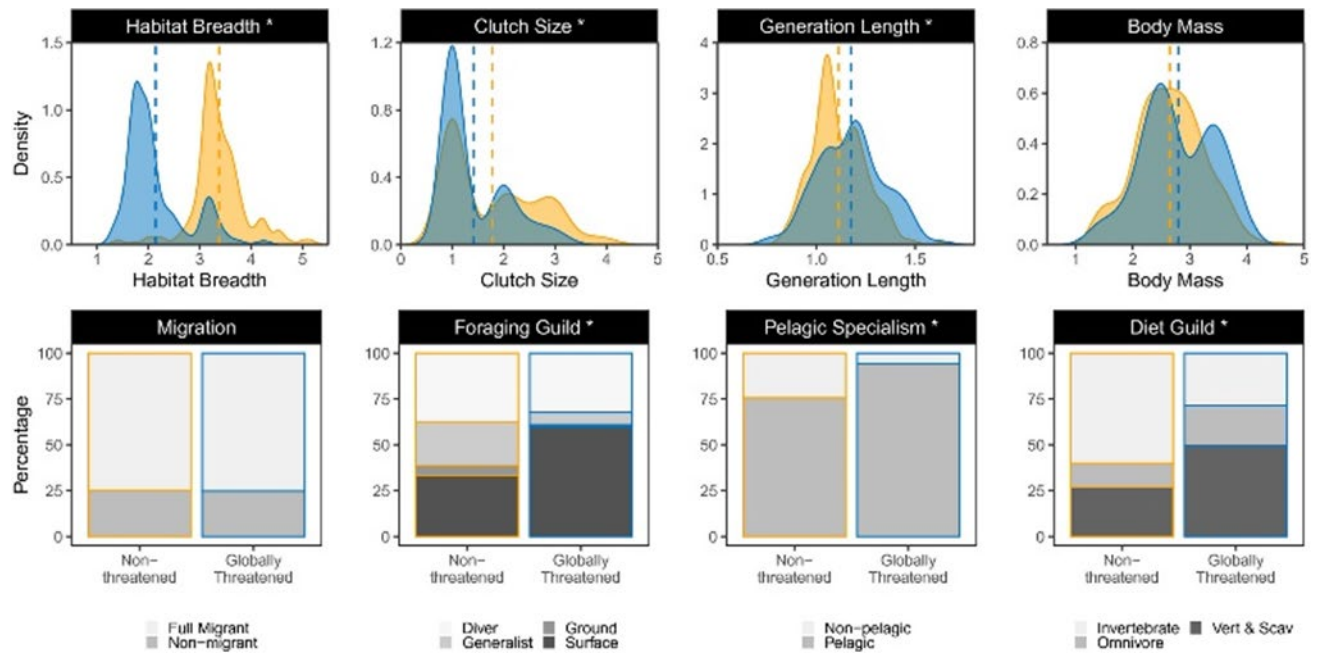
728   *Figure 2 Distributions of continuous traits and proportion of categorical traits. Orange*

729   *represents non-threatened species, while blue represents threatened species. Dashed lines are*

730   *the mean of each distribution. Habitat breadth, generation length and body mass x-axes are log-*

731   *transformed. Asterisks indicate the traits with significant differences between threatened and*

