



Bycatch-threatened seabirds disproportionally contribute to community trait composition across the world

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ABSTRACT

Human pressures in the ocean are restructuring biological communities, driving non-random extinctions, and disrupting marine ecosystem functioning. In particular, fisheries bycatch, the incidental mortality of non-target species, is a major threat to seabirds worldwide. Direct bycatch data are often scarce. Instead, leveraging trait-based analyses with fine-scale fisheries data could answer fundamental questions about spatial patterns of bycatch-threatened species and facilitate targeted conservation strategies. Here, we combine a dataset of species' traits and distribution ranges for 361 seabird and sea duck species with spatially resolved fishing effort data for gillnet, longline, trawl, and purse seine gears. First, we quantify geographic patterns of seabird community traits. Second, we describe how community traits could shift under local extinction scenarios in areas where bycatch-threatened seabirds spatially overlap with fishing activities. These objectives allow us to highlight the collective contribution of species currently threatened from bycatch to ecosystem functioning. We reveal distinct spatial variation in the community weighted mean of five seabird traits (body mass, generation length, clutch size, diet guild, and foraging guild) are evident. Moreover, our results show that fisheries bycatch is selectively removing a distinct suite of traits from the community within particular oceanic regions. Specifically, fisheries bycatch is threatening species with larger body masses, slower reproductive speeds (smaller clutch sizes and longer generation lengths), and specialised diet and foraging guilds. The spatial non-uniformity of the community trait shifts suggests that within specific marine regions, communities have limited redundancy and therefore may have less insurance to buffer against declines in ecosystem functioning. Our extinction scenario warns that seabirds currently threatened from fisheries bycatch substantially contribute to community functional composition. Management actions that incorporate species' traits and fine-scale fisheries datasets as tools for marine spatial planning will add an important dimension when evaluating the success of conservation initiatives.

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1. Introduction

Trait-based approaches can be used to uncover community structure and to increase our understanding of ecosystem functioning (Tavares et al., 2019; Wieczynski et al., 2019). Traits are attributes of organisms measured at the individual level, such as body mass and foraging guild (Gallagher et al., 2020; Violle et al., 2007). When traits relate to species' roles in ecosystems, they can be used to infer species' contributions to ecosystem functioning (Gallagher et al., 2020; Pigot et al., 2020). For example, diet and foraging strategy directly link to functions, e.g., trophic regulation of populations and nutrient storage (Tavares et al., 2019). When such traits are coupled with spatial data on species' distributions, they can be applied in trait analyses, for instance community-weighted means (CWM), to characterise community functionality (Duarte et al., 2017; Weigel et al., 2016). In turn, these patterns can broadly infer what, where, and how resources are acquired and consumed, and thus derive spatial patterns of functionality (Pimiento et al., 2020). Moreover, revealing spatial patterns of community contributions to ecosystem functioning can highlight regions where conservation strategies will provide the greatest gains for enhancing biodiversity and maintaining and restoring ecosystems (Butt and Gallagher, 2018; Miatta et al., 2020).

Biodiversity can help stabilise ecosystem functioning under anthropogenic pressures across spatio-temporal scales (Tilman et al., 2014). For example, the insurance hypothesis suggests diverse communities can buffer ecosystems against declines in their functioning because multiple species perform similar roles (redundancy), therefore providing greater insurance that some species will maintain functioning even if others fail (Yachi and Loreau, 1999). However, anthropogenic pressures in the ocean are restructuring biological communities and causing worrying population declines (McCauley et al., 2015). Moreover, these pressures cause non-random extinctions because species vulnerability depends on their traits, such as large body size, small geographic range, and foraging specialisation (Cooke et al., 2019; Duffy, 2003; Gross and Cardinale, 2005; Richards et al., 2022, 2021). Indeed, the most functionally important species are often the most prone to extinction (Rao and Larsen, 2010). Consequently, their loss could generate waves of ecological change, shifts in community composition, and disruptions to marine ecosystem functioning (Cardinale et al., 2012; Chapin et al., 2000; Mace et al., 2012; McCauley et al., 2015).

Fisheries bycatch, the incidental mortality of non-target species, is a profound threat to marine ecosystems, and to seabirds in particular (Alverson et al., 1994; Dias et al., 2019; Lewison et al., 2004; Marchowski, 2022; Marchowski et al., 2020; Stempniewicz, 1994). As wide-ranging foragers, seabirds overlap and interact with a variety of fishing gears and fleets during the breeding, non-breeding, and migration stages of their annual cycle (Clay et al., 2019; Komoroske and Lewison, 2015; Orben et al., 2021; Żydelski and Richman, 2015). Consequently, bycatch is driving seabird population declines worldwide (Anderson et al., 2011; Dias et al., 2019; Skov et al., 2011). For instance, gillnet fisheries alone cause an estimated 400,000 seabird mortalities annually (Żydelski et al., 2013).

As top predators, seabirds play a key role in marine ecosystem functioning by contributing to: (1) nutrients cycling through transporting nutrients via excretion across habitats and realms; (2) trophic regulation; and (3) community shaping through consuming large amounts of biomass (Pimiento et al., 2020; Tavares et al., 2019). Consequently, as fisheries bycatch targets a distinct suite of seabird traits, the non-random losses could result in significant changes in community functional composition and cause dramatic shifts in ecosystem functioning (Richards et al., 2022, 2021). Thus, quantifying the patterns of community traits across the world allows us to explore the present spatial variability in the functional contributions of species. Moreover, simulating a 'worst-case' bycatch-driven extinction scenario, which assumes the local extinction of bycatch-threatened seabirds, could illustrate their collective contribution to ecosystem functioning (Komoroske and Lewison, 2015; Pimiento et al., 2020).

Here we combine a dataset of five traits across 361 seabird and sea duck species with global seabird range maps and a spatially resolved fishing effort dataset for gillnet, longline, trawl, and purse seine gears to: (1) quantify geographic patterns of seabird community traits; and (2) describe how community traits could shift under a 'worst-case' extinction scenario in areas where bycatch-threatened seabirds spatially overlap with fishing activities. Collectively, these objectives allow us to identify the oceanic regions where bycatch-threatened species contribute disproportionately to the community composition of functional traits, and comment on the potential consequences of their extinction for sustaining ecosystem functioning.

2. Methods

2.1. Extinction scenario

Our 'worst-case' extinction scenario follows an approach previously applied to a diversity of marine and freshwater species, and assumes the extinction of all seabirds currently threatened from fisheries bycatch in areas where they spatially overlap with fishing activities (Pimiento et al., 2020; Toussaint et al., 2016). While it is unlikely that all bycatch-threatened seabirds will be lost from communities overlapping with fishing activities, this extinction scenario offers the opportunity to highlight the collective contribution of bycatch-threatened seabirds to ecosystem functioning (Pimiento et al., 2020). To identify bycatch-threatened seabirds, we extracted the species listed as threatened from subsistence and large-scale bycatch effects (threats 5.4.3 and 5.4.4) within the International Union for Conservation of Nature (IUCN) threat classification scheme (IUCN, 2012). A total of 146 seabird species were classified as threatened from bycatch, representing 40% of the 361 seabirds analysed in the present study.

