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RESEARCH ARTICLE

Geographic range size, water temperature, and extrinsic threats predict the extinction risk in global cetaceans

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Abstract

Despite the fact that cetaceans provide significant ecological contributions to the health and stability of aquatic ecosystems, many are highly endangered with nearly one-third of species assessed as threatened with extinction. Nevertheless, to date, few studies have explicitly examined the patterns and processes of extinction risk and threats for this taxon, and even less between the two subclades (Mysticeti and Odontoceti). To fill this gap, we compiled a dataset of six intrinsic traits (active region, geographic range size, body weight, diving depth, school size, and reproductive cycle), six environmental factors relating to sea surface temperature and chlorophyll concentration, and two human-related threat indices that are commonly recognized for cetaceans. We then employed phylogenetic generalized least squares models and model selection to identify the key predictors of extinction risk in all cetaceans, as well as in the two subclades. We found that geographic range size, sea surface temperature, and human threat index were the most important predictors of extinction risk in all cetaceans and in odontocetes. Interestingly, maximum body weight was positively associated with the extinction risk in mysticetes, but negatively related to that for odontocetes. By linking seven major threat types to extinction risk, we further revealed that fisheries bycatch was the most common threat, yet the impacts of certain threats could be overestimated when considering all species rather than just threatened ones. Overall, we suggest that conservation efforts should focus on small-ranged cetaceans and species living in warmer waters or under strong anthropogenic pressures. Moreover, further studies should consider the threatened status of species when superimposing risk maps and quantifying risk severity. Finally, we emphasize that mysticetes and odontocetes should be conserved with different strategies, because their extinction risk patterns and major threat types are considerably different. For instance, large-bodied mysticetes and small-ranged odontocetes require special conservation priority.

KEYWORDS

cetaceans, comparative analysis, extinction risk, geographic range size, human threat, intrinsic trait, mysticetes, odontocetes, sea surface temperature

1 | INTRODUCTION

Human activities are causing a global biodiversity crisis, with species disappearing at rates that are up to 1000 times higher than that in the fossil record (Barnosky et al., 2011). In particular, over 600 vertebrate species have possibly gone extinct in the last half millennium, marking the arrival of the sixth mass extinction (Ceballos et al., 2015; Pimm et al., 2014). Analyses of past and ongoing extinction events have consistently reported the non-random distribution of extinction risk among species, and various factors were identified relating to the risk of species to extinction (Murray et al., 2011; Purvis et al., 2000). Therefore, investigating the key processes underlying species extinctions can help us identify species at risk of extinction and also assist in conserving species that are prone to future extinction (Cardillo & Meijaard, 2012). Moreover, compared to reactive and species-specific management, the development of preventative strategies based on statistical models can offer cost-effective, large-scale and rapid conservation measures, especially for endangered species with worldwide distributions (Cardillo & Meijaard, 2012; Murray et al., 2011).

With nearly 90 extant species, cetaceans are widespread and play an essential role in the ecological balance of marine and some freshwater ecosystems (Jefferson et al., 2015; SMM, 2022). Cetaceans as a group are also highly in danger among vertebrate groups, with nearly one-third of species assessed as threatened on the IUCN Red List (IUCN, 2022). Nevertheless, compared to high-profile land vertebrates (e.g., birds, mammals, amphibians, and reptiles), cetaceans have been frequently under-represented in global conservation prioritization, due to the relative paucity of information on their population dynamics, species' ecology, and extinction susceptibility (Jefferson, 2019; Pompa et al., 2011; Reeves, 2017). In recent years, some species have apparently become extinct (e.g., baiji, *Lipotes vexillifer*), or have declined precipitously to the edge of extinction (e.g., vaquita, *Phocoena sinus*) (Jaramillo-Legorreta et al., 2019; Turvey et al., 2007). Therefore, with updated knowledge of the distribution of cetaceans (Avila et al., 2018; Schipper et al., 2008), there is an urgent need to obtain information to understand what drives cetaceans to an elevated risk of extinction.

Both theory and empirical evidence have long suggested the non-random distribution of extinction risk among species clades, and have predicted that species with certain intrinsic traits (life-history and ecological traits) or under specific extrinsic threats are more vulnerable to extinction (Cardillo & Meijaard, 2012; Purvis et al., 2000). For cetaceans, evidence revealed that larger species generally have higher extinction risk, as they have slow life histories, increased hunting pressure, and weak recovery capacity from population declines (Brownell et al., 2018; Davidson et al., 2012). In addition, environmental factors such as temperature seasonality, net primary productivity and heatwaves can also influence food availability, fitness and even birth rates of cetaceans (Davidson et al., 2012; Wild et al., 2019). Furthermore, populations of cetaceans are vulnerable to both direct and indirect anthropogenic threats, including hunting (although this is not as extensive as in the past), ship strikes,

entanglement in fishing gear, habitat degradation, pollution, and climate change (Avila et al., 2018; Brownell et al., 2019; Jefferson & Curry, 1994; Pirotta et al., 2019; Read, 2005; Read et al., 2006; Reeves et al., 2013; Reijnders, 2003; Schipper et al., 2008; Smith & Reeves, 2012). Undoubtedly, both intrinsic traits and extrinsic factors affect how populations of cetaceans respond to these threats, and considering them together can reveal spatial contingencies in extinction risk (Davidson et al., 2012).

To date, many efforts have been made to assess the threatened status and drivers of extinction in cetaceans, which also highlight the importance of diverse conservation strategies to maximize biodiversity at different scales. For instance, for endangered or high-risk species, their conservation relies on knowledge of the specific threats, ecology, and biology of that species or of specific populations (Jaramillo-Legorreta et al., 2019; Turvey et al., 2007). By contrast, some studies have tried to assess threats for all or some marine species through mapping the geographic patterns of worldwide human impacts on ecosystems and species (e.g., risk maps; Avila et al., 2018; Halpern et al., 2015; Pompa et al., 2011; Schipper et al., 2008). However, such evaluations of global risks to species are generally inadequate, since the influence of threats depends not only on the ecological characteristics of each species, but also on the scale and severity of such threats (Murray et al., 2011). Contrary to the above studies, Davidson et al. (2012) combined both intrinsic and extrinsic factors to explore the drivers of extinction risk in marine mammals. However, they mixed cetaceans with other biologically distinctive phylogenetic groups (e.g., pinnipeds of Carnivora) and did not take a phylogenetic comparative view on extinction risk (Davidson et al., 2012). Hence, our current knowledge on the patterns of extinction risk in global cetaceans and underlying drivers are still fragmented and limited, and need to be extended to reach a more generalized understanding.

Extinction risk varies considerably among species, and the underlying threatening processes often show remarkable variation among small taxonomic groups (Böhm et al., 2016; Cardillo et al., 2008; Shuai et al., 2021). For example, Cardillo et al. (2008) showed a great deal of heterogeneity among mammal clades, supporting the view that tightly focused extinction risk models might be more precise. In fact, a narrow focus may help maximize the generality of the results while permitting specific guidance for conservation action (Cardillo et al., 2008; Shuai et al., 2021). For extant cetaceans, they are made up of two subclades (considered as suborders in the past): the Mysticeti, composed of the baleen whales, and the Odontoceti, formed by a more diverse species group, including toothed whales, dolphins, and porpoises (Jefferson et al., 2015; McGowen et al., 2020). These two groups show considerable morphological differences (e.g., baleen plates vs. teeth) and also large variations in species' predatory habits, body size, social structures, and preferred habitats (Jefferson et al., 2015; SMM, 2022). For instance, odontocetes are generally smaller than mysticetes, and are active predators with much more developed social structure (Jefferson et al., 2015). It is likely that odontocetes may experience a variety of threats and conditions that are either intensified or only

exist within their ranges compared to mysticetes, and vice versa (e.g., Avila et al., 2018). However, the correlates of extinction risk in these two cetacean subclades have rarely been considered in any previous studies and the underlying threatening processes remain largely unknown.