732   *non-threatened species identified from Table 3.*
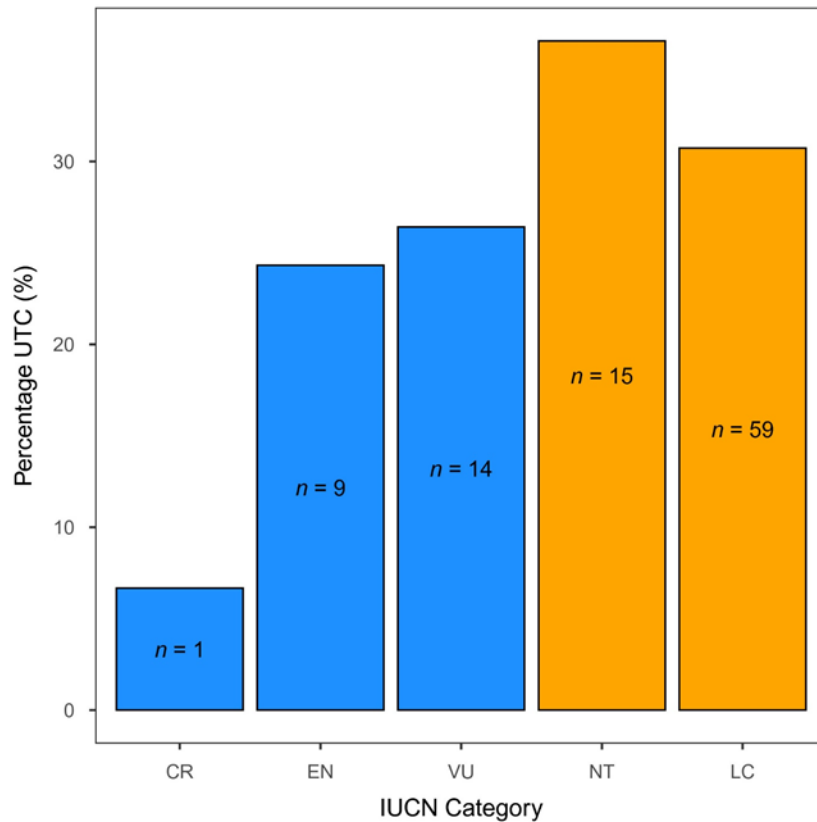
Figure 3 Proportion of seabird species with unique trait combinations (UTC) for each IUCN category. Orange represents non-threatened categories and blue represents threatened categories. 'CR' is Critically Endangered, 'EN' is Endangered, 'VU' is Vulnerable, 'NT' is Near Threatened, and 'LC' is Least Concern. 'n' indicates the number of species with UTCs in each IUCN category.
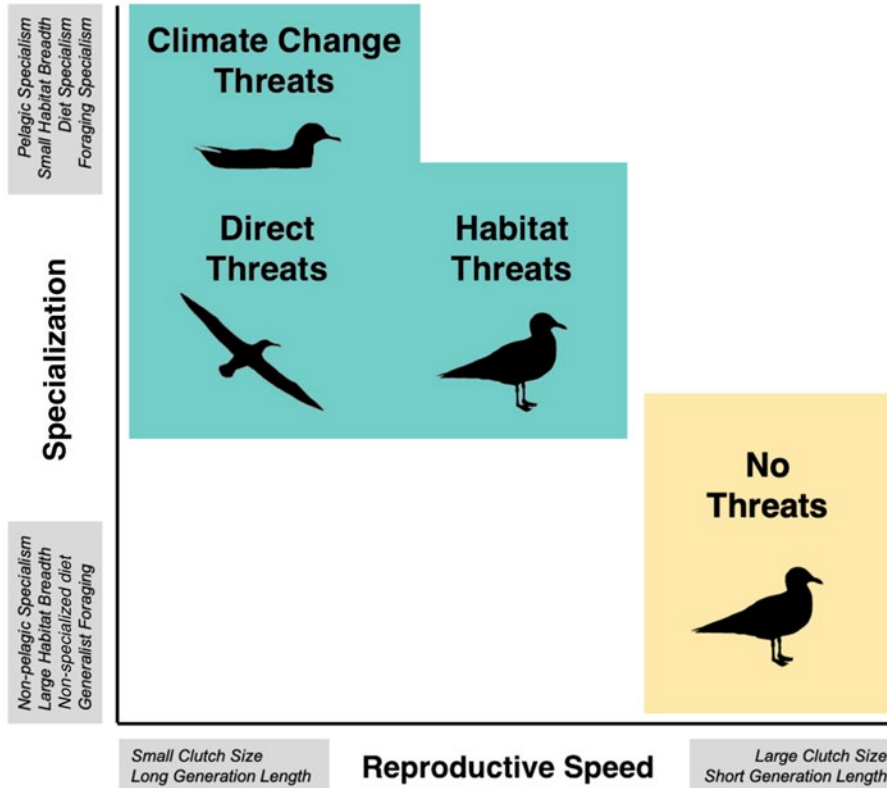
Figure 4 Generalised pattern of traits that predict vulnerability of seabirds to varying