2.2. Spatial data

To identify areas where fisheries and seabirds and sea ducks overlap, we first extracted distribution polygons for 361 seabirds and

sea ducks (Fig. 1A), from BirdLife International data zone (BirdLife International, 2017), available upon request from <http://datazone.birdlife.org/species/requestdis>. Here, we recognize seabirds as those which use marine habitats, through feeding at sea, either nearshore or offshore. These spatial polygons represent the coarse distributions that species likely occupy, and are presently the best available data for the ranges of all seabirds. We subset the spatial data to only retain the extant, native, resident, breeding season and non-breeding season polygons. We created a 1° resolution global presence-absence matrix (PAM; Fig. 1D) based on the seabird distribution polygons using the package ‘letsR’ and function *lets.presab* (Vilela and Villalobos, 2015) for further analyses. All land was removed from the presence-absence matrix using the *wrld.simpl* polygon from the package ‘maptools’ (Bivand and Lewin-Koh, 2018) and function *lets.pamcrop* from the package ‘letsR’ (Vilela and Villalobos, 2015).

Next, we downloaded spatio-temporal fishing effort data from Global Fishing Watch (globalfishingwatch.org). Global Fishing Watch analyses fishing activity data using the Automatic Identification System (AIS). While AIS is a safety device used onboard vessels to avoid collisions, it also transmits data about a vessel’s identity, type, location, speed and directions (Kroodsmma et al., 2018). These data are processed by Global Fishing Watch using convolutional neural networks to characterise fishing vessel identity, gear types, and periods of fishing activity with 94–97% accuracy when compared with labelled data (Guiet et al., 2019; Kroodsmma et al., 2018). We extracted the daily fishing activity data for gillnets, longlines, trawls, and purse seines from Global Fishing Watch. These gear types were selected because they cause the greatest seabird bycatch mortalities worldwide (Dias et al., 2019). The extracted vessels ranged in size from 1.98 to 7765 gross tonnes. Fishing activity between 2015 and 2018 across the four gear types was aggregated per 1° global grid cell to produce a single fishing activity layer (Fig. 1B). We focus on the combined distribution of fishing activity because the IUCN

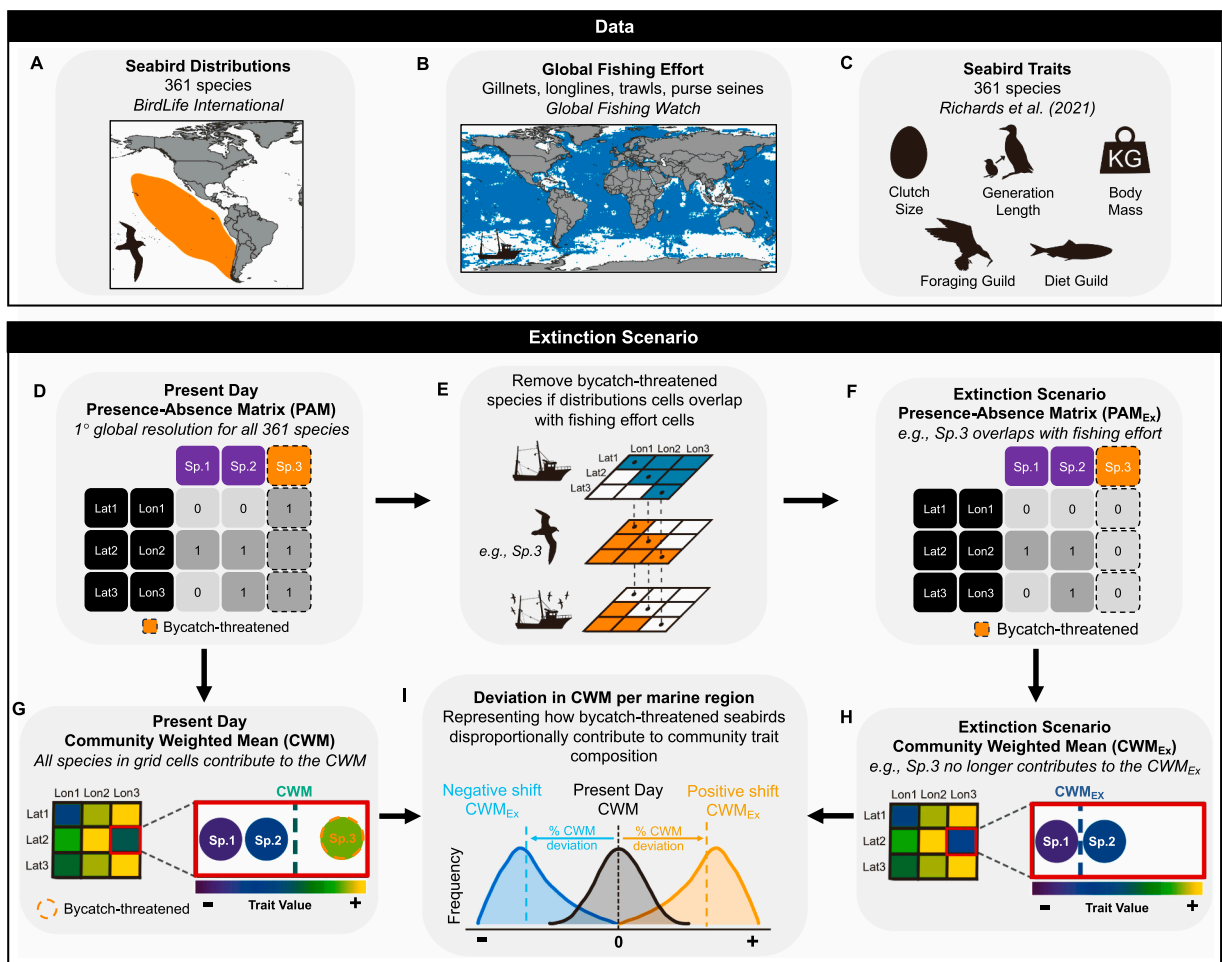


Fig. 1. Conceptual diagram representing the methodology used in the present study. In our analysis, we used spatial data on global (A) seabird distributions and (B) fishing effort, and a (C) dataset of seabird traits. We constructed a (D) present-day presence-absence matrix (PAM) based on the global distributions of extant seabird ranges. To simulate an extinction scenario and create an (F) extinction presence-absence matrix (PAM_{Ex}), distribution cells of bycatch-threatened seabirds that overlapped with fishing effort cells were removed (E). Coupling these two presence-absence matrices (PAM, PAM_{Ex}) with the seabird trait data, we computed the (G) present day community weighted mean (CWM) and an (H) extinction scenario community weighted mean (CWM_{Ex}). To quantify the extent that bycatch-threatened seabirds disproportionately contribute to community trait composition, we calculated the percentage deviation between the present-day CWM and the extinction scenario CWM_{Ex} for each marine region (I).

threat classification scheme database does not specify species' vulnerability to specific gear types.

