

23 **Abstract**

24 The interactive effects of multiple threats are one of the main causes of biodiversity
25 loss, yet our understanding of what predisposes species to be impacted by multiple
26 threats remains limited. Here we analyse a global dataset of over 7000 marine,
27 freshwater, and terrestrial vertebrate populations, alongside trait, threat and
28 geographical data, to identify the factors influencing the number of threats a species
29 is subjected to at the population level. Out of a suite of predictors tested, we find that
30 body mass and latitude both are broadly available for vertebrate species, and
31 influence the number of threats a population is subjected to. Larger bodied species
32 and those nearer the equator are typically affected by a higher number of threats.
33 However, whilst this pattern broadly holds across ecosystems for most taxa,
34 amphibians and reptiles show opposing trends. We suggest that latitude and body
35 mass should be considered as key predictors to identify which vertebrate populations
36 are likely to be impacted by multiple threats. These general predictors can help to
37 better understand the impacts of the Anthropocene on global vertebrate biodiversity
38 and design effective conservation policies.

39 **Keywords:** Conservation, extinction, life history, living planet database, multiple
40 stressors, population dynamics, traits.

41

42 **Introduction**

43 The Anthropocene is characterised by the strong influence of human activities on the
44 structure and functioning of Earth's natural systems (Steffen *et al.*, 2011; Dirzo *et al.*,
45 2014). Threats like climate change, habitat loss, exploitation, pollution, or invasive
46 species, directly or indirectly caused by human activities, are reshaping the
47 biosphere at an unprecedented rate and scale (Scholes *et al.*, 2018; Díaz *et al.*,
48 2019; IPCC, 2021). Although the individual effects of these threats can have strong
49 impacts (Kroeker *et al.*, 2010; Newbold *et al.*, 2015; Hughes *et al.*, 2017), about 80%
50 of species are exposed to more than one threat simultaneously (IUCN 2021). The
51 pervasiveness of multiple threats is of particular concern because of the
52 unpredictability of their interactive effects (Darling & Côté, 2008; Côté *et al.*, 2016).
53 Yet, our understanding of the factors driving exposure to multiple threats remains
54 limited (Maxwell *et al.*, 2016; Hodgson *et al.*, 2017).

55 Whether a population is exposed to a threat is a result of the combined effects
56 of environmental factors, species life histories, and human activity (Purvis *et al.*,
57 2000; Cardillo *et al.*, 2005). Life history traits such as body mass, trophic level, or
58 habitat specificity have been linked to the vulnerability of species (Fisher & Owens,
59 2004; Di Marco *et al.*, 2015; Pacifici *et al.*, 2017). For instance, species with large
60 body mass are disproportionately targeted for exploitation (Pauly *et al.*, 1998;
61 Duncan *et al.*, 2002), making them more vulnerable to further threats. Likewise,
62 predators usually require large home ranges and also depend on the abundance of
63 their prey species, making them vulnerable to habitat loss, as well as being a
64 common target for hunting (Cardillo *et al.*, 2005; Wolf & Ripple, 2016). Moreover,
65 species with low habitat specificity have the potential to be more prone to be

66 exposed to multiple threats, given their wider range of distribution (Malcolm *et al.*,
67 2006; Ehrlén & Morris, 2015; Batt *et al.*, 2017). While the influence of all these traits
68 on the vulnerability to species extinction has been largely explored (Purvis *et al.*,
69 2000; Fisher & Owens, 2004; Cardillo *et al.*, 2005), how these contribute to the
70 predisposition of species to being exposed to multiple threats remains unknown.

71 The exposure of species to threats can also depend on environmental factors.
72 For instance, the prevalence and impact of anthropogenic threats differs in marine,
73 terrestrial and freshwater systems (Díaz *et al.*, 2019). While in freshwater and
74 terrestrial ecosystems habitat loss is the most prevalent threat (Newbold *et al.*, 2015;
75 Birk *et al.*, 2020), exploitation represents the most pressing threat for marine species
76 (Halpern *et al.*, 2015). On top of that, local and global threats show distinct spatial
77 clustering worldwide (Bowler *et al.*, 2020; Harfoot *et al.*, 2021). Many local threats
78 are directly linked to human populations (e.g., habitat loss, hunting, etc.), so their
79 presence is likely to change in line with human population density across different
80 latitudes (Santini *et al.*, 2017). Global threats (e.g. climate change) are also non-
81 uniformly distributed, particularly across latitude (Harfoot *et al.*, 2021; IPCC, 2021),
82 making it challenging to predict them using simple proxies (Sunday *et al.*, 2012).