anthropogenic threats based on the results presented in Table 4. Silhouettes represent seabird

families with high frequencies of species at risk to each threat type. 'Climate' threats encompass

climate change and severe weather. 'Direct' threats directly impact the survival and fecundity of

seabirds, while 'habitat' threats modify or destroy habitats. 'No threats' encompasses species

with no identified IUCN threats. Reproductive speed is the trade-off between clutch size and

generation length. Specialisation encompasses pelagic specialism, habitat breadth, diet guild,

and foraging guild.

748
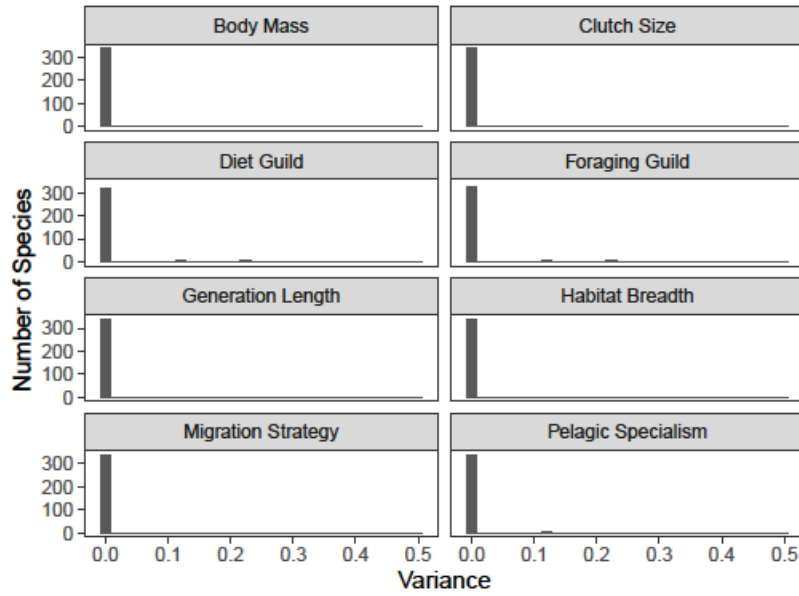
*Figure S3.1 Variance for continuous traits and coefficient of unalikability for categorical traits*

between the 15 imputed trait datasets.


751
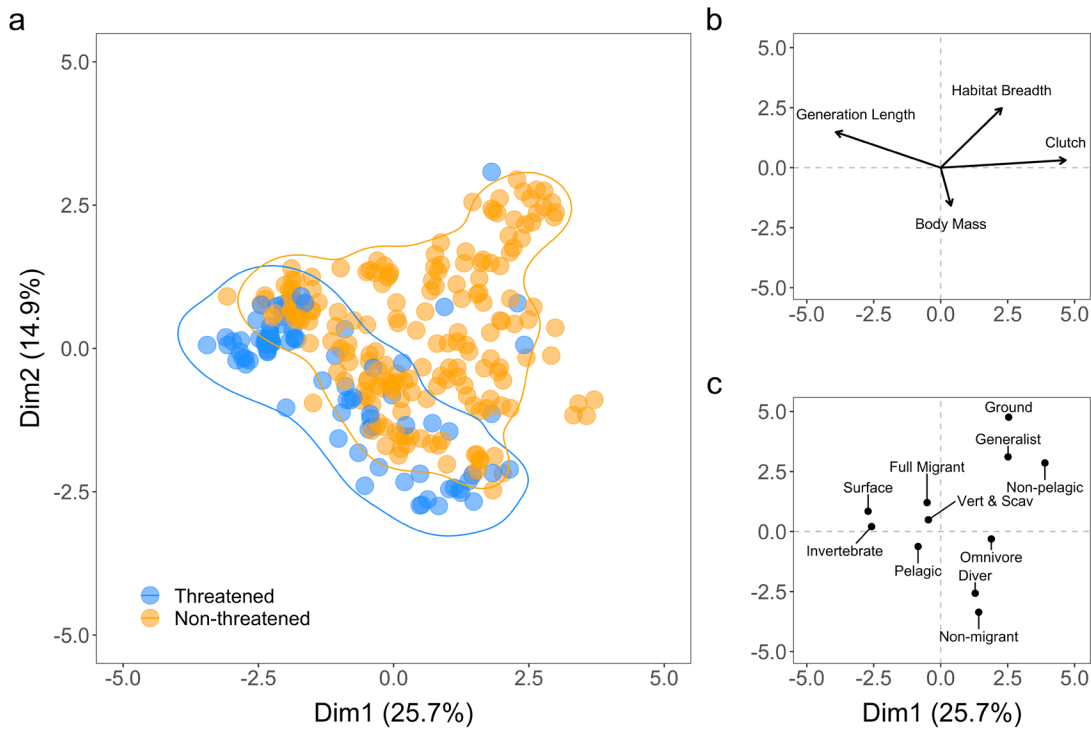
Figure S3.2 Mixed data PCA biplot of seabird traits excluding imputed data. a) Points are the

