1 # Species traits predict extinction risk across the

2 # Tree of Life

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Summary

Biodiversity is eroding at unprecedented rates due to human activity[1]. Species' trajectories towards extinction are shaped by multiple factors, including life-history traits[2] as well as human pressures[3]. Previous studies linking these factors to extinction risk have been narrow in their taxonomic and geographic scope[4], thus limiting the ability for identifying global predictors. We studied the relation between 12 traits and the extinction risk of almost 900 species representing 15 groups across the tree of life (vertebrates, invertebrates and plants) at a global scale. We show that threatened species share narrow habitat breadth, poor dispersal ability, low fecundity, small altitudinal range, and are affected by a large human footprint. Other traits either show contrasting responses among groups (body size, offspring size, and change in human footprint), or relations were found for only a limited number of taxa (generation length, diet breadth, microhabitat). Our study suggests that in the absence of data on the precise distribution and population trends of species, traits can be used as predictors of extinction risk and thus help guide future research, monitoring and conservation efforts.

Main

We are currently facing the sixth mass extinction at the planetary scale. Species are becoming extinct at rates 1000 to 10000 faster than background extinction rates[1]. Not only species, but functions they provide and that benefit humanity are at risk, with unpredictable consequences towards our own well-being. And yet, we are mostly unaware of what species are most at risk and why, with many becoming extinct even before description: the Centinelan extinctions. This lack of knowledge can be partly circumvented if we know which characteristics, or traits, are common to endangered species and which allow species to be resilient to anthropogenic change.

The vulnerability of species to extinction largely depends on their life-history strategies (intrinsic traits), and biotic and abiotic conditions species face (extrinsic traits)[2,3,5]. All studies linking the extinction risk of species to intrinsic and extrinsic factors have focused, however, on few species or narrow geographic ranges. Due to societal and knowledge biases[6,7], well-studied groups include vertebrates, namely mammals[2,3] and birds[8,9] and the best-known region is the Palearctic realm[4,10]. The relations between traits and extinction risk across the tree of life have never been analyzed at a global taxonomic and geographic scale.

A global trait analysis

48   Here, we compiled a dataset of 12 traits commonly related to extinction risk (Table S1): body size,

49   offspring size, fecundity, generation length, diet breadth, trophic level, dispersal ability, microhabitat,

50   habitat breadth, altitudinal range, human footprint within the species range as of 2009[11], and the

51   relative change in human footprint over a period of 16 years (1993-2009)[11]. Traits were quantified for

52   874 species in five groups of each of vertebrates (mammals, birds, reptiles, amphibians, and fishes),

53   invertebrates (dragonflies, butterflies, grasshoppers, spiders and snails) and plants (bryophytes, ferns,

54   gymnosperms, monocots and legumes) (Table S2-4). Each of the 15 taxonomic groups included 10

55   species in each of six biogeographic realms, five threatened and five non-threatened, as long as data on

56   extinction risk was available, namely global assessments in the International Union for the Conservation

57   of Nature (IUCN) Red List of Threatened Species (see methods, Table S5). We used these data to identify

58   global predictors of extinction risk across taxa and space.

59   For all groups, we first standardized trait values to ensure comparability. We then inspected the

60   existence of relationships between traits with pair plots and Spearman rank correlations (Fig. S1). As no

61   strong correlations were found we used all traits in subsequent analyses. We modelled the extinction

62   risk as a binary response variable (threatened versus non-threatened following the IUCN Red List

63   categories: threatened: EX, CR, EN, VU and NT, non-threatened: LC; note that our grouping is different

64   from the usual for IUCN). Significant differences between threatened and non-threatened species were

65   tested both within and for all taxonomic groups. Within groups, significant differences were detected

66   with null models, by comparing the mean and the standard deviation of trait values of threatened

67   species with a distribution of simulated data, sampled across all the possible values for that trait and

68   group. We applied Bayesian mixed models to detect significant relationships between traits and

69   extinction risk across taxa. The mixed models were used to relate threat status against each trait, while

70   controlling for the non-independent effects of taxonomy (using the taxon grouping as a random effect in

71   the models). We inferred significance in either positive or negative relationships between the extinction

72   risk status and each trait when 95% of the posterior distributions of the estimates were not intercepting

73   the zero value. We also related the geographical range size of species to extinction risk (Fig. S2), but we

74   excluded it from further analyses because this trait is used to determine extinction risk in most IUCN Red

75   List assessments. Moreover, range size itself may often not be the driver, but a consequence of

76   trajectories towards extinction, such as population size and trend. Range and population size could only

77   be used without circular reasoning if pre-disturbance values were known, which is almost invariably not

78   the case.

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80   Predicting extinction risk

81   Five traits were found to be consistently (similar sign across groups) and significantly (p < 0.05, or almost

82   significantly, p < 0.1) related with extinction risk (Table 1): habitat breadth, dispersal ability, fecundity,

83   altitudinal range, and human footprint.

84   The association between habitat breadth and extinction risk was negative, highly significant (Table 1)

85   and found across all taxa (Fig. 1). Species occurring in a narrower range of habitats have fewer

86   opportunities to expand to and survive in alternative suitable living conditions and are consequently

87   more likely to be threatened[12,13]. In fact, habitat breadth, together with geographical range size and

88   abundance, is one of the three classical dimensions of rarity[14]. In a previous meta-analysis[4] habitat

89   breadth was the only factor, besides geographical range size, that was consistently found to correlate

90   with extinction risk. This trait should be very relevant in the face of generalized natural ecosystem

91   destruction with consequent habitat loss for numerous species. With increasing levels of habitat loss

92   occurring across all biomes, species that adapt to alternative habitat types will inevitably fare better.

93   We identified a negative association between dispersal ability and extinction risk (Table 1), indicating

94   that species with poor dispersal ability are more likely to be at risk than those dispersing easily. The

95   pattern was common across tested taxa (mammals, birds, dragonflies, grasshoppers, spiders, and

96   bryophytes) but stronger in grasshoppers, spiders and bryophytes (Fig. 1). In the face of localized

97   threats, species with a better capacity to colonize new areas have a lower risk of extinction[15,16].