Since the pioneering work of Purvis et al. (2000), comparative extinction-risk analysis has been widely used to assess the relative plight of biodiversity and to make conservation recommendations. However, extinction-risk studies to date have typically focused on land mammals, birds, reptiles, and other terrestrial biota (Böhm et al., 2016; Cardillo et al., 2008; Jones et al., 2003; Owens & Bennett, 2000; Purvis et al., 2000; Wang et al., 2018), with relatively few studies on the fauna in aquatic environments (Bland, 2017). To fill this gap, we provide the first and most comprehensive analyses on the patterns and processes of extinction and threats for global cetaceans (both freshwater and oceanic species) using a cluster of six intrinsic traits, six environmental factors, and two human-related threat indices. Our study has three specific objectives. First, we attempted to identify the patterns and correlates of extinction risk in global cetaceans. Second, we examined whether the correlates and processes of extinction risk and major threat types differed between the two subclades of cetaceans, that is, mysticetes and odontocetes. Finally, after revealing the key drivers of extinction risk in cetaceans, we provided proactive guidelines for cetacean conservation and effective population management.

2 | MATERIALS AND METHODS

2.1 | Data collection

We collected the threat status of 90 cetacean species as of March 2022 based on the IUCN Red List of Threatened Species assessment (IUCN, 2022). We excluded nine Data-Deficient species, and then used the following categories of IUCN threat status: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR). Since the contribution of Purvis et al. (2000), comparative studies on extinction risk generally constructed threat status into an ordinal response factor with a higher rank corresponding to greater extinction risk (Böhm et al., 2016; Cardillo et al., 2008; Ducatez & Shine, 2017; Jones et al., 2003; Matthews et al., 2011; Wang et al., 2018). To keep it simple and consistent, we therefore followed their ideas and coded threat status from 0 (LC) to 4 (CR) (Table S1).

We collected data on six intrinsic traits for all cetaceans to reflect basic aspects of ecological requirement and habitat choice of species, including active region, geographic range size, maximum body weight, maximum diving depth, maximum reproductive cycle, and maximum school size. These data were generally derived from Jefferson et al. (2015), SMM (2022), the Animal Diversity Web (<https://animaldiversity.org/>), the IUCN Red List (IUCN, 2022), the regional databases (e.g., Department of Agriculture, Water and the Environment of the Australian Government, <https://www.awe.gov>

[au/environment/biodiversity](https://www.awe.gov.au/environment/biodiversity)), and related publications (e.g., Avila et al., 2018; Davidson et al., 2012).

More specifically, Davidson et al. (2012) showed that most at-risk species often occur in coastal areas. Following this idea, we quantified the *main active region* of all cetaceans as freshwater (coded as 1, e.g., river dolphins), coastal waters <200m in depth (2) (e.g., finless porpoises), or oceanic waters (3) considering the primary distribution or core habitats of species. In case of some species inhabiting different regions, we considered the one where the largest portion of the habitats they reside in. Second, previous studies have shown that species with smaller range sizes are often at higher risk of extinction, all else being equal (e.g., Harnik et al., 2012). We hence calculated *geographic range size* (km²) by extracting the extent of occurrence of species from the IUCN shapefiles and geo-data of recent studies (e.g., Avila et al., 2018) within ArcGIS 10.2 (ESRI, 2016). Since the regular and periodic occurrence of many cetaceans often show seasonal and annual shifts, we followed previous studies (Davidson et al., 2012) and mapped the maximum range extents of species. Moreover, body size and diving depth were also possible predictors of extinction risk, as large species or shallow-water species may face more barriers in their environments, such as human persecution (Davidson et al., 2012; Payne et al., 2016). To account for the influences of these variables, we collected the overall *maximum body weight* (t) and *maximum diving depth* (m) for all cetaceans from the reported records in the above resources. Fourth, in aquatic mammals, social group size may reduce extinction risk due to the advantages of sociality in reducing predation and enhancing foraging (Davidson et al., 2012). Therefore, we considered *maximum school size* as the maximum number of individuals in a typical social group that is most commonly seen in the wild. Lastly, a recent review showed that a high reproductive frequency (short inter-birth interval) of species communities can support demographic resilience in adverse conditions (Beauchard et al., 2017). We thus collected the *maximum reproductive cycle* of cetaceans as the maximum inter-birth interval in years. For the unavailable data of the reproductive cycle of six species (e.g., *Mesoplodon bowdoini*), we took the estimates based on mean values of their congeners, as done in other studies (Newbold et al., 2013; Wang et al., 2018).

Here we did not include population size as a variable for two reasons. First, the population sizes of cetaceans are largely raw estimates and could be incomplete or inaccurate due to sampling difficulties. Moreover, the extinction risk assignment of cetaceans is entirely based on population size (Criteria A and C), which could introduce circularity into correlative analyses. The above data were available for almost all cetaceans with the exception of *Berardius minimus* (NT), a newly described species of the genus *Berardius* in 2019 (Yamada et al., 2019). We hence excluded this species, leaving a total of 80 cetacean species for further analyses.

We also obtained six environmental factors from chlorophyll concentration raster and sea surface temperature raster of 2020 and 2003 (0.1-degree resolution, NASA Earth Observations, <https://neo.sci.gsfc.nasa.gov/>) based on the findings and hypotheses of published literature for all cetaceans. For instance, previous

studies showed that the spatial distribution of risk in aquatic mammals was strongly correlated with mean annual net primary production (Davidson et al., 2012), and that water temperature was a main factor influencing the distribution of many lower latitude cetaceans (Kaschner et al., 2006). Therefore, to infer the annual productivity and temperature of species' environment, we converted the range maps of cetaceans into occurrence grids at a resolution of 0.1° in ArcGIS 10.2, and then extracted *mean chlorophyll* (mg/m³) and *mean surface temperature* (°C) by averaging the monthly raster data of the year 2020 across the distribution range of each species. Moreover, the small realized thermal niches reflecting narrow temperature range have proven to increase the extinction risk in extant marine species (Collins et al., 2018), and the seasonal shift in primary productivity may create a mismatch for species to track its prey (Sequeira et al., 2014). We thus calculated the ranges of maximum and minimum values of chlorophyll concentration raster and sea surface temperature raster of 2020 across the distribution range of each species to represent *chlorophyll seasonal variation* (mg/m³) and *temperature seasonal variation* (°C), respectively. Lastly, climate changes have had severe impacts on marine ecosystems, including increases in ocean temperature (0.13°C on average per decade), fluctuations in chemical composition and primary productivity, and are likely to impact marine apex predators (MacLeod, 2009; NOAA, 2022; van Weelden et al., 2021). Following the idea of Szesciorka et al. (2020), we considered the *chlorophyll interannual trend* (mg/m³) and *temperature interannual trend* (°C) as the differences of mean chlorophyll or mean surface temperature between 2020 and 2003 to reflect interannual environmental changes.