83 Understanding the role life history traits and the environmental factors
84 influencing the predisposition of vertebrate populations to be exposed to multiple
85 threats is therefore the first step to manage their effects (Maxwell *et al.*, 2016). Here,
86 we study multiple threats by identifying factors that best predict the number of threats
87 a population is affected by. To do this, we use population-level threat data from the
88 Living Planet Database (Loh *et al.*, 2005), containing spatially explicit data for 7826
89 populations of 2667 vertebrate species, across the seven continents and all major

90 ecosystems. To test the influence of life history on the predisposition of species to be
91 exposed to multiple threats, we supplemented the threat data with traits which are
92 broadly available and comparable across different taxa: body mass, trophic level,
93 and habitat specificity. To test the influence of environmental factors, we also
94 supplemented the data with human population density, latitude, and system
95 (freshwater, marine or terrestrial) as proxies. We then used multilevel Bayesian
96 models to determine which factors have the strongest influence on the predisposition
97 of populations to be exposed to multiple threats.

98 **Materials and Methods**

99 *Threats data*

100 To determine the number of threats vertebrate populations are exposed to, we used
101 the Living Planet Database (LPD hereafter). The LPD
102 (http://livingplanetindex.org/data_portal) contains information on over 25,000
103 vertebrate populations around the world, comprising all vertebrate classes across
104 marine, freshwater, and terrestrial systems and providing population-specific
105 information such as spatial location, abundance, and threat exposure. Data are
106 collected from scientific literature, online databases, and grey literature published
107 since 1970, with at least two years of abundance; detailed inclusion criteria for the
108 LPD can be found in Collen et al., (2009). If the data source was a report of paper,
109 the entire article would be screened and the information was usually extracted from
110 the discussion. For population data shared directly from a data provider, threat
111 information was recorded in the database template form that was provided. A
112 population did not have to be in decline for a threat to be recorded.

113 Of the 25,054 population time series making up the LPD (including
114 confidential records), 7826 contained data relating to population threat exposure.
115 Based on information from the data source, for each publication we first identified
116 whether the population was threatened, not threatened or whether its threat status
117 was unknown. In this study, we only considered those populations for which threat
118 status information was available. Threats were identified as direct or indirect human
119 activities or processes that impacted the populations for at least 50% of the surveyed
120 years, according to the original source of the time series. If the population was
121 threatened, the number of threats at which the population was exposed was
122 recorded, from one to three. The information within the data sources was sometimes
123 quantitative, e.g. stating number of individuals hunted annually, but most often it was
124 reported in a qualitative way, e.g. a describing a general pattern of hunting that
125 impacts the populations. For this reason, and because the impact of the threat was
126 rarely quantified in the data sources, broad categories describing the threat to the
127 population were recorded.

128 *Body mass data*

129 Body mass data were collated from a number of pre-existing databases and the
130 scientific literature (see Table S1 for a full list of sources utilised). When minimum
131 and maximum values were given, maximum was taken to ensure measures were
132 most likely those of mature individuals, and thus in line with commonly reported
133 measures from the other databases. Most data sources did not contain sex-specific
134 body mass measurements; however, where sex was indicated an average of the
135 male/female record was taken to account for dimorphism. Finally, where multiple
136 records of the same species were present between datasets, the mean was taken,
137 with all records then standardised to reflect a common unit (g, grams).

138 For some taxa body mass data were unavailable, and so were estimated
139 using allometric regression equations using length measurements when possible
140 (Feldman *et al.*, 2016; Stark *et al.*, 2020). We used the general equation $W = a L^b$,
141 where W = body mass, L = length, and a and b are the intercept and slope of a
142 regression line over log-transformed weight-at-length data, respectively (Froese,
143 2009; Ripple *et al.*, 2017). This method was applied to 47 amphibian species using
144 snout to vent length (SVL) records and clade-specific regression coefficients in
145 FishBase (Froese, 2009; Santini *et al.*, 2018; Stark *et al.*, 2020). A further 320 fish
146 species' mass were estimated, based on maximum total length (TL) and regression
147 coefficients in FishBase (Froese, 2009). Where a measure other than TL was listed
148 (e.g., standard length (SL), fork length (FL)), regression coefficients were used to
149 convert these to total length before estimating body mass.