98   Consequently, species groups with high dispersal capability, such as birds and dragonflies, often have a

99   lower number of threatened species compared to other groups. In addition, shifts in species'

100   distributions caused by climate change are likely to exacerbate the extinction of poor dispersers[17,18]. This

101   trait might be very relevant in predicting which species will be able to adapt to increasing levels of

102   fragmentation of natural habitats. As fragmentation is one of the consequences of habitat loss, its

103   effects are increasing at global scales, and having good dispersal ability might prove crucial to the

104   survival of many species.

105   The model relating fecundity to extinction risk included mostly data from vertebrates (mammals, birds,

106   reptiles, amphibians, and fishes) and one invertebrate group (snails, table S3). Fecundity was negatively

107   associated with extinction risk (Table 1), indicating that species with lower reproductive output are more

108   at risk, with the strongest signal for mammals (Fig. 1). Populations of species with low reproductive

109   output are presumed to decline in the face of demographic threats, due to diminished capacity to

110   compensate for higher mortality rates[19]. Mammal families with higher proportions of species threatened

111   by hunting and fishing have smaller litter sizes[20]. Although our model for fecundity includes no plant

112   species due to lack of data, it is likely that species with lower reproductive output are also more

113   threatened in plants[21]. Species with higher reproductive output will probably fare better in the future

114   independently of any particular threat.

115   Altitudinal range, often a measure of climatic tolerance, was marginally negatively correlated with

116   extinction risk (Table 1). The modest significance of this trait could be a consequence of the small

117   number of species for which data were available. The signal was stronger for bryophytes and, to some

118   extent, butterflies (Fig. 1). Species with lower climate tolerance have fewer chances to be able to exploit

119   new ranges for survival, and thus confronting higher extinction risk[22]. This trait in particular might be

120   very relevant during the current climate emergency, as it might indicate which species will be able to

121   adapt in the future to changing temperature and precipitation patterns.

122   The human footprint index was positively related to extinction risk (Table 1), indicating that species with

123   higher mean human pressure within their ranges are more likely to be threatened. The pattern was

124   consistent across taxa, but stronger in birds, dragonflies, snails and bryophytes (Fig. 1). This result was

125   expected and reflects the fact that most organisms, independently of their traits, are sensitive to human

126   pressure. Synanthropic or bred/cultivated species are obvious exceptions, benefiting from human

127   pressure across their range[23].

128   While the previous five traits were found to be global predictors of extinction risk, some were found to

129   differ in their signal according to the species group (Supplementary discussion). They either showed

130   contrasting responses between groups (body size, offspring size, and change in human footprint) or

131   relations were found for only a limited number of taxa (generation length, diet breadth, microhabitat).

132   In some cases a similar trait might in fact reflect different competitive advantages depending on the

133   group, such as larger body sizes being targeted by hunting in the case of mammals and birds, but

134   constituting a competitive advantage for many plant taxa[4]. In other cases, either data are missing or

135   have little contrast for some taxa, preventing general trends to be found. Future studies with more data

136   might help clarify and further support some of the trends already found.

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Future directions

139   In this work, we were able to study the relationships between all the main traits found in the past to

140   influence extinction risk, and the threat level of species covering numerous branches of the tree of life

141   from many parts of the world. Notable exceptions are fungi and marine taxa, for which knowledge is

142   scarcer. Inevitably, there are still gaps in both the knowledge available on traits (e.g. fecundity, dispersal

143   ability) in some taxa and of geographic coverage (mainly tropical species) in others. Yet, our results are

144   not only robust, but also generalizable for a wide spectrum of terrestrial organisms.

145   Our study supports the view that extinctions do not affect species randomly, but extinctions are rather

146   mediated by species traits[23]. We show that across the tree of life, species with a higher extinction risk

147   are those with narrow habitat and climatic niches, poor dispersal capacity , and low fecundity. On top of

148   this, the presence of human activity increases the probability that the species become threatened.

149   These results emphasize two different aspects of extinction: firstly, with species extinctions, we might

150   not only lose species but also their particular functions in ecosystems, which in turn, could lead to

151   further co-extinctions. Secondly, high human impact on ecosystems is generally not compatible with

152   species survival.

153   With the understanding of key biological factors contributing to species vulnerability, we will be able to

154   identify species that are more prone to extinction, even in the absence of data that are most commonly

155   used but often unavailable, such as geographic range size or current population trends. These two

156   factors have been considered as the most important for extinction assessments according to the IUCN

157   Red List criteria. Yet, often they are unknown or biased, with figures above 50% Data Deficient species

158   reported for invertebrates, which represent the vast majority of species[24]. Using traits as surrogates for