Despite the fact that many river cetaceans are at the edge of extinction, previous studies on cetaceans regularly excluded these species from their extinction risk models (e.g., Davidson et al., 2012) or risk maps (e.g. Avila et al., 2018), due to the comparatively coarse resolution of their geo-spatial layers to cover their extrinsic conditions. Here, we artificially chose the available grid cells within inland waterways or estuaries to derive these environmental factors for river cetaceans. We did not include extreme environmental values, for instance minimum and maximum chlorophyll, because these values were multi-correlated with mean values (Pearson's $r > .6$) and would add complexity to our models.

Following previous studies, we employed the IUCN threat classification scheme to identify the key drivers of extinction risk in cetaceans (e.g., Ducatez & Shine, 2017; González-Suárez et al., 2013; Owens & Bennett, 2000). This threat classification scheme sorts the threats of each species into 12 major categories, for instance (4) Transportation and service corridors, and each threat category contains a few specific threat types, such as (4.3) Shipping lanes (IUCN, 2022). Moreover, the IUCN threat classification scheme also assigns each threat type with four different impact levels (no, low, moderate, and high) to reflect the intensity of threats to each species (IUCN, 2022). We ranked these impact levels from 0 (no) to 3 (high), and also reclassified threat types into seven basic and relevant categories that are commonly recognized for cetaceans (Table S2), including climate change, fisheries bycatch, habitat shifts, intentional

hunting, overfishing, pollution, and shipping lanes (Avila et al., 2018; Schipper et al., 2008).

The relationship between the number of threats and extinction risk is often questionable because many factors, including threat scale, intensity and location, will influence the impacts of multiple stressors on species (Ducatez & Shine, 2017; Greenville et al., 2021). Taking cetaceans as an example, in contrast to environmental stressors (e.g., climate change, habitat shifts, and pollution), fisheries bycatch and intentional hunting, and to a lesser extent shipping traffic, are more serious stressors as they can directly cause injury and mortality, which can directly harm populations (Jefferson et al., 2015; SMM, 2022). Therefore, to account for the variation in their intensities and to simplify the analyses, we weighted these seven threat types with ordinal stress scores (fisheries bycatch and intentional hunting = 3, shipping lanes = 2, and the rest environmental stressors = 1). Finally, we derived a *human threat index* for each species by multiplying the IUCN impact level with stress score for a corresponding threat type. That is, when a species is under a high impact from fisheries bycatch, the human threat index for this threat type would be 3 (high impact level) × 3 (stress score) = 9, or 1 × 1 = 1 for pollution with a low impact level.

Maps of geographic patterns of human impacts on ecosystems and species (or risk maps) have also been widely used to identify risk hotspots, visualize threat levels, and quantify the major threats of a specific species (González-Suárez et al., 2013; Halpern et al., 2015; O'Hara et al., 2021; Pompa et al., 2011; Schipper et al., 2008). Nevertheless, most of these studies mapped only a few threats, and did not allow the analysis of threats specific to species. With most recent species-specific geo-spatial layers of human threats for marine mammals (Avila et al., 2018), we derived the variable of *threat coverage* (%) as the proportion of core habitat of a focal species affected by all above threats superimposed. These data were collected by assigning threats to countries where species were reported, refining their spatial allocation with species' distribution, and summarizing the relative proportion of species core habitat affected by different threats, which allows the comparison of the risk intensity exposed to each species (see Avila et al., 2018 for details).

2.2 | Data analyses

Previous studies showed that declines or extinctions in vertebrates are generally non-random so that closely related species may share similar risk to extinction (Cardillo et al., 2008; Murray et al., 2011). In our study, nearly all predictors showed significant phylogenetic signals (Blomberg's $K > 0$, Pagel's λ close to 1, $p < .05$), suggesting that close relatives are more similar than random pairs of species (Table S3). To control for the shared ancestry, we built phylogenetic generalized least squares (PGLS; Orme, 2013) models to relate the threat categories of cetaceans to the focal explanatory variables. The technique is a modification of generalized least squares using knowledge of phylogenetic relationships to produce an estimate of expected covariance in cross-species data (Symonds

& Blomberg, 2014). For PGLS models, we employed the maximum likelihood method to optimize Pagel's λ (a reflection of phylogenetic signal) and set two branch length modifiers (κ and σ) to constant 1 to assume a Brownian motion model of evolution (Orme, 2013). PGLS has been shown to outperform equivalent non-phylogenetic approaches, because the latter will improperly introduce more similar residuals from closely related species into the regression analysis (Bland, 2017; Böhm et al., 2016; Cardillo, 2021; González-Suárez et al., 2013; Matthews et al., 2011). PGLS also has advantages over other phylogenetic comparative approaches, such as independent contrasts (Symonds & Blomberg, 2014). For instance, PGLS is more flexible, which can either correct for phylogeny or not based on the extent of phylogenetic signal in the data (Symonds & Blomberg, 2014). We conducted PGLS analyses using "pgls" function (package *caper*, Orme, 2013) in R version 4.0.2 (R Core Team, 2021).

The phylogenetic tree for these 80 species (Figure 1) was constructed using the latest cetacean tree provided by McGowen et al. (2020). For 11 species that were absent from this latest tree, they were placed by their closet congeners with information obtained from publications (e.g., Vollmer et al., 2019 for *Lagenorhynchus* species) and experts' suggestions. We employed the species' phylogenetic tree rather than the taxonomic "phylogeny" (Davidson et al., 2012) in our analyses because the former is an actual representation of the true evolutionary process of species.

To retain the most relevant predictors and to improve model fit, we carried out PGLS analyses in the following four steps. First, we conducted univariate PGLS analyses on each of the six intrinsic traits and eight external factors against risk categories to evaluate the relative contribution of each predictor on extinction risk. We directly excluded the variables showing weak correlations with the risk categories of species ($p \geq .1$) from the following analyses. Second, since multi-collinearities may lead to similar underlying processes, we tested for collinearity between the remaining potential predictors in the first step ($p < .1$), and only retained relevant variables with low correlations (Spearman's $\rho < |.50|$; Cohen, 2013). Here, we compared the relative importance of the highly correlated variables through the Akaike information criterion corrected for small sample size (AIC_c) analysis (Burnham & Anderson, 2004). For instance, many factors (e.g., maximum diving depth) were highly correlated with geographic range size (Tables S4 and S5). We only retained range size because it is more explanatory ($AIC_c = 224.893$) on extinction risk of cetaceans than other variables ($AIC_c = 244.157$ – 261.258 ; Table S5). Third, for the relevant predictors identified through the second step, we built a set of candidate models considering all possible combinations among these predictors, and then carried out model selection by ranking the AIC_c and Akaike weight (w_i) of all candidate models (Burnham & Anderson, 2004). We also evaluated the goodness-of-fit of each model by calculating the corresponding adjusted R^2 value. Since models may have similar explanatory abilities ($\Delta AIC_c \leq 2$), we finally applied a model-averaged approach for models in the 95% confidence set to estimate the relative importance of predictors (w_+), and their weighted estimates of regression coefficients (θ) as well as unconditional standard errors (Burnham & Anderson, 2004).