principal component scores of each seabird species. Ellipses indicate the 95% confidence

intervals for globally threatened (blue) and non-threatened (orange) seabird species.

755   *Coordinates of b) continuous and c) categorical traits. Coordinates were rescaled to match the*

756   *mixed data PCA.*
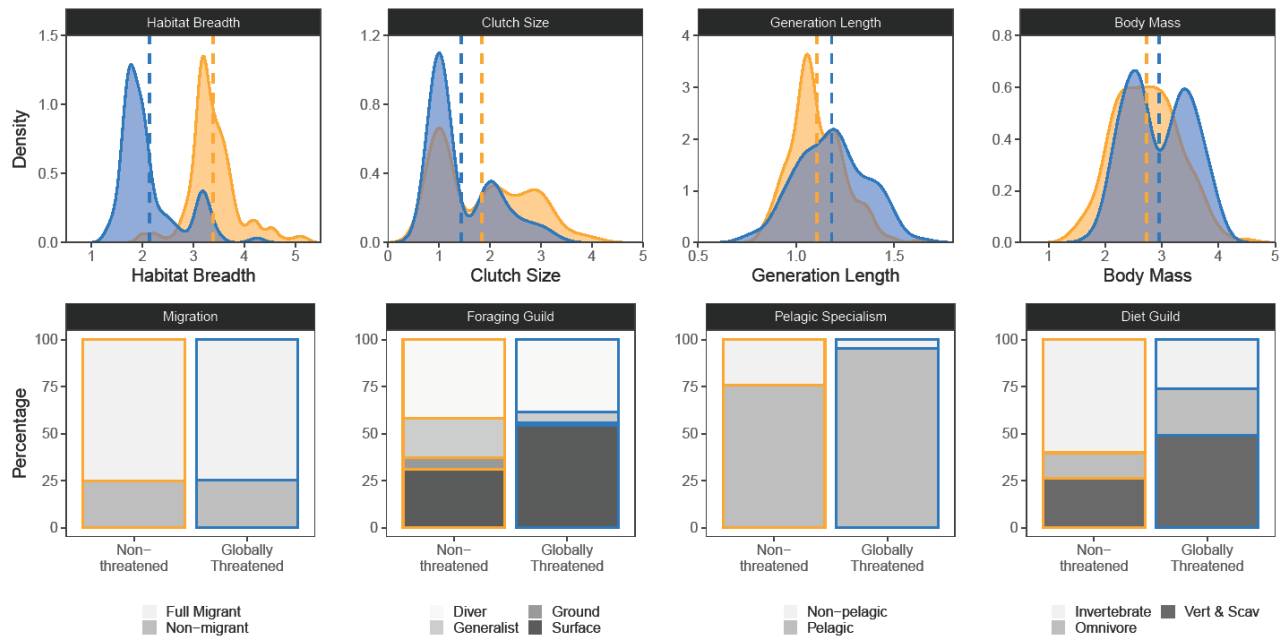
758   *Figure S3.3 Distributions of continuous traits and proportion of categorical traits, excluding*