159   extinction risk will help reduce this knowledge gap, allowing prioritization of future research, monitoring
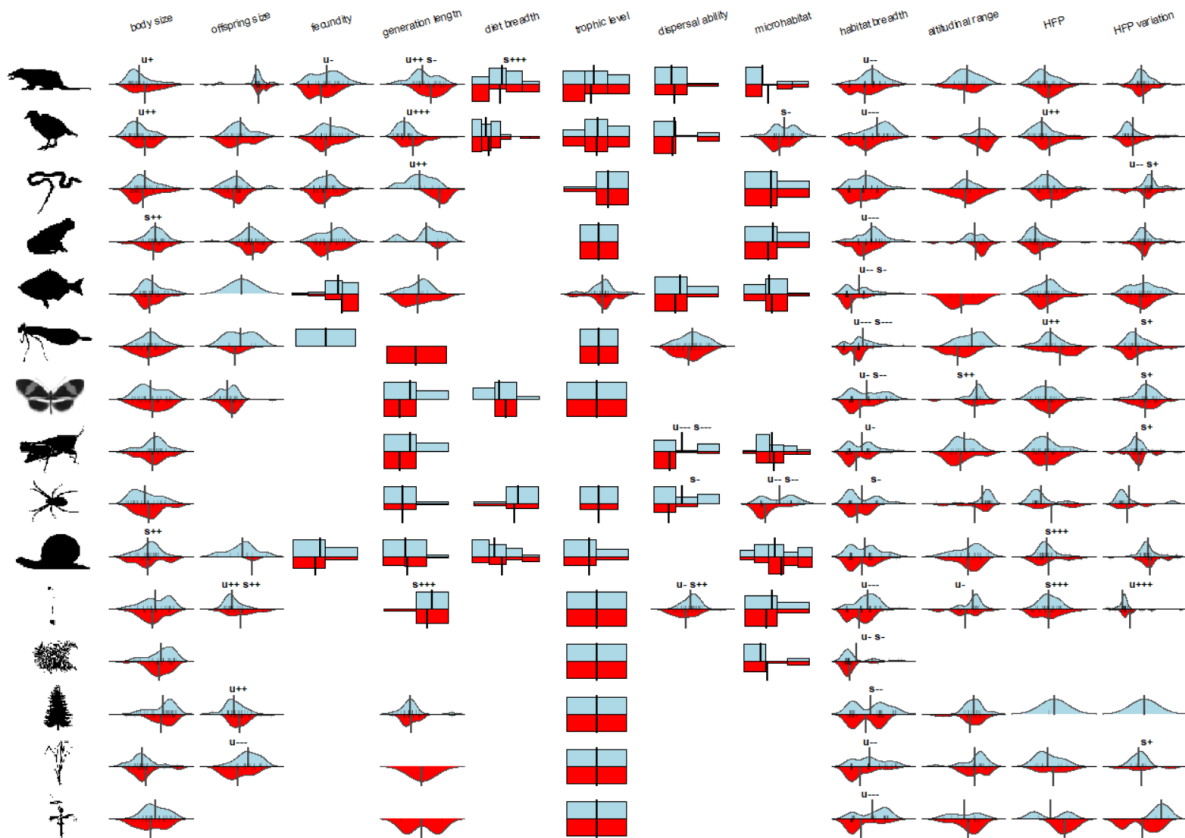
160   and conservation efforts.

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Figure 1: Beanplots of density of trait values between non-threatened (blue, upper side) and threatened (red, lower side) species. Small vertical bars represent one species' value; darker bars indicate several species with the same trait value. The large vertical bar is the mean trait value. Null models show whether the mean (u) or standard deviation (s) of trait value of threatened species is higher (+++, ++, +) or lower (---, --, -) than expected. Significance codes: +++ or --- x < 0.01; ++ or -- 0.01 <= x < 0.05; + or - 0.05 <= x < 0.1.

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175 **Table 1:** Results of the MCMCglmms relating the value of each trait with extinction risk.

Trait	Sign	pMCMC	N species
Body size	0	0.666	825
Offspring size	0	0.182	438
Fecundity	-	0.0467	333
Generation length	0	0.384	340
Diet breadth	0	0.77689	214
Trophic level	0	0.689	266
Dispersal ability	-	0.00543	335
Microhabitat	0	0.802	545
Habitat breadth	-	<0.0001	874
Altitudinal range	-	0.0653	314
Human footprint	+	0.000857	561
Change in Human footprint	0	0.73131	561

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Supplementary materials

Methods

Because our goal was to find general trends, we selected 1) species belonging to a variety of taxonomic groups covering most of the multicellular tree of life (vertebrates, invertebrates and plants), and 2) traits that were generalizable across taxa, not considering others that would be specific for some groups (e.g., brain size).

Selection of species

As a first step in selecting the species, we identified a range of taxa that would capture a wide range of life-histories and geographical locations. We restricted our species pool to the species already assessed for the global IUCN Red List of Threatened Species[TM] (www.iucnredlist.org), excluding those that were assessed as Data Deficient. We also restricted our analysis to the multicellular branch of the tree of life. Since very few assessments of fungi exist, we also excluded these. Finally, we restricted the analysis to terrestrial and freshwater species given that the few marine species assessed would require different stratified sampling and analyses. We therefore chose five vertebrate, five invertebrate, and five plant groups. Vertebrate groups comprised "Mammals" (Class: Mammalia), "Birds" (Class: Aves), "Reptiles" (Class: Reptilia), "Amphibians" (Class: Amphibia) and freshwater "Fishes" (Class: Actinopterygii). The invertebrate groups comprised "Dragonflies" (Order: Odonata, including damselflies), "Butterflies" (Suborder: Rhopalocera), "Grasshoppers" (Order: Orthoptera), "Spiders" (Order: Araneae), and land "Snails" (Class: Gastropoda). In the selection of the plants we followed the recent baseline study[25] with the following embryophytes (land plants): "bryophytes", excluding hornworts (Divisions: Bryophyta and Marchantiophyta), "pteridophytes " (Classes: Lycopodiopsida, Polypodiopsida), "Gymnosperms" (Classes: Pinopsida, Cycadopsida, Gnetopsida), "Monocots" (Class: Liliopsida), and finally the "Legumes" (Order: Fabales) serving as a representative of the largest group of plants, eudicots (Table S5).

To guarantee global spatial representativeness of the dataset, we selected, whenever possible, 10 species per group from each of six biogeographic realms (Table S5). Of the 10 species, we randomly selected from the global IUCN database equal numbers of threatened (one of each of Near Threatened, Vulnerable, Endangered, Critically Endangered or Extinct) and non-threatened (five Least Concern) species.

206   As not all taxa have global coverage in the IUCN Red List, we had to restrict our dataset to smaller

207   regions in the case of butterflies, grasshoppers, spiders, snails, and bryophytes. All species of spiders,

208   snails and bryophytes were selected from Europe, due to very low numbers of assessments from other

209   geographical realms. For grasshoppers, most assessments came from the Afrotropics and Palearctic, and

210   therefore 30 species were selected from each. In butterflies, no Nearctic species were included due to

211   unavailability of data from that group by the time we made the selection (IUCN version 2018-2), and

212   very few from the Indo-Malay region were included. In total, our dataset included 874 species.