Finally, we built an extinction scenario presence-absence matrix (PAM_{EX}; Fig. 1F) representing the coarse distributions where seabirds could become locally extinct due to bycatch. To achieve this, we removed all cells where the distributions of seabirds listed as threatened from bycatch by the IUCN threat classification scheme overlapped with the fishing activity layer (Fig. 1E). To ensure consistency between the species' distribution and fishing activity layer, we re-projected all spatial data to a raster format with the same coordinate reference system (WGS84) and resolution (1° x 1° global grid cells). To achieve this, we used the package 'raster' and function *rasterFromXYZ* (Hijmans, 2019).

2.3. Present-day and extinction scenario community weighted means

To map and describe the global distribution of seabird traits, we selected five traits (Table 1; Fig. 1C): *body mass*, the median mass in grams; *generation length*, the age at which a species produces offspring in years; *clutch size*, the number of eggs per clutch; *diet guild*, the dominant diet of the species (omnivore, invertebrate, vertebrate & scavenger); and *foraging guild*, the dominant foraging strategy of the species (diver, surface feeder, ground feeder, generalist). Traits for 340 seabirds were extracted from Richards et al. (2021), and we further compiled traits for 21 sea ducks following the same approach. Next, we calculated the community weighted mean (CWM; Fig. 1G) for each 1° grid cell with the function *functcomp*, package 'FD' (Laliberté et al., 2014; Laliberté and Legendre, 2010). To calculate the extinction scenario community weighted mean (CWM_{EX}; Fig. 1H), we removed all bycatch-threatened seabirds from grid cells overlapping with fishing activities.

Community weighted means describe the typical characteristics within a set of species by combining information on species' traits and distributions (Duarte et al., 2017). For continuous traits (body mass, clutch size, generation length), CWM and CWM_{EX} are the mean trait value of all species present in each 1° grid cell, and for categorical traits (foraging and diet guild), CWM and CWM_{EX} are the most dominant class per trait within each 1° grid cell. We do not weight the CWM and CWM_{EX} by species relative abundances because these data were not available.

2.4. Contribution of bycatch-threatened seabirds to community trait composition

To quantify the contribution of bycatch-threatened seabirds to the community trait composition (Fig. 1I), we calculated the deviation between the present-day (CWM) and the extinction scenario (CWM_{EX}) community weighted means. Thus, quantifying the shift in the average traits of a community if bycatch-threatened seabirds were lost. For continuous traits (clutch size, body mass, generation length), we calculated the percentage deviation in CWM for each grid cell. For categorical traits, we calculated the proportion of each foraging guild (*diver*, *surface*, *ground*, *generalist*) and diet guild (*omnivore*, *invertebrate*, *vertebrate & scavenger*) category per grid cell as observed, and again after the removal of bycatch-threatened species for cells overlapping with fishing activities. We then calculated the percentage deviation between these values per grid cell.

To describe the spatial trends in bycatch-threatened species' contribution to community traits, we calculated the mean and standard deviation of community weighted mean shifts within ten global oceans and seas (Flanders Marine Institute, 2021). To test whether the shifts in community weighted mean were significantly different from zero in each marine region, we used a One-Sample Wilcoxon Signed Rank Test with function *wilcox.test* from package 'rstatix' (Kassambara, 2023). All analyses were completed in R version 4.0.4 (R Core Team, 2020).

3. Results

3.1. Spatial variation in community traits

We find large spatial variation in the community weighted mean (CWM) of body mass, generation length, clutch size, diet guild, and foraging guild traits across the globe (Fig. 2). The heaviest species are located in the Southern Ocean, driven by the presence of large albatross species. Species with small body masses are distributed in the Tropics, particularly near east India, due to the presence of many small gulls and shearwaters. Species with the longest generation lengths are concentrated in the Southern Ocean, driven by albatross species. Whereas, species with the shortest generation lengths and largest clutch sizes are distributed along coastlines,

Table 1

Description of the traits used in the present study and their relation to ecosystem functioning. Table modified from Richards et al. (2021).

Trait	Description	Ecosystem Function
Body Mass	Log ₁₀ (median body mass in grams)	Nutrient storage and transport
Generation Length	Log ₁₀ (generation length in years)	
Clutch Size	Number of eggs per clutch (the central tendency was recorded as the mean or mode)	Nutrient storage
Diet Guild	The dominant diet of the species <i>Omnivore; Invertebrate; Vertebrate & scavenger</i>	Nutrient storage; Trophic-dynamic regulations of populations
Foraging Guild	The dominant foraging guild of the species <i>Diver; Surface; Ground; Generalist</i>	Nutrient storage; Trophic-dynamic regulations of populations

