# 1 Body mass and latitude as global predictors of vertebrate

- 2 populations exposure to multiple threats
- 3 **Running title:** Global predictors of multiple threats
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curate and maintain the Living Planet Database. N.N. collated body mass data. P.C.
and N.N. performed analyses and produced the manuscript. All co-authors
contributed substantially to revisions.

17 Data and materials availability: The Living Planet Database (excluding confidential 18 records) is available at: www.livingplanetindex.org/data\_portal. The code and data 19 used in this study will be available at Zenodo upon acceptance and is available for 20 reviewers in <u>https://github.com/PolCap/LPD\_Threats</u>.

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## 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.

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

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# 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

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

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

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

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

165 Human population density data

To estimate the human influence across different latitudes, we obtained human population density (inhabitants/km<sup>2</sup>) information from HYDE3.2.001 (Hurtt *et al.*, 2011). The human population density represents the number of human habitants per km<sup>2</sup> per grid cells of 5' resolution. We used the country where the vertebrate populations were studied to obtain the human population density data of each time 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 the187 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	$y = Normal(\mu, \sigma^2), eq 1$
213	$\mu = \alpha_{Species} + \beta_{Factor}$ , eq 2
214	$\alpha_{species} \sim Normal(\bar{\alpha}, \sigma_{species}), eq 3$
215	We set weakly informed priors:

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

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

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

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

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

225 Results

226 General models

The number of threats which populations are exposed to is affected by a number of 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).

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

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

Latitude proved a strong predictor of the number of threats which populations are exposed to. Although we hypothesised that the potential reason for this pattern could be that the largest number of people live in lower latitudes (Kummu & Varis, 2011; Figure S4), human population density was a weak driver of threat number. 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 disproportionally 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 345 al., 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.



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

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

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370 371 Figure 3. Factors influencing the number of threats at which vertebrate 372 populations are exposed. (a-c) density plots of posterior distributions for the 373 effects of (a) system, (b) taxonomic class, and (c) trophic level, on the number of 374 threats. Each density plot is based on 1,000 samples from the posterior distribution 375 of the slope estimates (Table S2). The reported values are the highest posterior 376 density median values (circles), with 80% (thickest bars), 90%, and 95% (thinnest 377 bars) uncertainty intervals. n represents the sample size for that given threat in the 378 original dataset. (d-g) predictions of the number of threats as a function of the (d) 379 body mass (g), (e) latitude (absolute value), (f) human population density and (g) 380 habitat breadth. Lines represent the predictions from the multilevel Bayesian models 381 (Table S2), where thin lines correspond to the predictions drawn from each of the 382 250 posterior samples of the model, and the thick line represents the mean outcome 383 of the model.



Figure 4. Model predictions of threat number as a function of body mass.
Multilevel Bayesian model predictions of the number of threats as a function of body

390 mass (in grams). Ribbons display 95% confidence intervals.





Figure 5. Latitudinal trends of the number of threats. Multilevel Bayesian model
predictions of the number of threats as a function of the absolute value of latitude.
Ribbons display 95% confidence intervals.

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