Selection of traits

214   As predictors, we selected intrinsic and extrinsic traits of species whose relationship with extinction risk

215   has been hypothesized and tested in previous studies for some taxonomic groups (Table S1) but

216   excluded traits that are specific to a few taxa only (e.g. brain size). Intrinsic trait data were compiled

217   from the literature, including existing trait databases, and in some cases also measurements of

218   photographs of pinned specimens (usually the holotype or paratype of species) available online.

219   Different taxonomic groups differ in their life-history and ecological strategies. Therefore, for each

220   intrinsic trait, we selected trait "proxies" (Table S3), which are analogous traits[26] with the same function

221   across taxa but measured differently. The choice of proxies depended on the suitability of the trait as a

222   proxy (e.g., body length is a better proxy of body size than body mass in birds, due to large variation

223   within a species between seasons), and on the availability of data for that trait (e.g. dispersal ability of

224   birds and mammals being a binary trait distinguishing migratory and/or nomadic species from those not,

225   an ordinal trait reflecting the propensity to balloon in spiders and a continuous trait of seed size in

226   plants).

227   To measure the human footprint pressure and the change in human footprint within each species'

228   range, we used recently constructed $1km^2$ resolution raster maps of human footprint available for the

229   years 1993 and 2009[11]. In these maps, each raster cell is characterized by a score of cumulative human

230   footprint pressure, ranging from 0 (no human impact) to 50 (very high human impact). The score of a

231   grid cell is a function of the presence and/or magnitude of eight types of pressures: the extent of built

232   environments, human population density, electric infrastructure, crop lands, pasture lands, roads,

233   railways and navigable waterways[11]. To estimate the mean human footprint of 2009 across a species'

234   range, we averaged all grid cell values within each species polygon maps, retrieved from IUCN (see

235   below). To estimate the change in human footprint, we first constructed a map of the differences

236   between 2009 and 1993, with positive values indicating a positive change in human footprint (more

237   human impact in 2009 compared to 1993) and negative values indicating negative change, and then

238   averaged the scores across species' ranges. The species' range maps were obtained from the IUCN Red

239   List of Threatened Species. We only included maps with the following origin, presence, and seasonal

240   descriptors: "Native" or "Reintroduced"; "Extant", "Probably extant", or "Possibly extant"; and

241   "Resident", "Breeding season", "Non-breeding season" or "Seasonal presence uncertain".

242   When no trait data were available for the species, we used either the value of a closely related species

243   or the genus or family average; this latter approach was used when values for other taxa were available

244   in online trait databases. Genus and family averaging were never performed for binary data, habitat

245   breadth, altitudinal range, human footprint, change in human footprint, and geographical range size

246   variables.

247   Some groups lacked data completely for some traits, such as fecundity and offspring size for dragonflies

248   and spiders, and diet breadth for reptiles and amphibians. Trophic level was known for all species but in

249   some groups the trophic position resolution was finer (fishes), while for some others it was coarse or

250   invariant (dragonflies, spiders, plants).

251   Because offspring size is highly correlated with body size, we used instead a relative metric of offspring

252   size: the residuals of a regression between log(offspring size) and log(body size) within all groups.

253   Because the altitudinal range is often related to the geographical range size of species, we used the

254   residuals of a regression between log(altitudinal range) and the log(geographical range size).

255   The compiled dataset included data for 94% and 99% of the species for body size and habitat breadth,

256   respectively (Table S2). Particularly for invertebrate and plant species, data availability for some traits

257   was low, including offspring size (mean 50%, range 0% to 100%), fecundity (38%, 0-100%), generation

258   length (39%, 0-100%), diet breadth (24%, 0-100%), or dispersal ability (38%, 0-100%). The human

259   footprint and the change in human footprint were available for 64% of species, since species' maps are

260   available for many of the species on the IUCN website.

Trait transformation and standardization

262   We log-transformed count data (e.g. number of habitat types, number of diet types eaten), and

263   continuous data (body length, number of offspring), except the dispersal ability of dragonflies and

264   bryophytes, and residuals of offspring size and altitudinal range, since these traits were already log-

265   transformed when estimating their values. This ensured that the distribution of trait values followed a

266   near-normal distribution without observations spread far away from the main density of trait values. For

267   extinct species, which have geographical range sizes of 0 km^2, we replaced these 0's with 0.1, so that

268   log-transformation of these data points was possible. Likewise, altitudinal range values lower than 10m

269   were converted to 10m.

270 Within a given trait, the units and measurement scales were different across groups and it was

271 necessary to transform these data to guarantee comparability between taxa. All trait values within

272 groups were subject to a z-transformation, which includes rescaling of data (by dividing each data point

273 by the standard deviation) and recentering by subtracting the mean value from each observation. This

274 type of scaling preserves the mean and standard deviation of each trait.

Statistical analysis

276 We first modelled each trait separately (univariate models) per group. To check for significant

277 relationships between each trait distribution and extinction risk within groups, we ran null models. The

278 null model compared the mean and the standard deviation of the trait values of the threatened species

279 with the mean and standard deviation of 1000 null expectations when extracting the same number as

280 threatened species from the complete pool of threatened plus non-threatened. A deviation from the

281 null expectation was considered to have been met when either the mean or the standard deviation of

282 the threatened species were lower or higher than the 2.5th or the 97.5th percentiles of the null

283 distribution, in which case a significant negative or significant positive deviation was annotated

284 respectively.