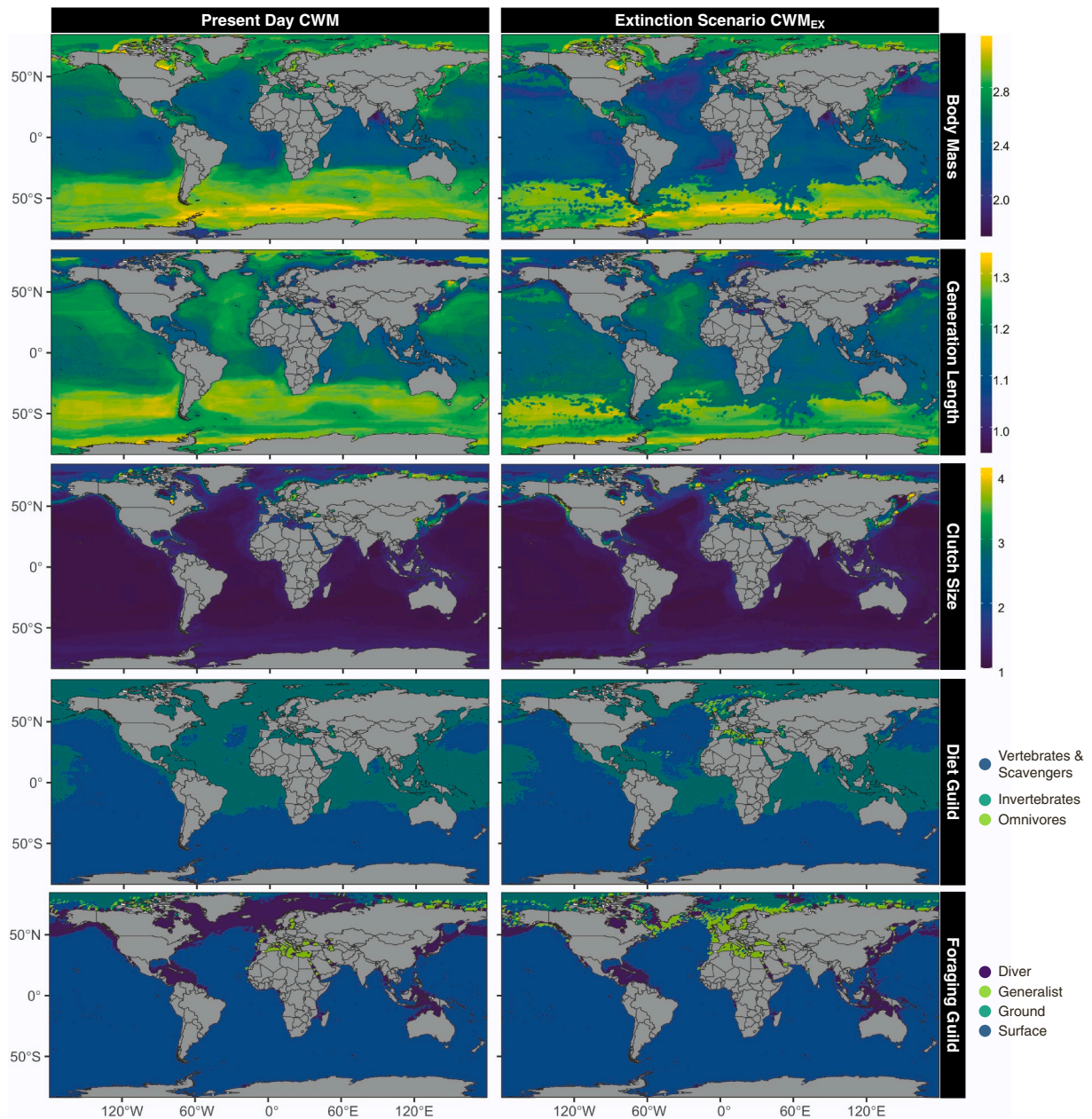


Fig. 2. Present-day Community weighted mean (CWM) of five traits based on the distributions of 361 presently extant seabird species (left panels), and extinction scenario community weighted mean (CWM_{EX}) following the predicted local loss of 146 species threatened from bycatch in areas where their distributions overlap with fishing activity (right panels). Therefore, the difference represents where bycatch- threatened species disproportionately contribute to community trait composition. For continuous data, CWM and CWM_{EX} is the mean trait value of all species present in each 1° grid cell. For categorical data, CWM and CWM_{EX} is the most dominant class per trait within each 1° grid cell. Body mass, generation length, and clutch size traits are $\log_{10}$ transformed, and truncated to the 0.1 - 99.9% range to aid visual clarity. Maps including all the data are in Appendix 1, Fig. S1.

particularly in the Northern Hemisphere, representing sea ducks, gulls, and cormorants. In contrast, species with the smallest clutch sizes are highly pelagic and distributed across all oceans, representing the distributions of many tubenoses and auks distinguished in laying a single egg per clutch. For diet guild, vertebrate & scavenger consumers dominate the Southern and Pacific Oceans, capturing the distributions of tubenoses and penguins, while invertebrate consumers dominate the Arctic, Atlantic, and Indian Oceans, representing gulls, cormorants, auks, and sea ducks. Omnivores are dominant only within small regions, such as the Caspian Sea and Black Sea, driven by distributions of omnivorous gulls. For foraging guild, surface foragers typically dominate most oceans south of $50^\circ N$, capturing the distributions of tubenose seabirds, whilst divers are the most dominant north of $50^\circ N$ and along the coast of Atlantic

Central America and Oceania, representing auks, cormorants, and sea ducks. Generalist gulls are concentrated around the coasts of Europe (Mediterranean Sea, Black Sea, Baltic Sea, North Sea) and ground foragers dominate in the high Arctic, driven by jaegers and gulls.

3.2. Contributions to community trait composition

Our results from the extinction scenario suggest that seabirds threatened from bycatch disproportionately contribute to the community composition of functional traits across the globe (Figs. 2 and 3). Specifically, bycatch-threatened seabirds with large bodies and slow reproductive speeds (longer generation lengths and smaller clutch sizes) contribute considerably to the community functional composition throughout the majority of the global oceans and seas, as indicated by significant shifts in the CWM of body mass, generation length, and clutch size (Fig. 3). Indeed, our analysis indicates that extinction due to bycatch could cause the erosion of larger body sizes by a mean of 1.1 – 9.4% across nine marine regions and longer generation lengths by a mean of 0.4 – 7.7% across all ten marine regions (Fig. 2). Moreover, clutch size could increase by a mean of 0.7 – 30.5% within seven regions. Bycatch-threatened seabirds that specialise in invertebrate diets dominate the community functionality in the North Atlantic Ocean, Mediterranean Region, and Baltic Sea, as illustrated by the 18.5 – 31% mean loss in invertebrate diet dominance following the bycatch-driven extinction scenario (Figs. 2 and 3). Moreover, the mean loss of 7.2 – 36.3% of diving dominance in the Baltic Sea, Mediterranean Region, Arctic, and North Atlantic Oceans suggest that bycatch-threatened seabirds with diving foraging specialisations contribute the greatest to the community functional composition (Figs. 2 and 3).

4. Discussion

Our bycatch-driven extinction scenario represents a worst-case outcome of fishing impacts. That is, it is unlikely that our underlying assumption will occur because the overlap of bycatch-threatened species with fishing activities does not directly equate to species extinction in those communities. However, this simplified extinction scenario warns that seabirds currently threatened from fisheries