To check whether the correlates and processes of extinction risk were different between these two subclades, we repeated all the above analyses for mysticetes and odontocetes separately (Table S1). The above analyses were conducted using the packages *caper* and *MuMin* (Barton, 2014; Orme, 2013). We refrained from performing multivariable PGLS and model selection for species groups which had less than three significant predictors in univariate analyses (Shuai et al., 2021). Prior to analyses, we log-transformed continuous variables to normalize value distributions and to equalize error variance (Chen et al., 2019; Zhong et al., 2022).

Based on the IUCN threat classification scheme, we classified the threats of cetaceans into seven major threat categories: climate change, fisheries bycatch, habitat shifts, intentional hunting, overfishing, pollution, and shipping lanes, with 0 representing not affected and 1 as affected by the threat (Ducatez & Shine, 2017). We then counted the total number of species that were impacted by each of these seven threats, and calculated the proportions for all cetaceans and the two subclades. We also reanalyzed the data for the threatened (i.e., CR, EN, VU) cetaceans and species subclades to check whether the number of threats attributed to a focal species differed between data-sufficient cetaceans and the threatened species group (one-way ANOVA), and whether the major threat types also showed variations between these two treatments of species.

3 | RESULTS

3.1 | The pattern of extinction risk in cetaceans

For the 80 cetacean species assessed by the IUCN Red List, 22 species (27.50%) were classified as threatened, including four CR species, 11 EN species, and seven VU species (Figure 1). The other 58 species were classified as non-threatened (72.50%), among which 49 species were LC and nine were NT (Figure 1).

Among the 80 assessed cetaceans, 13 species belonged to the mysticetes and 67 species were odontocetes (Table S1). The percentage of threatened species was higher in the mysticetes (5/13, 38.50%) than in the odontocetes (17/67, 25.37%).

3.2 | Extinction risk correlates of cetaceans

In the univariate PGLS analyses, geographic range size, maximum school size, chlorophyll interannual trend, mean surface temperature, temperature interannual trend, and threat index were the six most relevant predictors of extinction risk of global cetaceans after controlling for the multicollinearity among predictors (Table 1). The best multivariable PGLS model included geographic range size, mean surface temperature, and threat index, accounting for 60.11% of total variation (Table 2). Model averaging suggested that geographic range size ($w_+ = 1.00$, $\theta = -0.26 \pm 0.05$), mean surface temperature ($w_+ = 1.00$, 0.81 ± 0.24), and threat index ($w_+ = 0.99$, 0.09 ± 0.03) were still the three most important

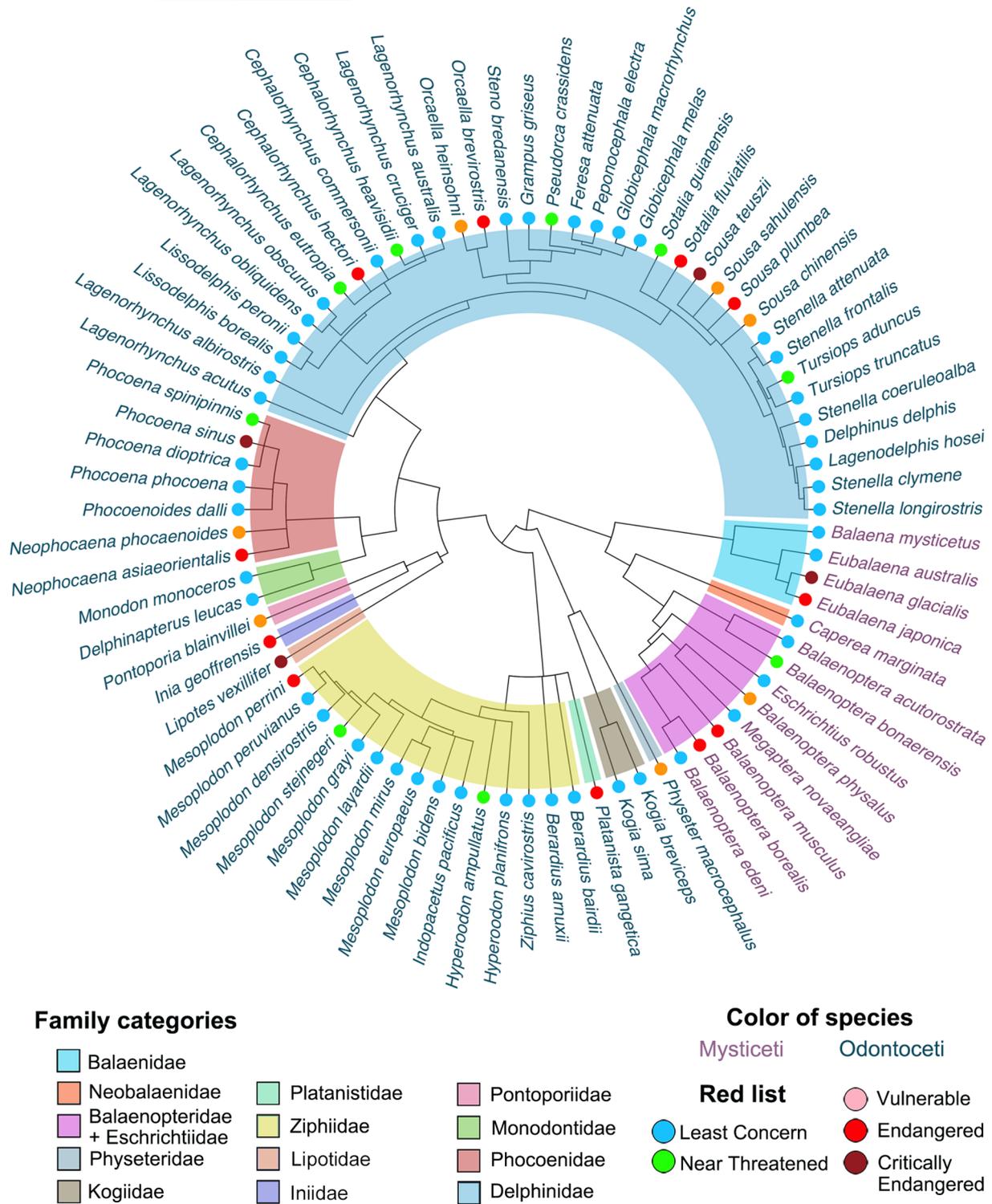


FIGURE 1 Phylogenetic tree of the 80 cetacean species based on the most recent global cetacean phylogenetic tree (McGowen et al., 2020). The color of circles exhibits the extinction risk of species derived from the IUCN Red List. See Table S1 for the complete list of cetacean species and the categories of Red List status. [Color figure can be viewed at wileyonlinelibrary.com]

variables consistently supported in the 95% confidence set ($p < .05$; Figure 2a; Table S6), indicating that species with small range size, living in warmer waters or under high human impacts would have a greater risk of extinction. However, the other three variables (maximum school size, chlorophyll, and temperature interannual

trends) showed comparatively less support ($p > .1$; Figure 2a; Table S6).