285 To test the relation between individual traits and extinction risk across taxa we used generalized linear

286 mixed effect models (GLMMs), in which we controlled the effect of taxonomy by allowing a random

287 intercept and random slope dependent on the taxonomic group. Since our response variable was binary,

288 our GLMM consisted of a logistic regression. The GLMMs were modelled within a Bayesian framework,

289 using Monte Carlo Markov Chains with R package MCMCglmm[27]. We used the default priors of package

290 MCMCglmm, which are weak priors. We ran simulations with 50,000,000 iterations, excluding the first

291 1,000,000 (burn-in). To ensure good mixing of chains, we only saved every 1000th iteration (thinning).

292 With these parameters, we observed good mixing of chains and thus, good convergence of posterior

293 parameters' distributions.

294 The random terms in the model add a new assumption to the overall model, which is that taxonomic

295 groups are sampled from a larger population of possible taxonomic groups and that the intercepts and

296 slopes of each group follow a normal distribution of intercepts and slopes around the population means

297 of the intercept and slope. The association between the trait and the probability of being threatened

298 was considered to be strong when 95% of the posterior distribution of a trait was not intercepting zero,

299 and moderate for 90%. All statistical analyses were performed in R version 3.6.1[28]. Beanplots were done

300 with package beanplot[29] and pairwise plots with packages ggplot2[30] and GGally[31].

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Supplementary discussion

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304 The distribution of body size values differed between threatened and non-threatened species in birds,

305 amphibians, snails, and marginally in mammals (Fig. 1). Overexploitation might explain the trends for

306 mammals and birds, as larger species are direct targets of hunting[20,32]. Particularly for mammals, as size

307 increases the importance of life-history traits in determining extinction risk increases in relation to

308 extrinsic traits[33]. Larger species within these generally large body-sized taxa (compared with, e.g.,

309 insects) also require more resources and these might quickly dwindle to unsustainable levels[33]. In

310 amphibians and snails, the standard deviations of body size values of threatened species were

311 significantly greater than the null expectation (Fig. 1), indicating that a larger proportion of threatened

312 species occur at both ends of the body size distribution for these groups. The conservation status of

313 small body-sized organisms could be explained by a particular set of life-history traits that may

314 predispose them to naturally restricted range size and narrow habitat breadth[34].

315 After accounting for body size, the relative offspring size of organisms showed mixed signals across taxa,

316 with the only significant values being found for plant groups, albeit with opposing signals (Fig. 1). In

317 bryophytes and gymnosperms offspring size was positively correlated with extinction risk, while for

318 monocots this relationship was negative. The size of an offspring in relation to the body size is an

319 indication of the investment in reproduction. The trade-off is between small and numerous, or large and

320 scarce. Larger species tend to invest more in large offspring, to compensate for higher mortality during a

321 very long juvenile stage[35]. However, when environmental conditions change rapidly, investing in only a

322 few descendants might be a bad option due to low variability under unpredictability. For monocots the

323 negative relation might be because 19 species in the dataset are orchids, which are characterized by the

324 smallest seeds among plants[35]. Orchids have very specific requirements for survival (their seeds require

325 the presence of mycorrhizal fungi to germinate) and therefore this relationship might be spurious and

326 phylogenetically driven, even if orchids are in fact generally in higher threat categories than most other

327 plant groups.

328 The change in human footprint indicates the rate of increase or decrease of human footprint in species'

329 ranges, with higher positive values showing a greater increase in impact, and higher negative values

330 showing a greater decrease in impact. Its influence on extinction risk was diverse, with no congruent

331 pattern across taxa (Fig. 1). Threatened bryophytes were characterized by significantly larger positive

332 changes in human footprint values than non-threatened bryophytes, while threatened reptiles were

333 characterized by significantly larger negative changes than non-threatened reptiles. This might be due to

334 recent impacts leading to large differences in the index that are still to be reflected in species

335   populations. The absence of a global trend indicates that the magnitude, rather than the rate of change

336   in human footprint is related to extinction risk.

337   Generation length had a very clear relationship with extinction risk for mammals, birds and reptiles (Fig.

338   1). Just as with fecundity, species with delayed life-cycles are more likely to be more threatened. For

339   organisms with slower life-cycles it takes longer to recover from low population numbers in the face of

340   demographic troughs[19]. The weak or nonexistent effect seen in invertebrates or plants taxa may be due

341   to lack of contrasts in data (either few data available, available just as ordinal values or showing low

342   natural variability).

343   The mean diet breadth between threatened and non-threatened species did not vary across groups (Fig.

344   1). However, the range of values differed between threatened and non-threatened mammals, indicating

345   that threatened species occurred at both ends of the range in diet breadth. As for seed size, phylogeny

346   might be playing a role, as diet specialists have been shown to be more at risk within bats[36], but not

347   within artiodactyls[37] for example. Further studies including the phylogenetic relations of species would

348   help clarify any general effects of diet breadth on extinction risk. As comprehensive phylogenetic trees

349   are currently available for only some of the taxa we studied this is not possible as of yet.

350   Microhabitat was a significant factor only for spiders (Fig. 1); spiders occurring at higher vertical strata

351   are less threatened. This effect seems to be due to the presence of organisms with higher capacity for

352   ballooning in this stratum. As ballooning depends on, first, building the right kind of silk strands (more

353   commonly found in web weavers) and second, finding the right place to take off (usually at higher

354   heights) spiders living on trees and other vegetation are often more prone to balloon than those living at

355   ground level[38]. Microhabitat therefore determines to a certain point dispersal ability and consequently

356   extinction risk in spiders.

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358 **Supplementary tables**

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360   Table S1: Traits studied, definition, examples, and hypotheses.