759   *imputed data. Orange represents non-threatened species, while blue represents globally*

760   *threatened species. Habitat breadth, generation length and body mass x-axes are log-*

761   *transformed. Habitat breadth and body mass have full trait coverage.*
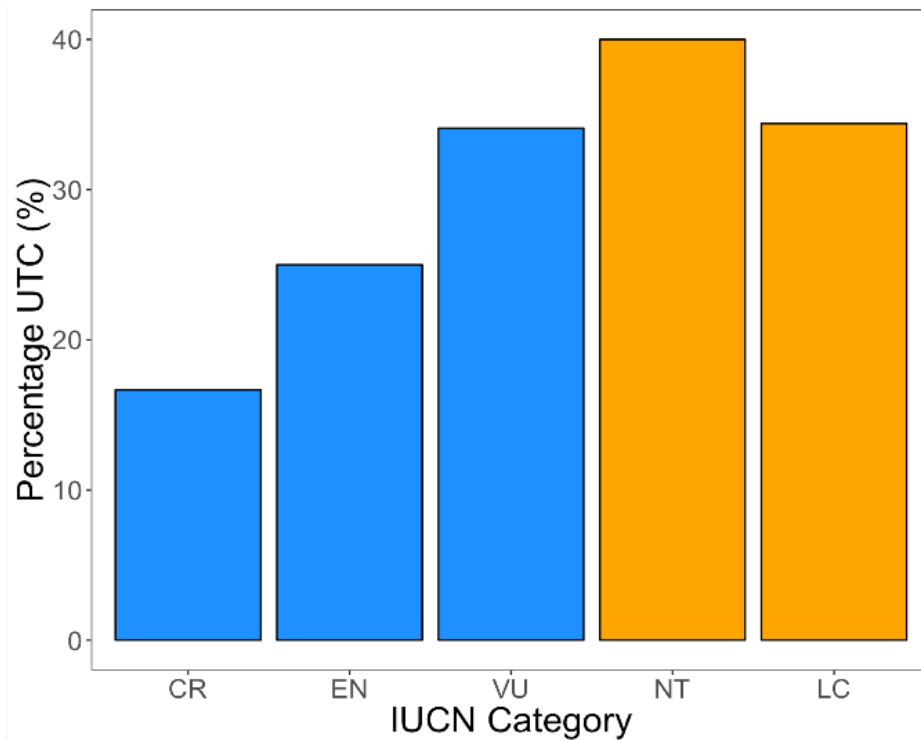
762
763 *Figure S3.4 Proportion of seabird species (281 sp.) with non-imputed unique trait combinations*

764 *for each IUCN category. Orange represents non-threatened categories and blue represents*