When dividing cetaceans into two subclades, the univariate PGLS analyses showed that maximum body weight was positively associated with extinction risk in mysticetes and negatively related

TABLE 1 Results of univariate phylogenetic generalized least squares models for predicting the risk of extinction in all cetaceans, mysticetes (Mysticeti), and odontocetes (Odontoceti). Variables underlined were excluded from the following multivariable analyses to avoid multicollinearities (Tables S4 and S5)

	All species (80 spp.)		Mysticeti (13 spp.)		Odontoceti (67 spp.)	
	Slope	t (p)	Slope	t (p)	Slope	t (p)
Intrinsic traits						
Active region	<u>-1.25</u>	<u>-5.55***</u>	-0.91	-0.76	<u>-1.34</u>	<u>-6.40***</u>
Geographic range size	-0.39	-8.67***	-0.06	-0.21	-0.36	-9.71***
Maximum body weight	-0.01	-0.18	0.75	2.14*	<u>-0.21</u>	<u>-2.26*</u>
Maximum diving depth	<u>-0.48</u>	<u>-5.90***</u>	-0.03	-0.06	<u>-0.51</u>	<u>-7.08***</u>
Maximum reproductive cycle	0.11	0.33	1.49	1.58	-0.17	-0.48
Maximum school size	-0.40	-4.17***	-0.09	-0.15	-0.38	-4.23***
Extrinsic factors						
Chlorophyll interannual trend	0.39	3.64***	-5.19	-1.71	0.41	4.21***
Chlorophyll seasonal variation	<u>-1.99</u>	<u>-3.79***</u>	2.30	0.56	<u>-2.24</u>	<u>-4.56***</u>
Mean chlorophyll	<u>2.08</u>	<u>4.33***</u>	2.61	1.05	<u>1.55</u>	<u>3.34***</u>
Mean surface temperature	1.29	3.99***	0.66	0.58	1.03	3.42**
Temperature interannual trend	1.25	3.55***	0.43	0.15	<u>1.32</u>	<u>3.95***</u>
Temperature seasonal variation	<u>-0.83</u>	<u>-4.48***</u>	0.47	0.83	<u>-1.16</u>	<u>-6.88***</u>
Threat coverage	<u>0.02</u>	<u>4.09***</u>	-0.01	-0.17	<u>0.02</u>	<u>5.06***</u>
Threat index	0.22	7.07***	0.16	1.58	0.23	7.79***

Note: Significant results are marked in bold: * $p < .1$; ** $p < .05$; *** $p < .01$; **** $p < .001$.

to that of odontocetes (Table 1), suggesting an elevated extinction risk in larger baleen species and smaller toothed whales. Moreover, body weight was the only important predictor of extinction risk for mysticetes, while this variable was excluded from the multivariable PGLS for odontocetes due to the strong collinearity with geographic range size (Table 1). For odontocetes, the best multivariable model included the variables of geographic range size, mean surface temperature, threat index, and chlorophyll interannual trend, accounting for 76.07% of total variation in the extinction risk (Table 2). Model averaging further showed that geographic range size ($w_+ = 1.00$, $\theta = -0.29 \pm 0.04$), mean surface temperature ($w_+ = 1.00$, 0.81 ± 0.18), and threat index ($w_+ = 0.90$, 0.07 ± 0.03) were the three most important predictors in the 95% confidence set for odontocetes (Figure 2b; Table S6).

3.3 | Major threats differ according to species extinction risk

The number of threats per species was 2.46 ± 1.23 (mean \pm SD, $n = 80$) for cetaceans worldwide, and was higher for odontocetes (2.58 ± 1.22) than for mysticetes (1.85 ± 1.10). When only considering the threatened species, the mean number of threats was increased (3.27 ± 1.09 , $n = 22$) for the threatened cetaceans, and was also higher for the threatened odontocetes (3.65 ± 0.90 , $n = 5$) than

for the threatened mysticetes (2.00 ± 0.63 , $n = 17$). The number of threats attributed to a focal species differed significantly between data-sufficient cetaceans and threatened species group ($n = 80$ vs. 22; $F = 6.98$, $df = 1$, $p < 0.01$).

For the data-sufficient species ($n = 80$), fisheries bycatch was consistently the most common threat to all three species groups ($29.79\% \pm 1.90\%$, Figure 3). Besides fisheries bycatch, the major threat types for odontocetes largely mirrored the results for all cetaceans, with pollution ranking as the second major threat (24.86% vs. 23.35%), followed by intentional hunting (18.50% vs. 18.78%), shipping lanes (9.25% vs. 12.69%), and habitat shifts (12.72% vs. 11.17%; Figure 3a). By contrast, shipping lanes was a more detrimental threat to mysticetes (37.50%), followed by intentional hunting (20.83%; Figure 3a).

Overall, the major threat types for data-sufficient species groups differed from those for the threatened species groups (Figure 3). Specifically, shipping lanes ranked as the second detrimental threat to all threatened cetaceans (23.61%), and was also a key threat to the threatened subclades (Figure 3b). Habitat shift and pollution had no impact on the threatened mysticetes, but were more influential for the threatened odontocetes (20.97% and 19.35%, respectively; Figure 3b). Among these seven threat types, climate change and overfishing had weak effects on all species and threatened ones across all these species groups ($0.86\% \pm 0.71\%$, Figure 3).

	<i>k</i>	AIC _c	ΔAIC _c	<i>w</i> _{<i>i</i>}	Adjusted R ²
All species					
RS+MST+TI	4	203.169	0	0.2644	.6011
RS+MST+TI+MSS	5	203.867	0.698	0.1864	.6011
RS+MST+TI+TIT	5	204.638	1.469	0.1268	.6001
RS+MST+TI+CIT	5	204.778	1.610	0.1182	.5995
RS+MST+TI+MSS+TIT	6	205.225	2.056	0.0946	.6006
RS+MST+TI+MSS+CIT	6	205.779	2.610	0.0717	.5982
RS+MST+TI+TIT+CIT	6	206.821	3.652	0.0426	.5956
RS+MST+TI+MSS+TIT+CIT	7	207.613	4.444	0.0287	.5953
RS+MST	3	209.305	6.137	0.0123	.5649
RS+MST+CIT	4	209.306	6.138	0.0123	.5715
RS+MST+MSS	4	210.527	7.358	0.0067	.5627
RS+MST+TIT	4	210.547	7.378	0.0066	.5650
RS+MST+MSS+CIT	5	210.850	7.681	0.0057	.5680
RS+MST+TIT+CIT	5	211.531	8.362	0.0040	.5662
RS+MST+MSS+TIT	5	211.672	8.503	0.0038	.5635
RS+TI+MSS+TIT	5	211.737	8.568	0.0036	.5594
RS+TI+TIT	4	212.099	8.930	0.0030	.5577
RS+MST+MSS+TIT+CIT	6	213.056	9.887	0.0019	.5629
Odontoceti					
RS+MST+TI+CIT	5	132.13	0	0.2459	.7607
RS+MST+TI	4	132.304	0.174	0.2254	.7552
RS+MST+TI+MSS	5	132.553	0.423	0.1990	.7563
RS+MST+TI+CIT+MSS	6	133.008	0.878	0.1585	.7595
RS+MST+CIT	4	134.164	2.034	0.0889	.7488
RS+MST+CIT+MSS	5	135.379	3.249	0.0484	.7458
RS+MST	3	137.223	5.094	0.0193	.7320
RS+MST+MSS	4	137.884	5.755	0.0138	.7311

Abbreviations: AIC_c, Akaike information criterion corrected for small sample size; CIT, chlorophyll interannual trend; MSS, maximum school size; MST, mean surface temperature; RS, geographic range size; TI, threat index; TIT, temperature interannual trend.