Trait	Definition	Examples of traits	Hypothesis	References
Body size	Typical size of an adult organism.	body mass, body length, plant height, plant mass, shell length	Larger organisms are more vulnerable because 1) they tend to have lower population densities, 2) require more resources; and 3) slower life cycles.	[4]
Offspring size	Typical size of an offspring.	size at birth, egg size, seed size	Organisms with larger offspring than expected by body size are more vulnerable to extinction because offspring size is often correlated with lower fecundity and slower life cycles with less capacity to adapt to new conditions.	[4]
Fecundity	Reproductive output.	Number of offspring per reproductive event, number of reproductive events in a year	Species with larger fecundities can compensate for the effects of higher mortality rates, particularly in the face of changing environment.	[4]
Generation length	Typical length of the life cycle, from birth until reproduction.	generation length, age at maturation, max longevity	Species with slow life cycles are more vulnerable to extinction, due to their weaker capacity to recover normal population numbers after a disturbance.	[4]
Diet breadth	Degree of narrowness of diet or of substrate used	Number of food types ingested, diversity of prey, breadth of soil conditions	Species with narrow diet breadths are more vulnerable because they are less able to shift diets when resource abundance fluctuates or decreases.	[26] [41]
Trophic level	Trophic position	herbivore/omnivore/carnivore	Organisms at higher trophic levels are more vulnerable because biomass available is reduced. Furthermore, they are affected by disturbance at lower trophic levels.	[4]
Dispersal ability	Capacity to disperse	Migrant? or not, dispersal speed, dispersal distance	Organisms with low dispersal ability are more vulnerable because they do not have the mechanisms to find suitable habitat around a changing environment.	[22,27,42,43]
Microhabitat	Typical vertical stratum occupied in a habitat.	nest position, foraging stratum, vertical position in the water column	Organisms that occupy lower strata in a habitat are more likely to face less extinction risk because they are less dependent on other species providing them verticality (like trees, bushes, etc.). On the other hand, species living on the ground may face higher predation pressure. Benthic organisms may be more vulnerable than those in the water	[44,45]

			column due to loss of good quality substratum and benthic vegetation.	
Habitat breadth	Range of habitat types occupied.	number of habitat types	Species capable of occupying a broad range of habitats are less likely to become extinct, because they may shift preferential habitat when one is reduced.	[14]
Altitudinal range	Range of altitude levels occupied.	Vertical distance between lower and higher limits	Species with broader altitudinal ranges are able to adapt to different altitudinal strata and shift or survive in different altitudes when conditions change.	[46]
Human footprint	Degree of human footprint within the range.	mean human footprint within the range, mean human population density, road density	Species living in areas with higher human influence are more likely to be threatened due to increased levels of habitat fragmentation, exploitation levels, etc.	[5,30]
Change in human footprint	Degree of human footprint change within the range.	Mean increase in human footprint change within the range, mean increase in human population density, mean increase in road density	Species living in areas in which human presence has increased in recent years are more likely to be threatened due to increased levels of habitat fragmentation, exploitation levels, etc.	[5]

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363   **Table S2**: Number of species for each trait in each taxonomic group.

	Body size	Offspring size	Fecundity	Generation length	Diet breadth	Trophic level	Dispersal ability	Microhabitat	Habitat breadth	Altitudinal range	Human footprint
Total	*842*	*415*	*334*	*344*	*214*	*743*	*335*	*551*	*874*	*314*	*562*
Mammals	60	59	58	58	59	60	35	60	59	16	55
Birds	59	0	58	59	60	60	60	60	60	17	50
Reptiles	60	43	60	11	0	45	0	44	59	15	51
Amphibians	60	60	60	6	0	18	0	57	60	21	55
Fishes	60	2	56	9	0	59	29	60	60	5	51
Dragonflies	60	5	1	1	0	60	60	0	60	7	34
Butterflies	59	47	0	10	17	60	0	0	60	19	44
Grasshoppers	51	0	0	5	0	0	60	60	60	27	56
Spiders	39	0	0	39	39	39	39	39	39	36	33
Snails	60	9	41	39	39	42	0	59	60	29	56
Bryophytes	52	46	0	60	0	60	52	59	60	36	57
Ferns	50	0	0	0	0	60	0	53	60	0	0
Gymnosperms	58	57	0	44	0	60	0	0	60	32	1
Monocots	60	41	0	1	0	60	0	0	59	32	14
Legumes	54	46	0	2	0	60	0	0	58	22	5

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Table S3: Table of proxies used for each trait. A "-" indicates traits for which we could not find enough data/proxies.

Group	Body size	Offspring size	Fecundity	Generation length	Diet breadth	Trophic level	Dispersal ability	Microhabitat
Mammals	Adult body mass (g)	Neonatal mass (g)	Litter size (no. of offspring)	Maximum longevity (years)	Number of food types	1 = herbivore; 2 = omnivore, 3 = carnivore	1 = not a migrant; not nomadic; 2 = migrant or nomadic	Foraging stratum: 1 = marine; 2 = ground level, including aquatic foraging; 3 = scansorial; 4 = arboreal; 5 = aerial; categories from Elton traits database[47]
Birds	Body length (cm)	Egg volume (mm^3), estimated from egg height and diameter using the Hoyt equation[48]	Clutch size (no. of offspring)	Generation length (years)	Number of food types	1 = herbivore, 2 = omnivore, 3 = carnivore	1 = Not a migrant; 2 = altitudinal/full migrant	Index of foraging verticality from 0 (prevalence of foraging below water) to 1 (prevalence of foraging well above vegetation or other structures). Adapted from Elton traits database[47]
Reptiles	Adult body mass (g)	hatchling snout-vent length (mm)	Clutch size (no. of offspring)	Generation length (years)	-	1 = herbivore; 2 = omnivore; 3 = carnivore	-	Verticality: 1 = ground level (ground dwelling, among rocks, freshwater, leaf litter); 2 = upper level
Amphibians	Snout-vent length (mm)	Offspring size (mm)	Clutch size (no. of offspring)	Age at sexual maturity (years)	-	1 = carnivore	-	Verticality: 1 = exclusively ground level/ aquatic; 2 = arboreal or arboreal and/or aquatic and/or terrestrial)