150 *Trophic level data*

151 We broadly classified species according to their diet in three main categories:
152 omnivores, carnivores, or herbivores. For amphibians, birds, mammals and reptiles,
153 we used the data from Etard *et al.* (2020). For bony and cartilaginous fishes we
154 inferred trophic levels from dietary information obtained from the parameter *Feeding*
155 *Type* contained in *FishBase* (Froese, 2009). Following the description in Froese
156 (2009) we considered: that herbivores were those species with between 2.0 and
157 2.19; carnivores had trophic levels equal to or greater than 2.8; and omnivores had
158 trophic levels between 2.2 and 2.79.

159 *Habitat breadth data*

160 We estimated the habitat breadth as the number of distinct habitats a species utilises
161 according to the IUCN habitat classification scheme (Daskalova *et al.*, 2020; Etard *et*

162 *al.*, 2020). For amphibians, birds, mammals and reptiles, we used the data available
163 in Etard et al. (2020). For bony and cartilaginous fishes the number of habitats was
164 estimated using the *rredlist* package (Chamberlain, 2017).

165 *Human population density data*

166 To estimate the human influence across different latitudes, we obtained human
167 population density (inhabitants/km²) information from HYDE3.2.001 (Hurt et al.,
168 2011). The human population density represents the number of human habitants per
169 km² per grid cells of 5' resolution. We used the country where the vertebrate
170 populations were studied to obtain the human population density data of each time
171 series.

172 *Final dataset*

173 When merging the above datasets with the data from the LPD, not all the species
174 had the same information available. The variables that were accessible for most of
175 the species was latitude (7826 time-series) and body mass (7492), followed by
176 human population density (7361), habitat breadth (6330) and trophic level (4833;
177 Figure 2a). When accounting for the combined availability of the variables, trophic
178 level was the variable with the less availability (Figure 2b). 1087 populations were
179 missing for the combined factors of trophic level and habitat breadth, 112 for trophic
180 level and body mass, 97 trophic level, body mass and habitat breath, 67 trophic level
181 and human population density, 48 trophic level, human population density and
182 habitat breadth and only 1 for trophic level, human population density and body
183 mass (Figure 2b). Because of the low numbers of shared data between some of the
184 factors, we fitted each model (see *Statistical Analysis*) using the dataset with the
185 maximum number of data for each factor. That is, the size of the data set used for

186 each of the models was different depending on the data availability for each of the
187 factors tested.

188 *Statistical Analysis*

189 To quantify the effects of latitude, body mass, habitat breath, human population
190 density, system, taxon, and trophic level we developed a set of multilevel Bayesian
191 models, using number of threats as a response variable. Body mass was log-
192 transformed and we used the absolute value of latitude. Body mass, latitude, habitat
193 breath, and human population density were added as numeric fixed effects and were
194 all standardised by subtracting the mean from each value and dividing by its
195 standard deviation. System, taxonomic class, and trophic level were considered as
196 categorical variables: the first having three levels, marine, terrestrial, and freshwater;
197 the second having five, amphibians, birds, bony fishes, cartilaginous fishes,
198 mammals and reptiles; and the third having three levels, omnivores, carnivorous and
199 herbivorous.

200 First, to test the effects of each of the aforementioned factors on the number
201 of threats at which vertebrate populations were exposed we fitted individual models
202 for each of the factors. Then, because we found that the system and taxonomic
203 group had an influence on the number of threats at which populations were exposed
204 (see Results), we fitted individual models for each combination of taxonomic group
205 and system. To account for the non-independence of repeated measurements for
206 each species we included a random intercept for each species. Given the lack of
207 phylogenetic signal in the number of threats at which the populations were exposed
208 (Figure S1) we did not include a phylogeny in these models. Each model with
209 categorical factors (e.g. system, taxon and trophic level) was fitted with a zero

210 intercept to allow us to determine absolute effect of each category of the factors. The
211 general structure of the models was:

212
$$y = \text{Normal}(\mu, \sigma^2), \text{ eq 1}$$

213
$$\mu = \alpha_{\text{species}} + \beta_{\text{Factor}}, \text{ eq 2}$$

214
$$\alpha_{\text{species}} \sim \text{Normal}(\bar{\alpha}, \sigma_{\text{species}}), \text{ eq 3}$$