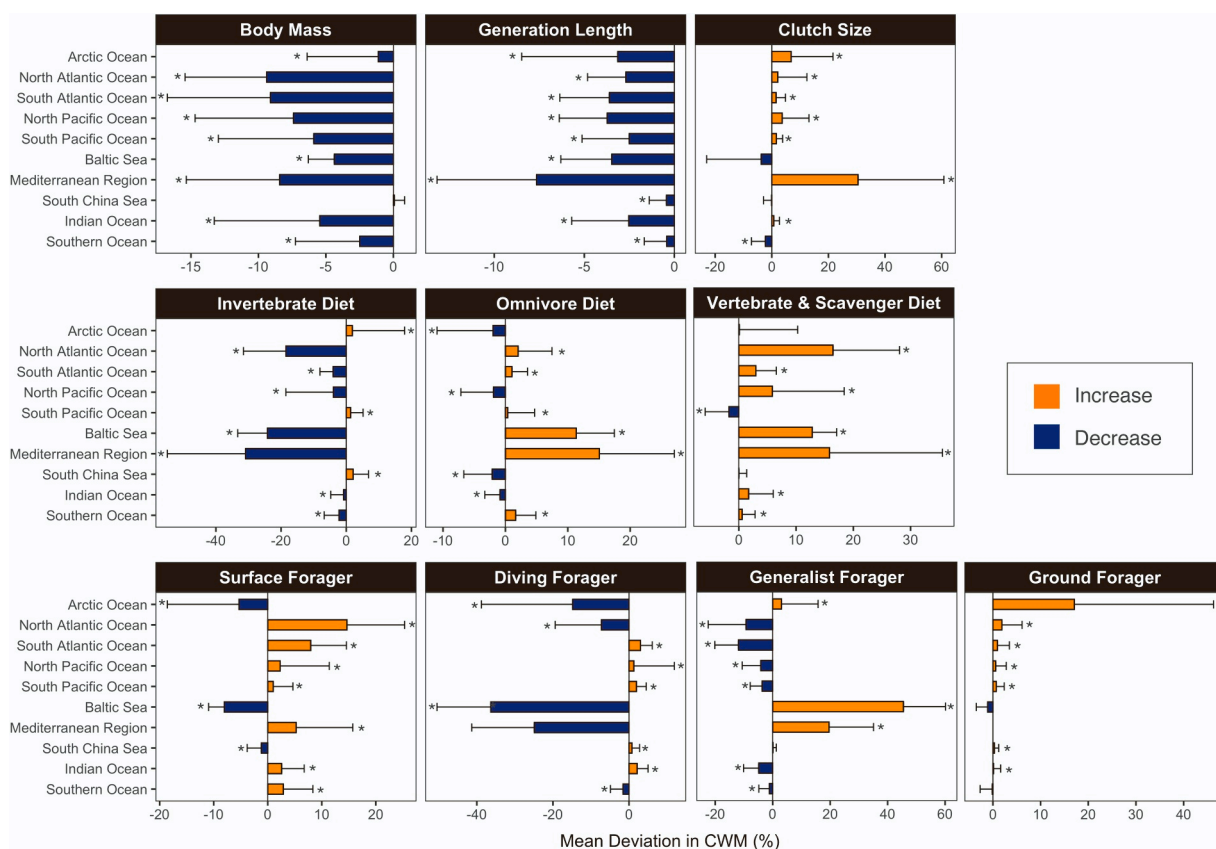


Fig. 3. Mean ($\pm$ standard deviation) shift in community weighted mean (CWM) within each marine region following removal of 146 bycatch-threatened species in areas where their distributions overlap with fishing activity. Orange represents a positive shift (increase in average trait value or frequency), and blue a negative shift (decrease in average trait value or frequency) in the CWM following removal of species threatened from bycatch. The marine region of South China Sea refers to South China and Eastern Archipelagic Seas. Stars indicate significantly nonzero averages.

bycatch contribute substantially to community functional composition, confirming wider research on marine megafauna (Pimiento et al., 2020). We find that fisheries bycatch is selectively removing a distinct set of species, and their traits, from communities across multiple oceanic regions. We therefore extend previous research focused on the global human-driven loss of species (Cooke et al., 2019; Pimiento et al., 2020; Richards et al., 2021) to resolve the spatial distribution of trait shifts for seabirds and sea ducks due to bycatch.

Predicted trait shifts due to fisheries bycatch varied among marine regions. The spatial non-uniformity of the community trait shifts suggests that some regions are highly sensitive to the loss of specific trait combinations and likely have limited redundancy (McLean et al., 2019). These regions might therefore have less insurance to buffer against declines in ecosystem functioning because they do not have redundant species to fill the empty niche space (Yachi and Loreau, 1999). Redundancy might further interact with the size of the community in different regions. For example, the large trait shifts observed in the Northern Hemisphere, coincide with the region of lowest seabird species richness and low functional diversity (Mott and Clarke, 2018; Richards, 2020). Thus, any species lost is likely to play a novel ecological role. For instance, fisheries are selectively targeting diving auks from within an already small species pool in the North Atlantic (Regular et al., 2013). Similarly, in the Southern Hemisphere, the loss of species with larger body masses and longer generation lengths are observed because fisheries threaten 90% of albatross species, and 65% of penguin species (Dias et al., 2019), which represent the majority of the largest, long-lived seabirds (Richards et al., 2022; Zhou et al., 2019). Moreover, these groups are species poor, therefore, there is limited redundancy to compensate for the loss of these species' traits. By contrast, the community composition of clutch size, foraging strategy, and diet guild remained relatively stable because high redundancy in the community traits compensates for the removal of threatened species. This redundancy arises from the fact that there are many species with average clutch sizes or common foraging strategies and diet guilds that are not threatened from bycatch.

The shifts in community traits could provide important insights into the magnitude and location of potential changes to ecosystem functioning. For example, body mass is strongly linked to nutrient transport and storage because large individuals hold and disperse large nutrient quantities (Anderson et al., 2011; Doughty et al., 2016; Tavares et al., 2019). Consequently, as fisheries remove species with larger body masses, changes to important zoogeographical cycles of major elements worldwide may arise (Graham et al., 2018; Schmitz et al., 2018; Speakman, 2005; Tavares et al., 2019; Wing et al., 2014). Moreover, shifts to species with faster reproductive speeds (decreased generation lengths and increased clutch size), such as gulls and terns, could have implications for nutrient storage and cycling, and food provisioning (Tavares et al., 2019). Additionally, the alteration of dominant foraging strategy and diet guild traits may modify trophic regulations and community structures, because, as top predators, seabirds influence marine food webs from the top down via direct and indirect pathways (Ripple et al., 2017). Thus, shifts in seabird communities due to losses to bycatch could have a range of ecological repercussions that could propagate through the species network, and could lead to a range of alterations to ecosystem function.

Species' traits can support marine spatial planning and when evaluating the success of conservation initiatives (Miatta et al., 2020). Moreover, several studies highlight the importance of including community and ecosystem functions into conservation policy because focusing on biodiversity metrics alone may exclude functionally and ecologically important locations (Bremner et al., 2006; Frid et al., 2008; Miatta et al., 2020; Rees et al., 2012). Thus, considering the traits of species assemblages in a quantitative framework offers valuable tools for advancing marine conservation outcomes (Miatta et al., 2020). While trait-based approaches do not directly quantify the ecosystem functions that seabirds deliver, here we show that a community weighted mean approach can highlight oceanic regions where bycatch-threatened species disproportionately contribute to community trait composition and that fishing activity non-randomly targets species with distinct traits. Future studies and management actions may consider quantifying the extent of trait and ecosystem function conservation as a result of bycatch mitigation successes at local scales in these regions. Despite high spatial overlap between seabird distributions and fishing activity, simple, innovative, and inexpensive mitigation solutions have substantially reduced bycatch across gear types and species (Croxall, 2008). These solutions include gear modifications that increase net visibility and deter species with scaring lines, and management actions including time-area closures that prohibit fishing in an area or at specific times (Senko et al., 2014). For example, the introduction of bird-scaring lines in a South African trawl fishery reduced albatross death rates by up to 95% (Maree et al., 2014). This example could provide a valuable case study to quantify the response of conserving a large proportion of vulnerable species for regional ecosystem functioning.