Group	Size	Egg/larval/spore size	Fecundity	Generation length	Diet breadth	Trophic position	Dispersal/Migrant	Habitat/Water column
Fishes	Body length (cm)	egg diameter (mm)	Minimum population doubling time: 1= more than 14 years; 2= 4.5-14 years; 3 = 1.4-4.4 years; 4 = less than 15 months	Generation length (years)	-	trophic position fish (average $\delta^{15}N$ signature)	Migrant (binary, not a migrant/migrant)	Water column verticality: 1 = demersal; 2 = benthopelagic; 3 = pelagic
Dragonflies	Hindwing length (mm)	Larval size (mm)	number of eggs	1 = less than a year; 2 = more than a year	-	1 = carnivore	Residuals of log(hindwing length) and log(abdomen length)[18]	-
Butterflies	Forewing length (mm)	Egg size (mm)	Number of eggs	1 = one generation per year; 2 = two generations per year	1 = monophagous; 2 = oligophagous; 3 = polyphagous	1 = herbivore	-	-
Grasshoppers	Total length (mm)	-	Number of eggs	1 = less than one year; 2 = more than a year	-	-	1 = flightless, 2 = dimorphic, 3 = winged	1 = troglobiont; 2 = terricolous; 3 = graminicolous/forbicolous; 4 = arbusticolous; 5 = arboricolous
Spiders	Body length (mm)	-	-	Generation length (years)	1 = stenophagous; 2 = euriphagous	1 = carnivore	Ballooning frequency: 1 = rare; 2 = occasional; 3 = frequent	Verticality index (Macias-Hernandez et al. 2020)
Snails	Heometric mean of the length and width of a shell (mm)[49]	Egg diameter (mm)	1 = 1-10 eggs; 2 = 10-100 eggs	1 = 1-2 years; 2 = 2-5 years; 3 = >5 years	Number of classes eaten. Classes = detritus/litter/living material/dead material/herbivore/canivore	1 = non-carnivore; 2 = carnivore	-	0 = caves and other subterranean habitats; 1 = under-rocks, 2 = rock level; 3 = above rocks; 4 = vegetation
Bryophytes	Shoot length (mm)	Spore diameter (um)	-	1 = annual or biannual, 2 = perennial	-	1 = producer	1 / log(spore size)[21]	1 = exclusively soil/rock; 2 = trees/walls/tree logs

Ferns	Height (cm)	-	-	-	-	1 = producer	-	1 = terrestrial/aquatic; 2 = soil or epiphytes; 3 = epiphytes/trunk
Gymnosperms	Height (cm)	Seed max diameter (mm)	-	Generation length (years)	-	1 = producer	-	-
Monocots	Height (cm)	Seed weight (Thousand kernel weight) (g)	-	Generation length (years)	-	1 = producer	-	-
Legumes	Height (cm)	Seed max diameter (mm)	-	Generation length (years)	-	1 = producer	-	-

Table S4: Proxies for Habitat breadth, Altitudinal range, Human footprint and Change in human footprint. All data extracted or derived from the IUCN Red List database.

Habitat breadth	Altitudinal range	Human footprint (HFP)	Change in human footprint	Geographical range size
Number of habitat types	Maximum - minimum elevation	Mean human footprint across geographical range	Mean change in HFP values across geographical range	Extent of Occurrence (km2).

Table S5: Number of species per taxonomic group and biogeographic realm.

|	Afrotropic	IndoMalay	Nearctic	Neotropic	Australasia	Palearctic
Mammals	10	10	10	10	10	10
Birds	10	10	10	10	10	10
Reptiles	10	10	10	10	10	10
Amphibians	10	10	10	10	10	10
Fishes	10	10	10	10	10	10
Dragonflies	10	10	10	10	10	10
Butterflies	10	2	0	16	16	16
Grasshoppers	30	0	0	0	0	30
Spiders	0	0	0	0	0	39
Snails	0	0	0	0	0	60
Bryophytes	0	0	0	0	0	60
Ferns	10	10	10	10	10	10
Gymnosperms	10	10	10	10	10	10
Monocots	10	10	10	10	10	10
Fabales	10	10	10	10	10	10