765 *globally threatened categories.*
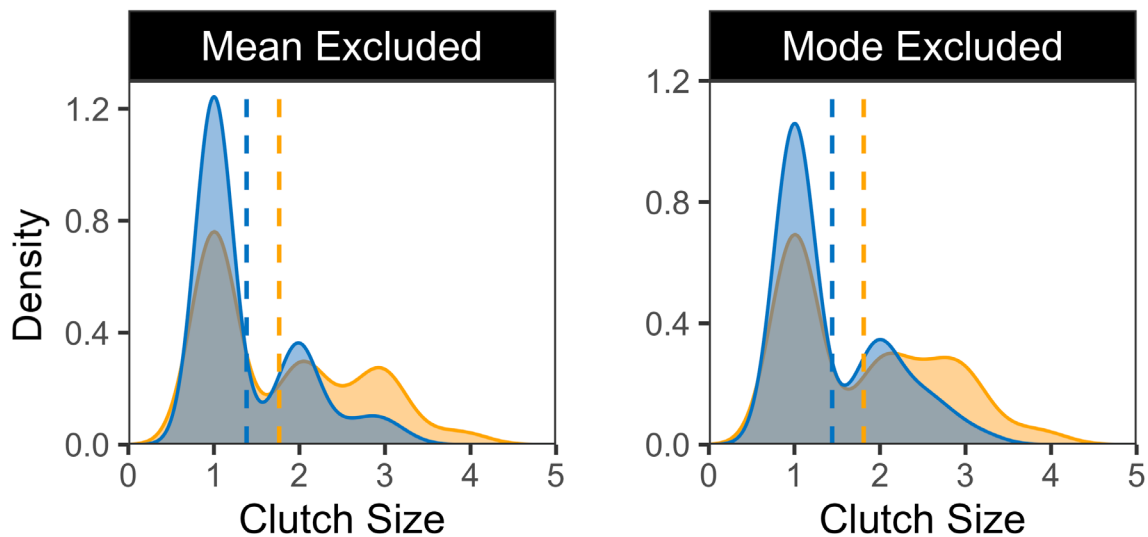
766
767 *Figure S3.5 Distributions of clutch size trait after excluding all compiled mean values (left), and*

768 *excluding all the compiled modal values (right). Orange represents non-threatened species,*

769 *while blue represents globally threatened species.*

TABLES

Table 1 Description of the traits used in the present study and their relation to ecosystem

functioning and species' vulnerabilities. Ecosystem function column modified from Tavares et al.

(2019). Imputation indicates the number of species imputed. Sources - 1: Cooke et al. (2019); 2:

BirdLife International; 3: Appendix S2;4: Wilman et al. (2014).

Trait	Description	Imputed	Ecosystem Function	Species' Vulnerability	Source
Body Mass	Log_{10} (median body mass in grams).	0	Nutrient storage and transport.	Strong predictor of extinction risk.	1
Habitat Breadth	Log_{10} (number of IUCN habitats listed as suitable).	0	Nutrient transport. Community shaping through organism dispersal.	Exposure to threats across multiple locations, or limited one location.	1
Generation Length	Log_{10} (generation length in years).	1	Nutrient storage.	The ability of populations to recover from threats.	2
Clutch Size	Number of eggs per clutch.	4	Nutrient storage.	The ability of populations to recover from threats.	1,3
Pelagic Specialism	Is the species a pelagic specialist? *Pelagic Specialist Non-pelagic Specialist*	60	Nutrient transport.	Exposure and interaction with marine threats, e.g. oil spills, bycatch.	4
Migration Strategy	Does migration occur? *Full migrant Non-migrant*	3	Nutrient transport. Community shaping through organism dispersal.	Exposure to threats across multiple locations, or limited one location.	2
Foraging Guild	The dominant foraging guild of the species. *Diver Surface Ground Generalist*	60	Nutrient storage. Trophic-dynamic regulations of populations.	The propensity of species to interact with threats, e.g. bycatch.	4
Diet Guild	The dominant diet of the species. *Omnivore Invertebrate Vertebrate & scavenger*	60	Nutrient storage. Trophic-dynamic regulations of populations.	Sensitive to overexploitation of specific foods (e.g. overfishing) and changes in lower trophic levels.	1

777   *Table 2 IUCN reclassified threat categories. 'Climate' encompasses climate change and severe*

778   *weather. 'Direct' threats directly affect survival and fecundity. 'Habitat' threats modify or*

779   *destroy habitat. 'No threats' encompasses species with no identified IUCN threats. 'Other'*

780   *threats are indirectly or not caused by humans. Modified from Gonzalez-Suarez, Gomez &*

781   *Revilla (2013).*

Threat Reclassification	IUCN Threat
Climate	Climate change and severe weather
Direct	Biological resource use
	Invasive & other problematic species & genes
	Human intrusions and disturbance
Habitat	Residential and commercial development
	Agriculture and aquaculture
	Energy production and mining
	Transportation and service corridors
	Natural system modifications
	Pollution
No Threats	No threats
Other	Geological events