We focus solely on fishing threats because bycatch is named a top threat to seabirds worldwide, however, seabirds face a diversity of threats throughout their life, including predation and displacement from invasive species, mortality and shifts in food resources due to climate change, and mortality following exposure to pollution (Dias et al., 2019). Future studies may consider investigating how managing and reducing threats through space and time conserves seabird traits and ecosystem functions. For example, coupling extensive seabird tracking data with colony-specific trait information and regional threat patterns could provide a powerful and informative tool for local management. Finally, since our approach assumed the complete removal of species that are threatened from bycatch in areas overlapping with fishing activities, i.e., local extinction of these species, future studies may consider investigating how reduced population sizes and changes in species' relative abundances caused by bycatch could influence community traits.

The Global Fishing Watch layers provides unprecedented understanding of the global fishing fleet and its spatiotemporal variations (Kroodsmas et al., 2018). Consequently, the dataset is an invaluable resource to advance our understanding of fisheries bycatch on seabirds and other marine organisms. For example, through integrating these fisheries data with seabird traits and distribution data, we provided a new perspective on the oceanic areas where bycatch-threatened species disproportionately contribute to community trait composition. Similarly, recent research employed the Global Fishing Watch data and biologging data to detect albatross association and encounters with commercial fishing vessels in the North Pacific Ocean, thus further revealing the fishing dataset's value as a novel conservation and management tool (Orben et al., 2021). We encourage use of fine-scale spatial datasets to provide additional perspectives for seabird research, and to expand on the present study. For example, fishing activity and seabird distributions vary at

different time scales, with distinct diurnal, seasonal, and annual patterns. Incorporating finer-scale data (e.g., biologging data) which encompasses these temporal signals is a direction for future studies that may provide further insights into the impacts of fishing on changes to seabird ecological strategies. Moreover, we focus on the combined distribution of gillnet, longline, trawl, and purse seine fishing activity on the overall shift in seabird traits because the IUCN threat classification scheme does not specify which gear types a specific species is vulnerable to. As greater detail becomes available on species vulnerability to bycatch, additional research may consider quantifying the response of ecological strategies in seabirds and sea ducks to the spatiotemporal variations in individual gear types, intensities, and illegal, unreported, and unregulated (IUU) fishing activities (Welch et al., 2022). Finally, the Global Fishing Watch data are fundamentally constrained by the limitations of AIS including incomplete satellite coverage in some regions, device tampering, and not all vessels carry an AIS transponder. However, as the AIS datasets are improved with time new patterns of seabird ecological strategy changes could be revealed.

5. Conclusion

In our extinction scenario, we show that bycatch-threatened seabirds disproportionately contribute to the community trait composition within specific oceanic regions. Fisheries bycatch is non-randomly threatening a distinct suite of seabirds according to their body size, reproductive speed, and diet and foraging guild. There are potentially significant implications for ecosystem functioning if bycatch-threatened seabirds and sea ducks are lost from their communities. Given almost one third of seabird species are impacted from bycatch and their populations are plummeting worldwide (Dias et al., 2019; Paleczny et al., 2015), management actions that incorporate species' traits and fine-scale fisheries datasets as tools for marine spatial planning will add an important dimension when evaluating the success of conservation initiatives.

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CRediT authorship contribution statement

Richards Cerren: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft. **Cooke Rob:** Formal analysis, Methodology, Writing – review & editing, Data curation. **Bates Amanda E.:** Funding acquisition, Methodology, Supervision, Writing – review & editing. **Bowler Diana E.:** Formal analysis, Methodology, Writing – review & editing. **Boerder Kristina:** Data curation, Writing – review & editing.

Declaration of Competing Interest

The work is all original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal. No part of the research has been published in any form elsewhere, unless it is fully acknowledged in the manuscript. The manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal. Any research in the paper not carried out by the authors is fully acknowledged in the manuscript. All sources of funding are acknowledged in the manuscript.

Data Availability

We have shared the link to data and code in the Data Sharing and Accessibility section of the manuscript.

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Data sharing and accessibility

Seabird traits were extracted from Richards et al. (2021), specifically <https://doi.org/10.5061/dryad.x69p8czhd>. Sea duck traits are available in Appendix 2. Species distribution polygons are available upon request from <http://datazone.birdlife.org/species/requestdis>. Fishing effort data are available for download from <https://globalfishingwatch.org/>. R code covering the major analytical steps is available on GitHub at <https://github.com/CerrenRichards/Seabird-Trait-Shifts>.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02792](https://doi.org/10.1016/j.gecco.2023.e02792).