Supplementary Figures
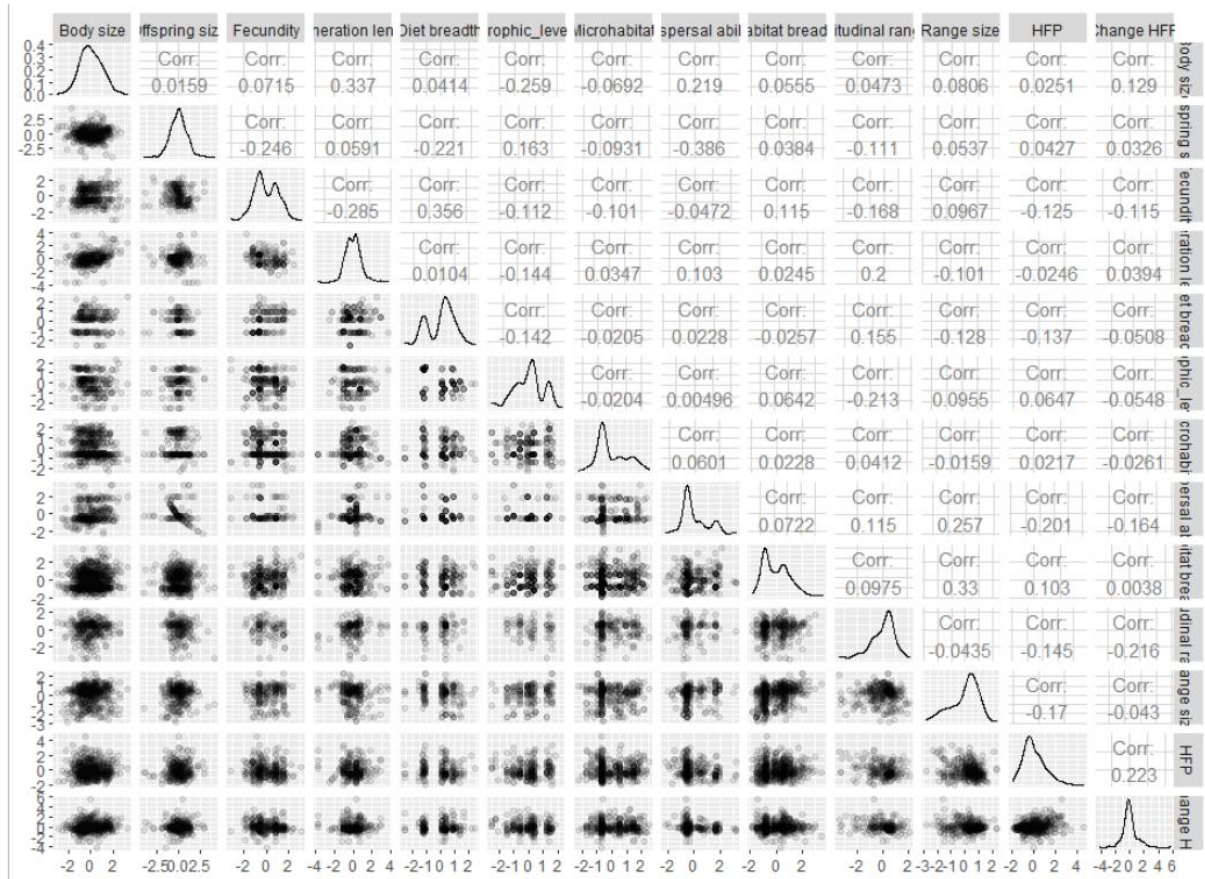
Figure S1: Pairwise correlations between traits. Upper panel: Spearman's rank correlation coefficient between each pair of traits. Diagonal: histogram of each trait. Lower panel: scatterplots of each trait. Higher density of datapoints is indicated by darker shades of gray.
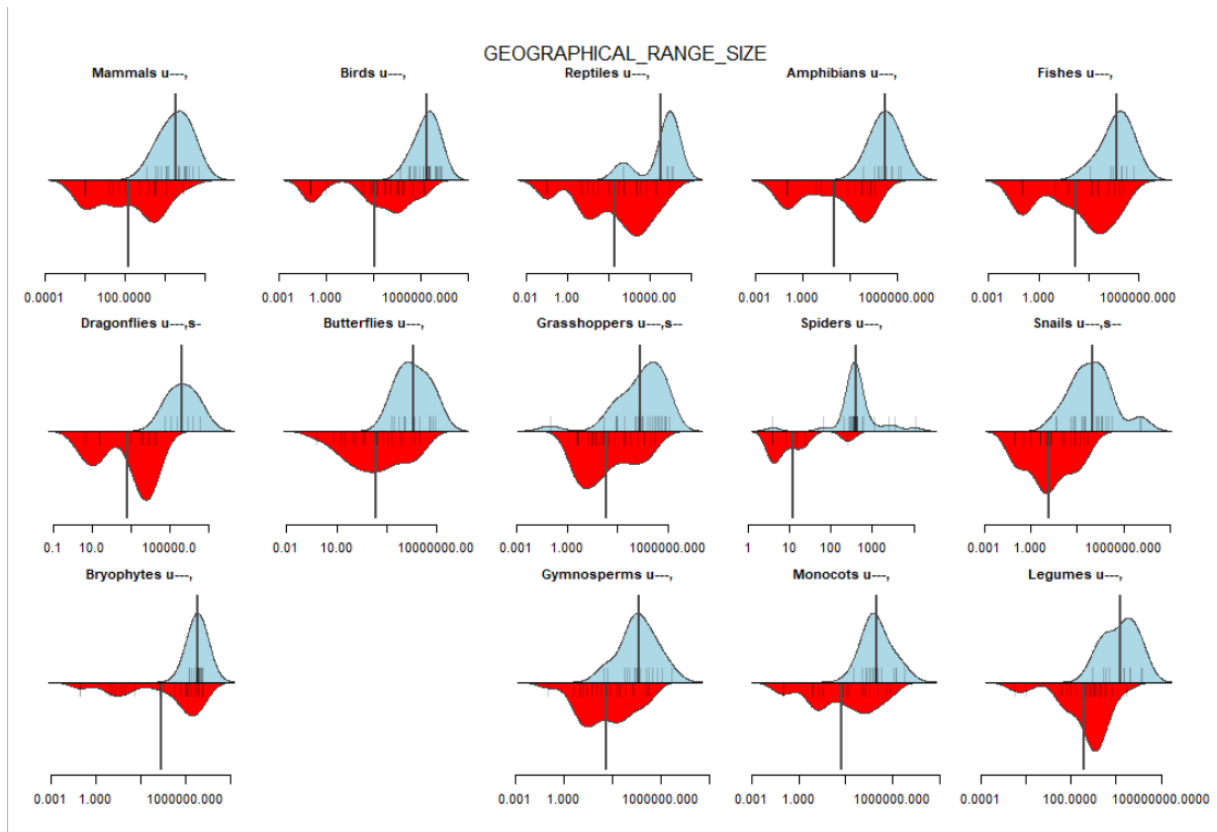
Figure S2: Beanplots of density of geographical range size values between non-threatened (blue, upper side) and threatened (red, lower side) species. Small vertical bars represent one species' value; darker bars indicate several species with the same trait value. The large vertical bar is the mean geographical range size value. Null models show whether the mean (u) or standard deviation (s) of threatened species is higher (+++, ++, +) or lower (---, --, -) than expected. Significance codes: +++ or --- x < 0.01; ++ or -- 0.01 <= x < 0.05; + or - 0.05 <= x < 0.1. The Bayesian model was highly significant (pMCMC < 0.0001, N = 506).

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Author contributions

FC and PC conceptualized the initial idea of the paper. All authors contributed to the acquisition of the data. FC conducted the formal analysis. FC and PC wrote the first draft of the manuscript, and all authors read, and contributed with suggestions.

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