4 | DISCUSSION

Our comparative study comprehensively investigated the correlates and processes of species extinction and threats for cetaceans at a global scale. We found that cetaceans with small range size, living in warmer waters or under high human impacts would have a greater risk of extinction. This result partly reflects previous findings, but for the first time, our study included freshwater cetaceans, incorporated phylogenetic uncertainty, and explored the taxonomic-specific vulnerabilities to threat processes for global cetaceans. We also tested, for the first time, whether the choices of species subclades impacted the assessment of major threats to this highly endangered taxon.

Our study also has three key advantages compared to previous studies on cetaceans. First, our study included four kinds of variables as putative predictors of extinction risk: life-history, ecological,

environmental, and human impacts (Murray et al., 2011). By contrast, previous studies on cetaceans often focused on extrinsic predictors (e.g., Avila et al., 2018; Halpern et al., 2008, 2015), and ignored how different species withstand extrinsic threatening processes. Second, our observed patterns can help predict the degree to which future species will face declines and extinctions with escalating anthropogenic pressure (Cardillo & Meijaard, 2012). For instance, it is predicted that the Chilean dolphin (*Cephalorhynchus eutropia*, NT) is actually highly endangered and requires urgent consideration due to its small range in South America and multiple threats affecting its populations (Jefferson, 2019). Finally, our study offers general and expansive patterns for global cetaceans, and hence avoids the pitfalls of researcher degrees of freedom, in which flexibility and subjectivity played strong roles in the selection of cetaceans to study and in examining the causes of species' endangerments (e.g., Brownell et al., 2019; Davidson et al., 2012).

TABLE 2 Results of multivariate phylogenetic generalized least squares models for predicting the risk of extinction in all cetaceans and odontocetes (Odontoceti). The table shows models with ΔAIC_c ≤ 10, model rank, change in AIC_c from the top model (ΔAIC_c), model weight (*w*_{*i*}), and adjusted R²

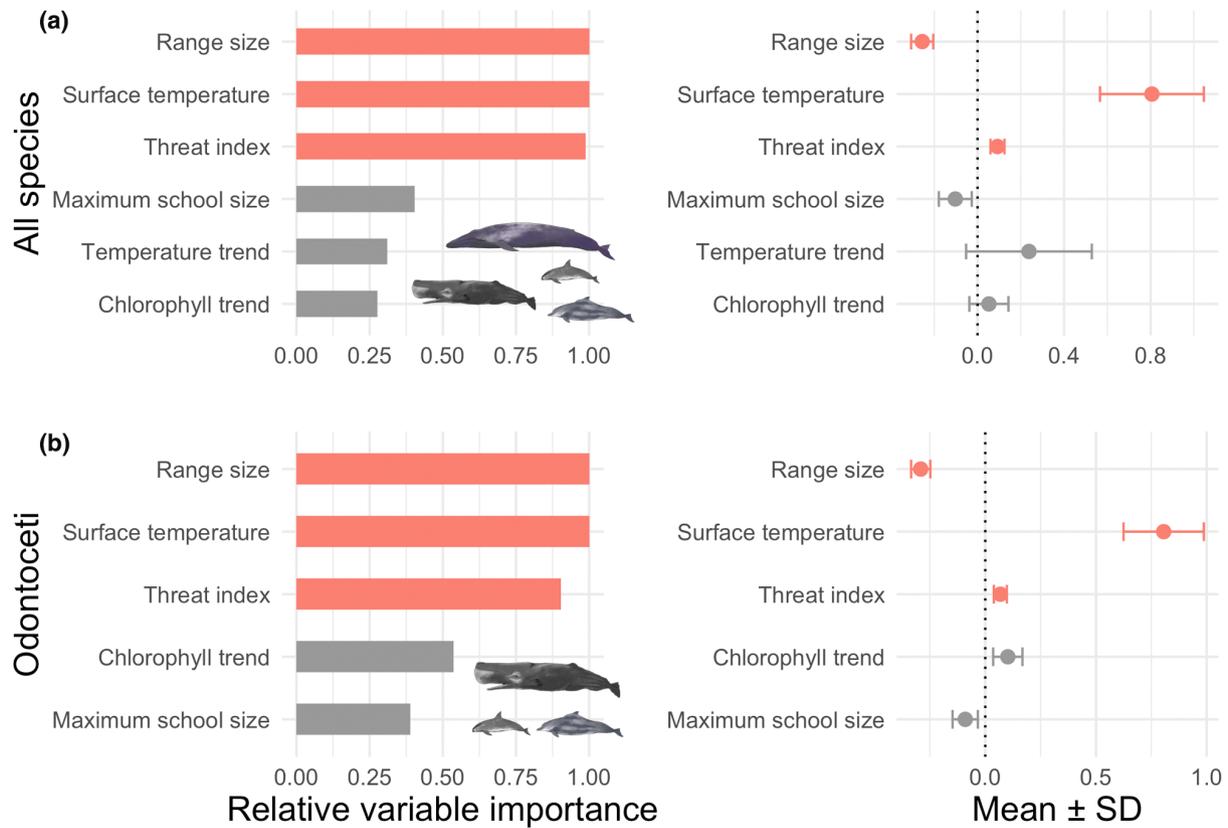


FIGURE 2 Relative variable importance, model-averaged parameter estimates and unconditional standard errors for the predictors in the 95% confidence set for all cetacean species (a) and odontocetes (Odontoceti, b). Significant predictors with $p < .05$ are marked in red. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16885)]

4.1 | Patterns of extinction risk in global cetaceans

As assessed by the IUCN Red List, 27.50% of the 80 cetaceans are currently threatened with extinction: a level of threat lower than that of amphibians (41%), but higher than that reported for mammals in general (26%) and birds (14%; IUCN, 2022). Importantly, small odontocetes are especially highly endangered and their extinction risk is largely underestimated considering intense human threats and small species' ranges (Bearzi et al., 2019). For instance, although listed as a CR species, baiji's extinction represents not only the first documented extinction of a 'megafaunal' vertebrate in over 50 years, but also the disappearance of the entire Lipotidae family (Jefferson et al., 2015; Turvey et al., 2007). Media reports also showed that in July 2021, the Mexican government essentially gave up maintaining the gillnet-free zone, the only conservation measures likely to prevent the extinction of the vaquita. Brownell et al. (2019) warned that without major conservation efforts, there would be grim prospects for CR small cetaceans and other at-risk megafauna.

4.2 | Correlates of extinction risk in global cetaceans

As expected, geographic range size was the leading factor in determining the extinction risk of cetaceans, a pattern which is widely

reported in previous studies (Chen et al., 2019; Davidson et al., 2009, 2012). Small-ranged species generally face a high risk of extinction, because range restriction may elevate their vulnerability to inbreeding, demographic, and environmental stochasticity (Davidson et al., 2012; Jenkins & Van Houtan, 2016). In addition, a confined range size can induce a high susceptibility of cetaceans to human-related threats, such as ship collision or fisheries bycatch, and such local impacts may cause global species extinctions (Di Marco & Santini, 2015; Jefferson, 2019; Smith & Reeves, 2012). In our study, the strong correlation between geographic range size and main active region suggests that small-ranged species (odontocetes in particular) prefer coastal or inshore/riverine regions, where intense human impacts occur compared to deep seas (Jefferson, 2019). The endemic baiji and vaquita are such vivid examples, whose ranges are quite small, but overlapping with extensive gillnet fishing activities (Jaramillo-Legorreta et al., 2019; Turvey et al., 2007). Therefore, to conserve small-ranged species, especially those in developing countries, effective local and transnational conservation measures, such as setting up marine-protected areas and implementing legislative protection are highly needed to protect their habitats and reduce their risk of extinction (Hoyt, 2012).