References

- Alverson, D.L., Freeberg, M.H., Pope, J.G., Murawski, S.A., 1994. A global assessment of fisheries bycatch and discards (No. 339). Rome.
- Anderson, O.R.J., Small, C.J., Croxall, J.P., Dunn, E.K., Sullivan, B.J., Yates, O., Black, A., 2011. Global seabird bycatch in longline fisheries. *Endanger. Species Res.* 14, 91–106. <https://doi.org/10.3354/esr00347>.
- BirdLife International, Handbook of the Birds of the World, 2017. Bird species distribution maps of the world. Version 2017.2 [WWW Document]. URL (<http://datazone.birdlife.org/species/requestdis>).
- Bivand, R., Lewin-Koh, N., 2018. maptools: Tools for Handling Spatial Objects.
- Bremner, J., Paramor, O.A.L., Frid, C.L.J., 2006. Developing a methodology for incorporating ecological structure and functioning into designation of Special Areas of Conservation (SAC) in the 0–12 nautical mile zone. *Liverpool*.
- Butt, N., Gallagher, R., 2018. Using species traits to guide conservation actions under climate change. *Clim. Change* 151, 317–332. <https://doi.org/10.1007/s10584-018-2294-z>.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67. <https://doi.org/10.1038/nature11148>.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000. Three-dimensional imaging of the face: a comparison between three different imaging modalities. *Nature* 405, 234–242. <https://doi.org/10.1093/asj/sjx227>.
- Clay, T.A., Small, C., Tuck, G.N., Pardo, D., Carneiro, A.P.B., Wood, A.G., Croxall, J.P., Crossin, G.T., Phillips, R.A., 2019. A comprehensive large - scale assessment of fisheries bycatch risk to threatened seabird populations. *J. Appl. Ecol.* 56, 1882–1893. <https://doi.org/10.1111/1365-2664.13407>.
- Cooke, R.S.C., Eigenbrod, F., Bates, A.E., 2019. Projected losses of global mammal and bird ecological strategies, 2279 *Nat. Commun.* 10. <https://doi.org/10.1038/s41467-019-10284-z>.
- Croxall, J.P., 2008. The role of science and advocacy in the conservation of Southern Ocean albatrosses at sea. *Bird Conserv Int* 18, 13–29. <https://doi.org/10.1017/S0959270908000300>.
- Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G., Croxall, J.P., 2019. Threats to seabirds: a global assessment. *Biol. Conserv* 237, 525–537. <https://doi.org/10.1016/j.biocon.2019.06.033>.
- Doughty, C.E., Roman, J., Faubry, S., Wolf, A., Haque, A., Bakker, E.S., Malhi, Y., Dunning, J.B., Svenning, J.-C., 2016. Global nutrient transport in a world of giants. *Proc. Natl. Acad. Sci.* 113, 868–873. <https://doi.org/10.1073/pnas.1502549112>.
- Duarte, L., Debastiani, V., Carlucci, M., Diniz-Filho, J., 2017. Analyzing community-weighted trait means across environmental gradients: should phylogeny stay or should it go? *Ecology* 99, 385–398. <https://doi.org/10.1111/jih.12426>.
- Duffy, E., 2003. Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.* 6, 680–687.
- Flanders Marine Institute, 2021. Global Oceans and Seas, version 1. Available online at (<https://www.marinerregions.org/>). <https://doi.org/10.14284/542> [WWW Document].
- Frid, C.L.J., Paramor, O.A.L., Brockington, S., Bremner, J., 2008. Incorporating ecological functioning into the designation and management of marine protected areas. *Hydrobiologia* 606, 69–79. <https://doi.org/10.1007/s10750-008-9343-y>.
- Gallagher, R.V., Falster, D.S., Maitner, B.S., Salguero-gómez, R., Vandvik, V., Pearse, W.D., Schneider, F.D., Kattge, J., Poelen, J.H., Madin, J.S., Ankenbrand, M.J., Penone, C., Feng, X., Adams, V.M., Alroy, J., Andrew, S.C., Balk, M.A., Bland, L.M., Boyle, B.L., Bravo-avila, C.H., Brennan, I., Carthey, A.J.R., Catullo, R., Cavazos, B.R., Conde, D.A., Ray, C.A., Rossetto, M., Sauquet, H., Sparrow, B., Spasojevic, M.J., Telford, R.J., Tobias, J.A., Violle, C., Walls, R., Weiss, K.C.B., Westoby, M., Wright, I.J., Enquist, B.J., 2020. Open Science principles for accelerating trait-based science across the Tree of Life. *Nat. Ecol. Evol.* 4, 294–303. <https://doi.org/10.1038/s41559-020-1109-6>.
- Graham, N.A.J., Wilson, S.K., Carr, P., Hoey, A.S., Jennings, S., MacNeil, M.A., 2018. Seabirds enhance coral reef productivity and functioning in the absence of invasive rats. *Nature* 559, 250–253. <https://doi.org/10.1038/s41586-018-0202-3>.
- Gross, K., Cardinale, B.J., 2005. The functional consequences of random vs. ordered species extinctions. *Ecol. Lett.* 8, 409–418. <https://doi.org/10.1111/j.1461-0248.2005.00733.x>.
- Guiet, J., Galbraith, E., Kroodsmas, D., Worm, B., 2019. Seasonal variability in global industrial fishing effort. *PLoS One* 14, 1–17. <https://doi.org/10.1371/journal.pone.0216819>.
- Hijmans, R.J., 2019. raster: Geographic Data Analysis and Modeling.
- IUCN, 2012. Threats Classification Scheme (Version 3.2) [WWW Document]. URL (<https://www.iucnredlist.org/resources/threat-classification-scheme>) (accessed 8.9.23).
- Kassambara, A., 2023. rstatix: Pipe-Friendly Framework for Basic Statistical Tests. R package version 0.7.2. (<https://CRAN.R-project.org/package=rstatix>).
- Komoroske, L.M., Lewison, R.L., 2015. Addressing fisheries bycatch in a changing world. *Front. Mar. Sci.* 2, 83. <https://doi.org/10.3389/fmars.2015.00083>.
- Kroodsmas, D.A., Mayorga, J., Hochberg, T., Miller, N.A., Boerder, K., Ferretti, F., Wilson, A., Bergman, B., White, T.D., Block, B.A., Woods, P., Sullivan, B., Costello, C., Worm, B., 2018. Tracking the global footprint of fisheries. *Science* 359 (1979), 904–908. <https://doi.org/10.1126/science.aao5646>.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*.
- Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology.
- Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004. Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol. Evol.* 19, 598–604. <https://doi.org/10.1016/j.tree.2004.09.004>.
- Mace, G.M., Norris, K., Fitter, A.H., 2012. Biodiversity and ecosystem services: a multilayered relationship. *Trends Ecol. Evol.* 27, 19–26. <https://doi.org/10.1016/j.tree.2011.08.006>.
- Marchowski, D., 2022. Bycatch of seabirds in the Polish part of the Southern Baltic Sea in 1970–2018: a review. *Acta Ornithol.* 56 <https://doi.org/10.3161/00016454AO2021.56.2.001>.
- Marchowski, D., Jankowiak, L., Ławicki, Ł., Wysocki, D., Chylarecki, P., 2020. Fishery bycatch is among the most important threats to the European population of Greater Scaup *Aythya marila*. *Bird. Conserv. Int.* 30, 176–193. <https://doi.org/10.1017/S0959270919000492>.
- Maree, B.A., Wanless, R.M., Fairweather, T.P., Sullivan, B.J., Yates, O., 2014. Significant reductions in mortality of threatened seabirds in a South African trawl fishery. *Anim. Conserv.* 17, 520–529. <https://doi.org/10.1111/acv.12126>.
- McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H., Warner, R.R., 2015. Marine defaunation: animal loss in the global ocean. *Science* 347, 1979. <https://doi.org/10.1126/science.1255641>.
- McLean, M., Auber, A., Graham, N.A.J., Houk, P., Villéger, S., Violle, C., Thuiller, W., Wilson, S.K., Mouillot, D., 2019. Trait structure and redundancy determine sensitivity to disturbance in marine fish communities. *Glob. Chang. Biol.* 25, 3424–3437. <https://doi.org/10.1111/gcb.14662>.
- Miatta, M., Bates, A.E., Snelgrove, P.V.R., 2020. Incorporating biological traits into conservation strategies. *Ann. Rev. Mar. Sci.* 13, 421–443. <https://doi.org/10.1146/annurev-marine-032320-094121>.
- Mott, R., Clarke, R.H., 2018. Systematic review of geographic biases in the collection of at-sea distribution data for seabirds. *Emu - Austral. Ornithol.* 118, 235–246. <https://doi.org/10.1080/01584197.2017.1416957>.
- Orben, R.A., Adams, J., Hester, M., Shaffer, S.A., Suryan, R.M., Deguchi, T., Ozaki, K., Sato, F., Young, L.C., Clatterbuck, C., Connors, M.G., Kroodsmas, D.A., Torres, L.G., 2021. Across borders: External factors and prior behaviour influence North Pacific albatross associations with fishing vessels. *J. Appl. Ecol.* 1–12. <https://doi.org/10.1111/1365-2664.13849>.
- Paleczny, M., Hammill, E., Karpouzi, V., Pauly, D., 2015. Population trend of the World's monitored seabirds, 1950–2010. e0129342 *PLoS One* 10. <https://doi.org/10.1371/journal.pone.0129342>.
- Pigot, A.L., Sheard, C., Miller, E.T., Bregman, T.P., Freeman, B.G., Roll, U., Seddon, N., Trisos, C.H., Weeks, B.C., Tobias, J.A., 2020. Macroevolutionary convergence connects morphological form to ecological function in birds. *Nat. Ecol. Evol.* 4, 230–239. <https://doi.org/10.1038/s41559-019-1070-4>.