215 We set weakly informed priors:

216
$$\mu \sim \text{Normal}(0,1), \text{ eq 4}$$

217
$$\bar{\alpha} \sim \text{Normal}(0,1), \text{ eq 5}$$

218
$$\beta_{\text{Factor}} \sim \text{Normal}(0,1), \text{ eq 6}$$

219
$$\sigma_{\text{species}} \sim \text{Exponential}(1), \text{ eq 7}$$

220 All models were fitted using the brms package v2.1.0 (Bürkner, 2017) in R
221 v4.0.0 (R Core Team, 2020). Models were run for 10000 iterations, with a warmup of
222 1000 iterations. Convergence was assessed visually by examining trace plots and
223 using Rhat values (the ratio of the effective sample size to the overall number of
224 iterations, with values close to one indicating convergence).

225 **Results**

226 *General models*

227 The number of threats which populations are exposed to is affected by a number of
228 factors (Figure 3). Among all the systems, freshwater and terrestrial species are

229 exposed to a higher number of threats (Figure 3a; Table S3). Reptiles are the
230 taxonomic class exposed to the highest number of threats, followed by amphibians,
231 birds, mammals, cartilaginous fishes, and then bony fishes respectively (Figure 3b;
232 Table S3). All trophic levels show similar degree of exposition to multiple threats,
233 with omnivores slightly less at risk than carnivores or herbivores (Figure 3c; Table
234 S3). Across all taxa and systems there is low evidence for the influence of body
235 mass on the number of threats (Figure 3d; Table S3). On the contrary, latitude has a
236 clear effect on the number of threats, with populations at higher latitudes being
237 exposed to a lower number of threats (Figure 3e; Table S3). However, human
238 population densities have a less clear effect, with a low certainty that the effect size
239 is different to zero (Figure 3f; Table S3). Finally, there is moderate evidence that
240 species with larger habitat breadth are exposed to a lower number of threats (Figure
241 3g; Table S3).

242 *System and taxa models*

243 The influence of body mass on the number of threats to which populations are
244 exposed varies across different systems and taxa (Figure 4). The number of threats
245 decreases with body mass in amphibians and reptiles independently of the system
246 they inhabit (Figure 4; Table S4). However, these estimates are highly uncertain for
247 freshwater amphibians and reptiles, and marine reptiles (Table S4). For all the other
248 taxonomic groups and systems, the number of threats increases with body mass
249 (Figure 4; Table S4), with high uncertainty in freshwater birds, freshwater and marine
250 bony fishes, and marine mammals (Table S4).

251 In line with the results of the general models, for most systems and taxa the
252 number of threats decreases at higher latitudes (Figure 5). However, for some

253 system and taxa combinations (notably terrestrial amphibians, birds, marine bony
254 fishes, marine cartilaginous fishes, and marine reptiles) the slope estimates are
255 again uncertain (Table S5). Our results also suggest that the number of threats could
256 increase with latitude in freshwater amphibians, freshwater mammals, and terrestrial
257 reptiles, although again these estimates were highly uncertain (Table S5).

258 **Discussion**

259 Identifying the factors determining the predisposition of species to be exposed to
260 multiple threats is crucial to maintain biodiversity (Gunderson *et al.*, 2016; Maxwell *et*
261 *al.*, 2016). To date, most studies have focused on identifying the factors that make
262 species more prone to extinction, rather than to multiple threats (Purvis *et al.*, 2000;
263 Cardillo *et al.*, 2005; Atwood *et al.*, 2020). Consequently, we currently lack
264 understanding of the (a)biotic factors which predispose species to multiple threats,
265 what could help pre-emptively design conservation actions. Here, using a global
266 collation of threat, trait, and geographic data from vertebrate populations, we show
267 that a suite of factors can be used to anticipate the number of threats which
268 vertebrate populations are exposed to. Among these, latitude and body mass are the
269 most readily available and with a strong predictive power. These results are the first
270 necessary step to develop predictive approaches to anticipate the number of threats
271 impacting wildlife populations using minimal data.

272 Latitude proved a strong predictor of the number of threats which populations
273 are exposed to. Although we hypothesised that the potential reason for this pattern
274 could be that the largest number of people live in lower latitudes (Kummu & Varis,
275 2011; Figure S4), human population density was a weak driver of threat number.
276 Human population density has long been considered a proxy for anthropogenic

277 disturbance factors (Santini *et al.*, 2017), and arguably the main cause for the
278 ongoing sixth mass extinction event (Ceballos *et al.*, 2020). This premise is based on
279 the assumption that areas with high human density increase the numbers of threats
280 to populations, driving populations beyond the point of recovery (Symes *et al.*, 2018).
281 However, our results suggest that human population density fails to capture the
282 patterns of threats distribution in our global data, and that latitude encapsulates
283 additional latent predictors which predispose populations to be impacted by multiple
284 threats.