Human threat index was another robust predictor of extinction risk of global cetaceans, indicating that species under strong cumulative effects of human threats have an elevated risk of extinction. In fact, humans have influenced the entire earth's oceans

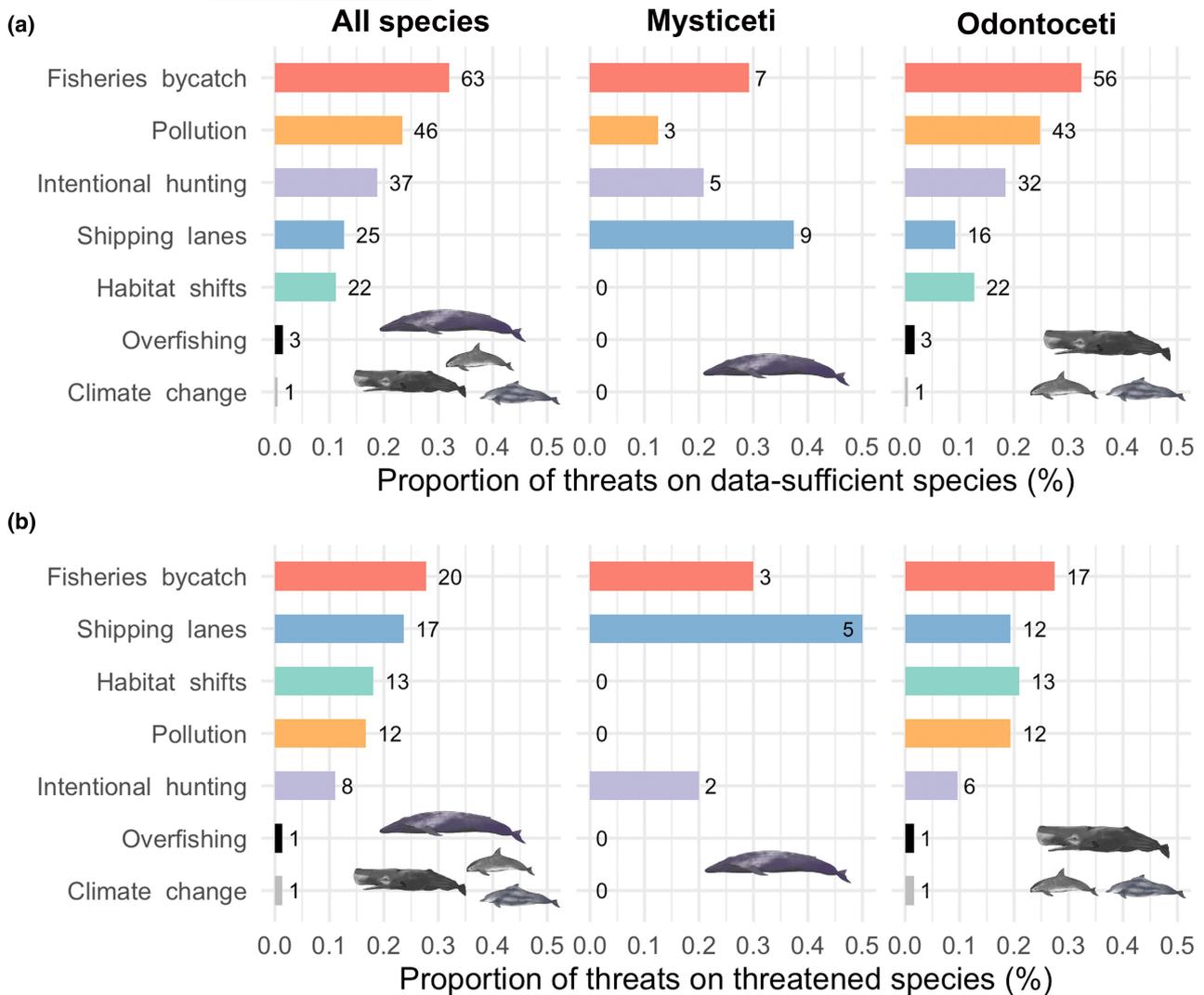


FIGURE 3 Bar charts showing the proportion of species affected by each of the seven major threat categories for three data-sufficient species groups (all cetaceans, mysticetes (Mysticeti) and odontocetes (Odontoceti, a) as well as their threatened species subsets (b). The numbers beside each bar illustrated the number of species for which each threat was listed. The data were collected from the IUCN Red List. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16385)]

and rivers, and nearly 97.7% of water regions experience multiple stressors (Halpern et al., 2015). In our study, almost all of the at-risk species and 74.13% of the 58 non-threatened cetaceans were affected by at least two human stressors, incurring the concern that more cetaceans will become endangered in the near future. For cetaceans, direct injury and mortality from entanglements (e.g., baiji), boat strikes (e.g., North Atlantic Right Whales, *Eubalaena glacialis*, Rolland et al., 2012), or intentional hunting (e.g., Amazon river dolphin, *Inia geoffrensis*; Mintzer et al., 2013) were generally considered as primary threats to their continued existence. In addition, water pollution and habitat alteration also induce the loss and fragmentation of both habitats and populations (e.g., Ganges river dolphin, *Platanista gangetica*; Sinha & Kannan, 2014), and hence are likely cause some populations to further decline or even lead to local extinction. Taking vaquitas as an example, the species can still persist on the planet if the removal of gillnets from their range can be achieved. Unfortunately, mismanagement and unsustainable/illegal

fisheries activities make such a miracle unlikely (Jaramillo-Legorreta et al., 2019).

Water surface temperature was also an important predictor of extinction risk in cetaceans, showing that species living in warmer areas have comparatively higher risk of extinction. Previous studies on territorial species predict that species in areas of lower temperatures are at higher risk, due to slower life histories (Chichorro et al., 2019; Flousek et al., 2015; Jiguet et al., 2010). However, this hypothesis was not supported in our study since water temperature was not related to the life-history parameters of cetaceans, such as body weight and reproductive cycle (Table S4). In fact, a pronounced dip in marine species richness, especially for pelagic species, has been observed around the equator (Chaudhary et al., 2021). For small-ranged or sedentary species (e.g., river dolphins), warm waters may impede them from tracking climate velocities to match their thermal preferences (Wild et al., 2019). Moreover, warmer waters generally show a greater extent of deoxygenation, and may decrease habitat

quality and food abundance for cetaceans (Breitburg et al., 2018). We also found that human threats were comparatively high in the warmer regions (Spearman $\rho = .32$, $p < .001$), which may in combination push cetaceans to the edge of extinction (Brownell et al., 2019; Whitehead et al., 2008). To cope with climate impacts, it is essential to reduce greenhouse gas emissions, improve environmental quality, and enhance coastal resilience (MacLeod, 2009; van Weelden et al., 2021). In fact, protecting cetaceans is climate positive because they can capture and store carbon, and help stabilize marine ecosystems (NOAA, 2022).