- Pimiento, C., Leprieux, F., Silvestro, D., Lefcheck, J.S., Albouy, C., Rasher, D.B., Davis, M., Svenning, J.-C., Griffin, J.N., 2020. Functional diversity of marine megafauna in the Anthropocene. *Sci. Adv.* 6 eaay7650.
- Rao, M., Larsen, T., 2010. Ecological Consequences of Extinction. *Lessons in Conservation* 3, 25–53. <https://doi.org/10.1126/science.1235225>.
- R Core Team, 2020. A language and environment for statistical computing.
- Rees, S.E., Austen, M.C., Attrill, M.J., Rodwell, L.D., 2012. Incorporating indirect ecosystem services into marine protected area planning and management. *Int. J. Biodivers. Sci. Ecosyst. Serv. Manag.* 8, 273–285. <https://doi.org/10.1080/21513732.2012.680500>.
- Regular, P., Montevercchi, W., Hedd, A., Robertson, G., Wilhelm, S., 2013. Canadian fishery closures provide a largescale test of the impact of gillnet bycatch on seabird populations. *Biol. Lett.* 9, 20130088. <https://doi.org/10.1098/rsbl.2013.0088>.
- Richards, C., 2020. The link between seabird traits and anthropogenic threats with implications for conservation. Memorial University of Newfoundland.
- Richards, C., Cooke, R.S.C., Bates, A.E., 2021. Biological traits of seabirds predict extinction risk and vulnerability to anthropogenic threats. *Glob. Ecol. Biogeogr.* 00, 1–14. <https://doi.org/10.1101/2020.09.30.321513>.
- Richards, C., Cooke, R., Bowler, D.E., Boerder, K., Bates, A.E., 2022. Species' traits and exposure as a future lens for quantifying seabird bycatch vulnerability in global fisheries. *Avian Conserv. Ecol.* 17, 34. <https://doi.org/10.5751/ACE-02033-170134>.
- Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J., McCauley, D.J., 2017. Extinction risk is most acute for the world's largest and smallest vertebrates. *Proc. Natl. Acad. Sci.* 114, 10678–10683. <https://doi.org/10.1073/pnas.1702078114>.
- Schmitz, O., Wilmers, C., Leroux, S., Doughty, C., Atwood, T., Galetti, M., Davies, A., Goetz, S., 2018. Animals and the zoogeochemistry of the carbon cycle. *eaar3213 Science* 362, 1979. <https://doi.org/10.1126/science.aar3213>.
- Senko, J., White, E.R., Heppell, S.S., Gerber, L.R., 2014. Comparing bycatch mitigation strategies for vulnerable marine megafauna. *Anim Conserv* 17, 5–18. <https://doi.org/10.1111/acv.12051>.
- Skov, H., Heinänen, S., Zydelski, R., Bellebaum, J., Bzoma, S., Dagys, M., Durinck, J., Garthe, S., Grishanov, G., Hario, M., Kieckbusch, J., Kube, J., Kuresoo, A., Larsson, K., Luigujoe, L., Meissner, W., Nehls, H., Nilsson, L., Petersen, I., Roos, M., Pihl, S., Sonntag, N., Stock, S., Stipniece, A., Wahl, J., 2011. Waterbird populations and pressures in the Baltic Sea. *Nordic Council of Ministers, Copenhagen*.
- Speakman, J.R., 2005. Body size, energy metabolism and lifespan. *J. Exp. Biol.* 208, 1717–1730. <https://doi.org/10.1242/jeb.01556>.
- Stempniewicz, L., 1994. Marine birds drowning in fishing nets in the Gulf of Gdańsk (southern Baltic): numbers, species composition, age and sex structure. *Ornis Svec.* 4, 123–132. <https://doi.org/10.34080/os.v4.23026>.
- Tavares, D.C., Moura, J.F., Acevedo-Trejos, E., Merico, A., 2019. Traits shared by marine megafauna and their relationships with ecosystem functions and services, 262 *Front Mar. Sci.* 6. <https://doi.org/10.3389/fmars.2019.00262>.
- Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and ecosystem functioning. *Annu Rev. Ecol. Evol. Syst.* 45, 471–493. <https://doi.org/10.1146/annurev-ecolsys-120213-091917>.
- Toussaint, A., Charpin, N., Brosse, S., Villéger, S., 2016. Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread, 22125 *Sci. Rep.* 6. <https://doi.org/10.1038/srep22125>.
- Vilela, B., Villalobos, F., 2015. letsR: a new R package for data handling and analysis in macroecology. *Methods Ecol. Evol.* 6, 1229–1234. <https://doi.org/10.1111/2041-210X.12401>.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116, 882–892. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>.
- Weigel, B., Blenckner, T., Bonsdorff, E., 2016. Maintained functional diversity in benthic communities in spite of diverging functional identities. *Oikos* 125, 1421–1433. <https://doi.org/10.1111/oik.02894>.
- Welch, H., Clavelle, T., White, T.D., Cimino, M.A., Van Osdell, J., Hochberg, T., Kroodsmas, D., Hazen, E.L., 2022. Hot spots of unseen fishing vessels. *Sci. Adv.* 8. <https://doi.org/10.1126/sciadv.abq2109>.
- Wieczynski, D.J., Boyle, B., Buzzard, V., Duran, S.M., Henderson, A.N., Hulshof, C.M., Kerkhoff, A.J., McCarthy, M.C., Michaletz, S.T., Swenson, N.G., Asner, G.P., Bentley, L.P., Enquist, B.J., Savage, V.M., 2019. Climate shapes and shifts functional biodiversity in forests worldwide. *Proc. Natl. Acad. Sci.* 116, 587–592. <https://doi.org/10.1073/pnas.1813723116>.
- Wing, S., Jack, L., Shatova, O., Leichter, J., Barr, D., Frew, R., Gault-Ringold, M., 2014. Seabirds and marine mammals redistribute bioavailable iron in the Southern Ocean. *Mar. Ecol. Prog. Ser.* 510, 1–13.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci.* 96, 1463–1468.
- Zhou, C., Jiao, Y., Browder, J., 2019. Seabird bycatch vulnerability to pelagic longline fisheries: Ecological traits matter. *Aquat. Conserv* 29, 1324–1335. <https://doi.org/10.1002/aqc.3066>.
- Żydelski, R., Richman, S.E., 2015. Foraging behavior, ecology, and energetics of sea ducks. *Ecology and conservation of North American sea ducks. Stud. Avian Biol.* 46, 241–266.
- Żydelski, R., Small, C., French, G., 2013. The incidental catch of seabirds in gillnet fisheries: a global review. *Biol. Conserv.* 162, 76–88. <https://doi.org/10.1016/j.biocon.2013.04.002>.