285 Global and local threats are distributed unevenly across the planet (Bowler *et*
286 *al.*, 2020). For instance, our results suggest that terrestrial and freshwater species
287 are exposed to a higher number of threats compared to marine ones. These findings
288 are in line with the millennia-long human impacts of terrestrial and freshwater
289 systems (McCauley *et al.*, 2015; Van Der Kaars *et al.*, 2017), but may also reflect the
290 difficulty of monitoring species in marine environments. In addition, the presence of
291 threats affecting species can vary within and across countries (Harfoot *et al.*, 2021),
292 often in relation to local governmental conservation policies (Barnes *et al.*, 2016;
293 Amano *et al.*, 2018). Climate change also shows complex spatial patterns, with some
294 mid-latitude regions projected to experience the highest increase in the temperature
295 of the hottest days, while the Arctic is expected to suffer the highest increase in the
296 temperature of the coldest days (IPCC, 2021). In these areas, where the impacts of
297 climate change are likely to become more intense, the interaction with other threats
298 is likely to increase in the coming decades (Bennett *et al.*, 2015). Given the
299 complexity of accounting for such multiple spatial drivers, latitude can provide a
300 simple proxy for multiple threats exposition.

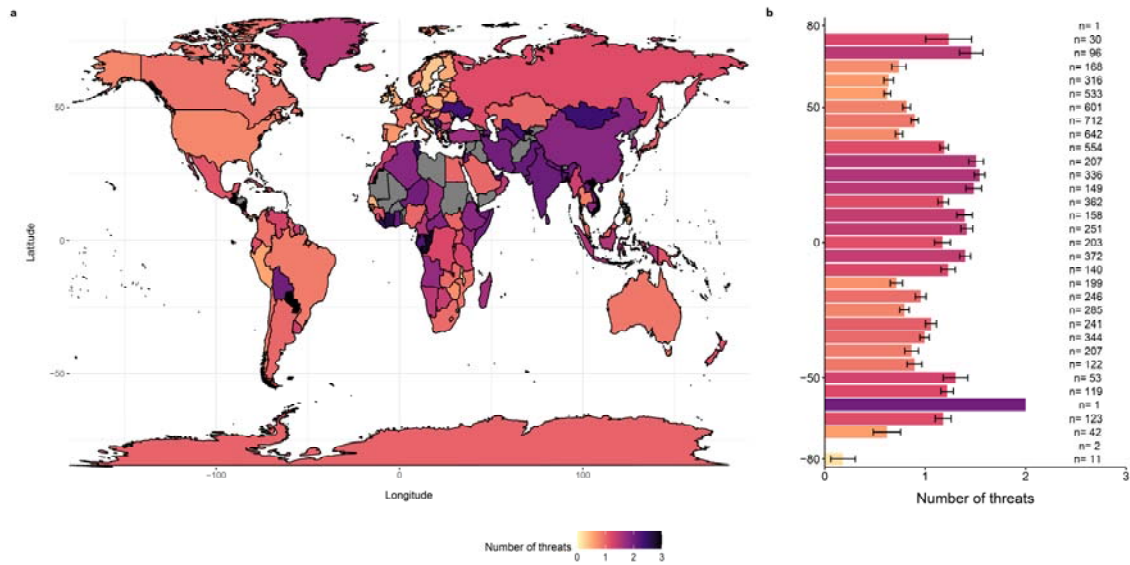
301 We also show that in most vertebrate groups larger species are exposed to a
302 greater number of threats. The greater vulnerability of larger species is often
303 attributed to different intrinsic and extrinsic factors (Fisher & Owens, 2004; Cardillo *et*
304 *al.*, 2005). For instance, larger species are disproportionately targeted for exploitation
305 and more affected by invasive species (Bennett & Owens, 1997; Duncan *et al.*,
306 2002). Also, species with larger body size often occupy higher trophic levels, which
307 are also associated with higher extinction risk (Böhm *et al.*, 2016; Collen *et al.*,
308 2011). However, our results support recent research (Atwood *et al.*, 2020) showing
309 that species with higher trophic levels are not necessarily exposed to a larger
310 number of threats. Because body size was the most readily available trait, and its
311 tight link with the life history of species (Gaillard *et al.*, 1989), conservation status
312 (Ripple *et al.*, 2017) and ecological processes (White *et al.*, 2007), our findings
313 validate its use as a proxy for multiple threats exposition.