Interestingly, the predictors of extinction risk were quite different between the two subclades of cetaceans. In particular, large-bodied mysticete species (e.g., blue whale, *Balaenoptera musculus*) were more vulnerable to extinction than their counterparts, corresponding to the finding of Davidson et al. (2012). Larger species generally have small population sizes and slow life histories (Purvis et al., 2000), and are highly vulnerable to human-related threats. Additionally, their past history of heavy exploitation by whaling operations has left them in a more vulnerable state. Blue whales and North Atlantic right whales are prominent examples; they are still at much reduced population sizes due to historical whaling, making them more vulnerable to current threats (Rolland et al., 2012). By contrast, geographic range size and water temperature were apparently less important to the Mysticeti group, as these species are highly migratory and are generally globally distributed (Jefferson et al., 2015; SMM, 2022). Odontoceti, however, forms a large proportion of the cetaceans and hence showed similar patterns as with the all-species group. Interestingly, we found that body size of odontocetes was negatively related to extinction risk, albeit that this variable was excluded due to the collinearity with geographic range size (Table S4). It suggests that small-bodied odontocetes (e.g., river dolphins, finless porpoises) also have higher risks of extinction, a pattern which was overlooked in previous studies (e.g., Davidson et al., 2012). Overall, conservation management of mysticetes and odontocetes should rely on different strategies, because their extinction risk was associated with different combinations of predictors.

Ranking threats based on species extinction risk provided new insights into understanding the major threats to cetaceans. Our findings for all data-sufficient cetaceans mirrored previous studies of mapping threats to marine mammals (Avila et al., 2018; Halpern et al., 2008, 2015). For instance, Avila et al. (2018) also showed that incidental catch was the biggest threat, followed by pollution and direct harvesting. However, such treatment will inevitably include a large proportion of unthreatened species (~70% of cetaceans), and may thus overestimate the impacts of certain threats on species (Ducatez & Shine, 2017). Moreover, the considerably larger ranges of unthreatened ones may also make it too coarse-grained to capture real human threats. Taking this bias into account, we focused on threatened cetaceans and found that shipping lanes were of more concern than pollution, especially for the baleen whales. In the last century, the world witnessed a nine-fold expansion of

large commercial vessels, which coincides with an increase in the amount of ship strikes on cetaceans (Pirotta et al., 2019; Schoeman et al., 2020). Our findings were overall in accord with the increasing concern that accidental mortality is a major factor in current extinction risk (Pirotta et al., 2019; Schipper et al., 2008), while pollution could be more detrimental in the near future.

Taken together, our phylogenetic comparative analyses showed that geographic range size, sea surface temperature, and human threat index were the best predictors of extinction risk in cetaceans. Previous studies on terrestrial vertebrates (e.g., land mammals, birds, reptiles) have frequently detected a higher extinction risk of small-ranged species than widespread ones (Böhm et al., 2016; Owens & Bennett, 2000; Purvis et al., 2000), which lead to a preoccupation with protecting species with restricted range distributions (e.g., $<10,000\text{km}^2$; Pimm et al., 2018). Nevertheless, our study emphasized that those "small-ranged" species of cetaceans (mean = $56,809,275\text{km}^2$ for threatened ones) were also highly vulnerable to global extinction, revealing that this less-known taxon could be underrepresented in traditional conservation actions. In fact, cetaceans require large ranges to retain seasonal habitats and viable populations (Reeves, 2017), which suggest that conservation policy should be taxon-specific on the basis of species ecology. Moreover, we found that cetaceans were highly susceptible to extrinsic threats, but the identified threat types for cetaceans (e.g., entanglements, shipping lanes) were largely different compared to those for land vertebrates (e.g., land conversion, species invasion; Murray et al., 2011). Therefore, for the persistence of cetaceans, conservation strategies should also differ from our establishment views from land species and reduce stress from specific human activities or disturbances as identified in our study (Jefferson, 2019; Smith & Reeves, 2012; Smith & Smith, 1998). Overall, our study provides insights into the extinction risk of cetaceans and we suggest that conservation strategies should account for the specific threat type and the ecology of the target taxa.

Although chlorophyll concentration, temperature trend, and variation were significant predictors of extinction risk in cetaceans, they were less important than geographic range size, water surface temperature, and threat index in our study. Actually, their poor predictions are perhaps partially because they influence the extinction risk of cetaceans through interacting with geographic range size (Tables S4 and S5), and partly due to the comparatively coarse-scale to reflect real environmental changes.

5 | CONCLUSION

Identifying key correlates of extinction risk and evaluating how they vary across species and space are essential for prioritizing conservation action and avoiding future extinctions (Shuai et al., 2021; Wang et al., 2018). Despite the fact that cetaceans form a small fraction of vertebrate taxa, the conservation of cetaceans worldwide is still challenging due to incomplete knowledge of species'

demography, life histories, and biogeography (Jefferson, 2019; Pompa et al., 2011; Reeves, 2017). Previous studies on the extinction risk of cetaceans have focused, however, on few species or specific regions (e.g., Brownell et al., 2019; Jaramillo-Legorreta et al., 2019; Jefferson, 2019; Turvey et al., 2007; Vanderlaan & Taggart, 2009), and less is known about the correlates of extinction risk in global cetaceans.

Our phylogenetic comparative analyses focused on all extant cetaceans and clearly showed that no single solution exists for the proactive conservation of cetaceans. Here we provide several additional ways forward. First, we showed statistically that cetaceans with small ranges require high conservation priority. Hence, creating large, unfragmented, and well-managed protected zones is important for supporting viable small-ranged cetaceans (Smith & Smith, 1998). Second, our study consistently highlighted that human threats, such as fisheries bycatch, also imperil many species. Therefore, managing fisheries, identifying high-risk areas, developing safety corridors, and limiting pollution are essential for reducing the risk of human threats within the distribution ranges of cetaceans (Brownell et al., 2019; Hoyt, 2012; Ritter & Panigada, 2019). Third, we should also pay considerable attention to the species living in warmer waters, especially those species that do not move long distances, since they may have lower ability to “escape” from climate change and human influences (Breitburg et al., 2018; Wild et al., 2019). Moreover, our study provided new insights into the conservation of endangered species by offering a cautionary tale that major threat types can be considerably different between data-sufficient species and threatened species. Therefore, further studies should consider the extinction risk when superimposing risk maps and quantifying risk severity for different species. In addition, we emphasized that mysticetes and odontocetes should be conserved with different strategies, because their extinction risk patterns and major threat types were considerably different. For instance, it is critical to protect large baleen whales by mitigating the impacts of shipping traffic in open seas, by limiting vessel speed, and re-routing shipping lanes in the overlapped habitats (Hoyt, 2012; Vanderlaan & Taggart, 2009). Finally, it is important to strengthen international cooperation and to promote the enactment and enforcement of transboundary fishery laws and regulations to assist in preserving a healthy and sustainable diversity of cetacean fauna (Gillespie, 2002). While at this point, the future may not look particularly bright for cetaceans, it has been pointed out that there is still ample time to change our ways and ensure a more secure future for these animals (Bearzi, 2020; Bearzi et al., 2019; Jefferson, 2019). It is true that we have lost some species and populations already, but there is still much that can be saved.

AUTHOR CONTRIBUTIONS

Yanping Wang, Bingyao Chen, and Chuanwu Chen designed the study. Bingyao Chen and Chuanwu Chen collected the data. Chuanwu Chen conducted the analyses and wrote the draft. Thomas A. Jefferson and Yanping Wang contributed to the writing of the paper.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from Dryad at <https://doi.org/10.5061/dryad.p5hqbzks7>.

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SUPPORTING INFORMATION

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

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