782

783 *Table 3 Output results from the Mann-Whitney U and Chi-Squared tests which test the difference*

784 *in the means (Mann-Whitney U) and independence (Chi-Squared) between the traits of*

785 *threatened and non-threatened species.*

Continuous Trait	Mann-Whitney U (W)	p-value
Body Mass	13814	0.06
Clutch Size	9431	0.00
Habitat Breadth	2077.5	0.00
Generation Length	15187	0.00
Categorical Trait	**Chi-squared (X^2)**	**p-value**
Diet Guild	28.812	0.00
Pelagic Specialism	15.565	0.00
Foraging Guild	27.733	0.00
Migration Strategy	$1.4119e^{-30}$	1.00

786

Table 4 SIMPER summary of top five traits contributing to the Bray Curtis dissimilarity between

threats. The proportion of species per trait is indicated as greater (+), smaller (-), or equal (=)

between each threat category. 'S' indicates small; 'M' indicates medium; and 'L' indicates

large.

791

Threat	Trait	Contribution (%)	Cumulative (%)	Climate Change	Direct	Habitat	No Threat
Climate Change vs. Direct	Non-pelagic Specialist	11.7	11.7	-	+		
	Pelagic Specialist	11.7	23.3	+	-		
	Vertebrate & Scavenger	7.5	30.8	+	-		
	Invertebrates	7.2	38.1	-	+		
	Habitat Breadth (M)	6.9	45.0	+	-		
	Clutch Size (S)	6.6	51.6	=	=		
	Generation Length (S)	5.1	56.7	+	-		
	Clutch Size (L)	4.9	61.6	-	+		
Climate Change vs. Habitat	Habitat Breadth (M)	8.6	8.6	+		-	
	Pelagic Specialist	7.6	16.3	+		-	
	Non-pelagic Specialist	7.6	23.9	-		+	
	Habitat Breadth (S)	6.3	30.2	-		+	
	Body Mass (L)	6.1	36.3	=		=	
	Body Mass (S)	6.0	42.3	=		=	
	Clutch Size (S)	5.9	48.1	+		-	
	Generation Length (S)	5.8	53.9	-		+	
Climate Change vs. No Threat	Invertebrates	11.3	11.3	-			+
	Pelagic Specialist	8.5	19.8	+			-
	Non-pelagic Specialist	8.5	28.2	-			+
	Omnivore	8.2	36.4	+			-
	Body Mass (L)	7.2	43.7	+			-
	Body Mass (S)	5.8	49.5	+			-
	Clutch Size (L)	5.6	55.1	-			+
	Clutch Size (S)	5.3	60.4	+			-
Direct vs. Habitat	Generation Length (S)	7.9	7.9		-	+	
	Clutch Size (S)	7.7	15.6		+	-	
	Non-pelagic Specialist	7.2	22.7		-	+	
	Pelagic Specialist	7.2	29.9		+	-	
	Invertebrates	6.5	36.4		-	+	
	Generation Length (M)	6.3	42.7		-	+	
	Vertebrate & Scavenger	5.1	47.8		+	-	
	Generalist	5.1	52.9		-	+	

Direct vs. No Threats	Omnivore	10.7	10.7	+	-
	Habitat Breadth (M)	10.3	21.0	-	+
	Habitat Breadth (S)	10.2	31.2	+	-
	Vertebrate & Scavenger	7.1	38.3	+	-
	Non-pelagic Specialist	6.4	44.7	-	+
	Pelagic Specialist	6.4	51.0	+	-
	Diver	5.1	56.2	+	-
	Invertebrates	4.9	61.1	-	+
Habitat vs. No Threats	Omnivore	8.4	8.4	+	-
	Habitat Breadth (M)	8.2	16.7	-	+
	Habitat Breadth (S)	8.1	24.8	+	-
	Invertebrates	7.1	31.9	-	+
	Generation Length (M)	6.0	37.9	+	-
	Generation Length (S)	5.9	43.8	-	+
	Clutch Size (S)	5.5	49.3	+	-
	Pelagic Specialist	5.1	54.4	+	-

792