314 Amphibians and reptiles were the exception to the abovementioned pattern,
315 with body size being inversely related with number of threats. These pattern may be
316 driven by the nature of the threats affecting them. Both groups are mostly affected by
317 habitat loss, while mammals, birds and fishes are mostly impacted by exploitation
318 (Díaz *et al.*, 2019; Harfoot *et al.*, 2021). While larger individuals are often the target
319 of exploitation (Pauly *et al.*, 1998; Duncan *et al.*, 2002), the lower dispersal ability
320 and more constrained range sizes of small organisms could make them more
321 vulnerable to habitat loss (Cardillo *et al.*, 2008; González-Suárez *et al.*, 2013; Pacifici
322 *et al.*, 2017). Moreover, our results suggest amphibians and reptiles are facing the
323 largest number of threats, mirroring recent reports suggesting that these are the
324 vertebrate groups experiencing the most dramatic decline (Daskalova *et al.*, 2020).
325 Despite these findings, amphibians and reptiles are the most understudied

326 vertebrate groups in global conservation assessments (Alroy, 2015). For instance,
327 about 25% of known reptiles and amphibian species are classified as data deficient
328 by the IUCN Red List (IUCN, 2021). Hence, our results adds evidence for the need
329 of global efforts to study these groups, to better understand the causes of their
330 decline and develop effective conservation policies (Gibbons *et al.*, 2000). Our
331 findings also highlight the importance of understanding the mechanisms that
332 predispose reptiles and amphibians to multiple threats as a key area for future
333 research.

334 Although our research uses the largest compilation of population-level threat
335 data, there are still gaps in our understanding of the drivers of multiple threats. While
336 the LPD draws from published literature, this also means its data inherits any biases
337 derived from its sources. This has resulted in the over-representation of well-studied
338 regions and taxa, with research also inclined towards populations within protected
339 areas and terrestrial ecosystems (Loh *et al.*, 2005; McRae *et al.*, 2017). In addition,
340 while here we only focused on the number of threats, their type (e.g. exploitation,
341 habitat loss), intensity and/or frequency also has a major influence on the population
342 trends and this information was not readily available. For instance, different threats,
343 or the same threat with different intensity and/or frequency, might interact in different
344 ways, causing different impacts on the populations (Darling & Côté, 2008; Côté *et al.*,
345 2016; Orr *et al.*, 2020). Not only that, but the timing (when threats impacted the
346 population over the time series) and the synchrony (the overlap on time between
347 multiple threats) of the threats might have a strong influence on populations
348 (Johnstone *et al.*, 2016; Jackson *et al.*, 2021). The limited data available on
349 disturbances nature and timing at the population-level hampered including such
350 information in our analyses. To this end, we advocate explicit reference to threats

351 within ecological research to enable the expansion of current databases and to keep
352 multiple threats processes at the forefront of developing research.



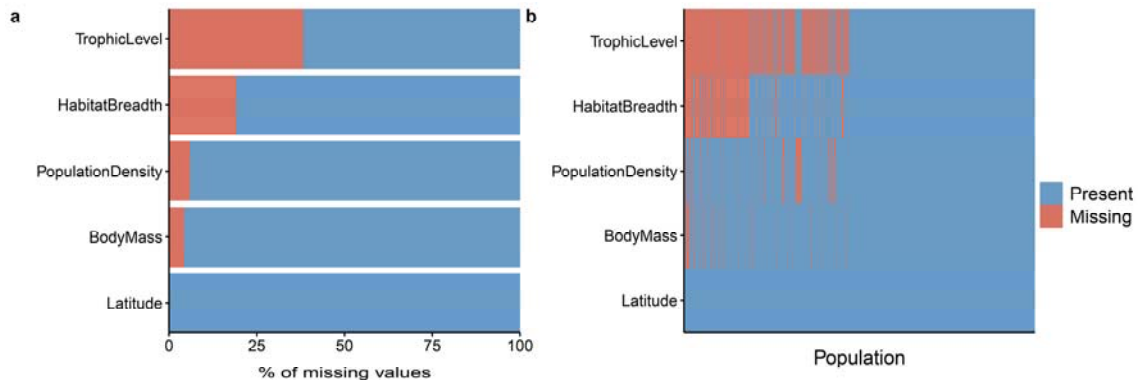
353 **Figure 1. Global distribution of the mean number of threats by country and**
354 **latitude.** Global overview of the mean number of threats, (a) within each country and
355 (b) by latitude with numbers alongside bars representing sample sizes for each 5°
356 latitude bin.
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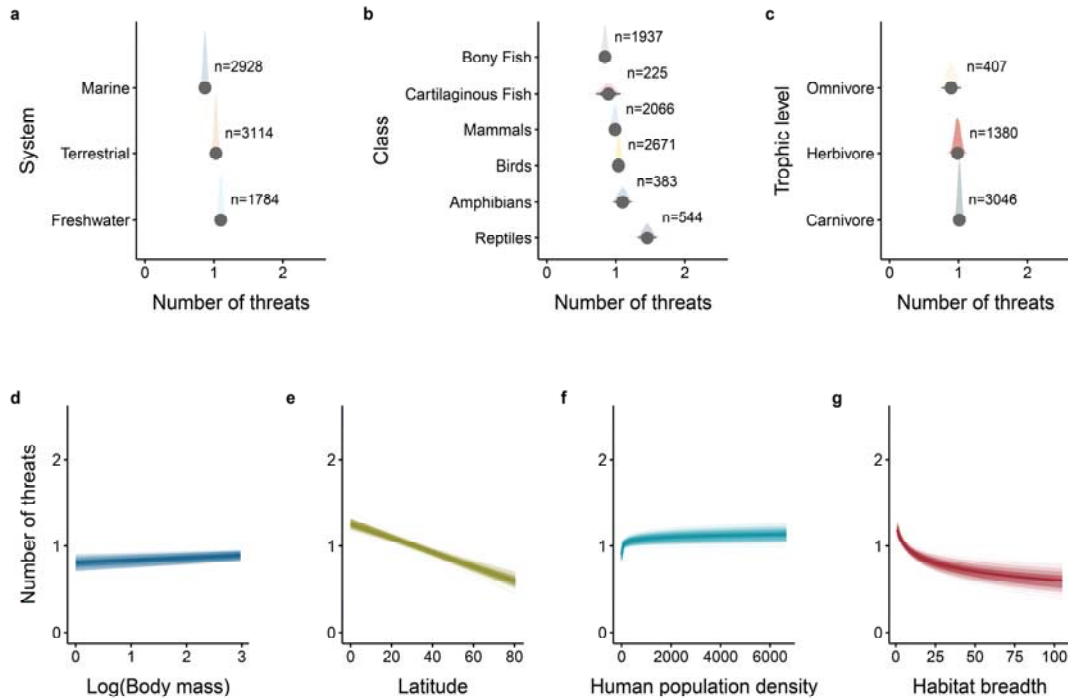


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363 **Figure 2. Patterns of missingness in the data.** The variable the most available for
364 the species in the subset of data from the Living Planet Database containing threat
365 information was body mass. (a) Proportion of missing and present values of the
366 different variables. (b) Total presence and absence of the different variables across
367 the dataset.

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Figure 3. Factors influencing the number of threats at which vertebrate populations are exposed. (a-c) density plots of posterior distributions for the

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effects of (a) system, (b) taxonomic class, and (c) trophic level, on the number of

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threats. Each density plot is based on 1,000 samples from the posterior distribution

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of the slope estimates (Table S2). The reported values are the highest posterior

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density median values (circles), with 80% (thickest bars), 90%, and 95% (thinnest

376

bars) uncertainty intervals. **n** represents the sample size for that given threat in the

377

original dataset. (d-g) predictions of the number of threats as a function of the (d)

378

body mass (g), (e) latitude (absolute value), (f) human population density and (g)

379

habitat breadth. Lines represent the predictions from the multilevel Bayesian models

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(Table S2), where thin lines correspond to the predictions drawn from each of the

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250 posterior samples of the model, and the thick line represents the mean outcome

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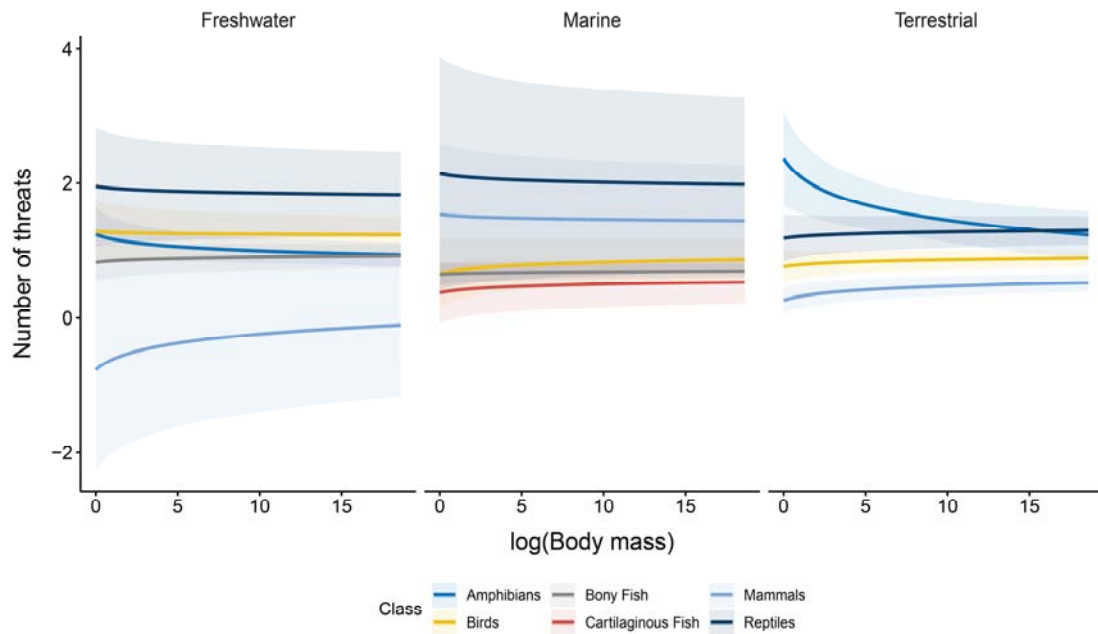
of the model.

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388 **Figure 4. Model predictions of threat number as a function of body mass.**

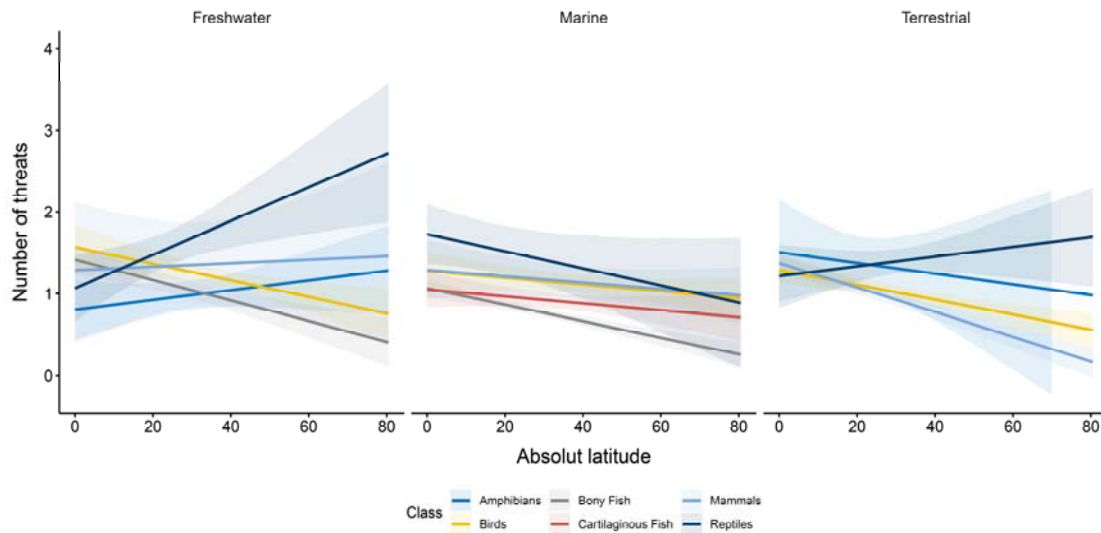
389 Multilevel Bayesian model predictions of the number of threats as a function of body
390 mass (in grams). Ribbons display 95% confidence intervals.

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Figure 5. Latitudinal trends of the number of threats. Multilevel Bayesian model

397 predictions of the number of threats as a function of the absolute value of latitude.

398 Ribbons display 95% confidence intervals.

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