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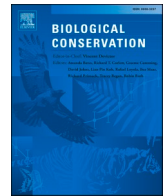
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Trait-based prediction of extinction risk across terrestrial taxa

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ABSTRACT

Species differ in their biological susceptibility to extinction, but the set of traits determining susceptibility varies across taxa. It is yet unclear which patterns are common to all taxa, and which are taxon-specific, with consequences to conservation practice. In this study we analysed the generality of trait-based prediction of extinction risk across terrestrial (including freshwater) vertebrates, invertebrates and plants at a global scale. For each group, we selected five representative taxa and within each group we explored whether risk can be related to any of 10 potential predictors. We then synthesized outcomes across taxa using a meta-analytic approach. High habitat specificity was a consistent predictor across vertebrates, invertebrates and plants, being a universal predictor of risk. Slow life-history traits – large relative offspring size, low fecundity, long generation length –, and narrow altitudinal range were also found to be good predictors across most taxa, but their universality needs to be supported with additional data. Poor dispersal ability was a common predictor of extinction risk among invertebrate and plant taxa, but not consistently among vertebrates. The remaining traits (body size, micro-habitat verticality, trophic level, and diet breadth) were useful to predict extinction risk but only at lower taxonomical levels. Our study shows that despite the idiosyncrasies among taxa, universal susceptibility to extinction exists and several traits might influence extinction risk for most taxa. Informing conservation prioritization at lower taxonomic scales should however include taxon-specific trait-based predictors of extinction risk.

1. Introduction

We are currently facing the sixth mass extinction at the planetary scale (Cowie et al., 2022), with species becoming extinct 1000 to 10,000 times faster than background rates (De Vos et al., 2015). Not only species, but the functions they provide and that benefit humanity are at risk, with unpredictable consequences towards ecosystem and human well-being (Carmona et al., 2021; Toussaint et al., 2021). Identifying the causes of species' decline is therefore a crucial step to use conservation

resources efficiently.

The main causes of decline are well identified and are human-driven: loss and conversion of habitat, excessive exploitation and persecution of many species, pollution, invasive species, and climate change (Secretariat of the Convention on Biological Diversity, 2020). But species differ in their intrinsic attributes (life-history and ecological strategies) and therefore may be more or less susceptible to a particular driver of extinction (Purvis et al., 2000a, 2005).

Hundreds of attributes have been tested as predictors of extinction

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risk in the past (Chichorro et al., 2019). Most effects of traits depend on interactions with other factors, such as the threatening process (González-Suárez et al., 2013; Murray et al., 2014), the taxonomic level (Purvis et al., 2005) and taxa (Chichorro et al., 2019), and the spatial scale and extent of the study (Purvis et al., 2005). Based on these earlier studies two traits seem to be consistent predictors of extinction risk (i.e., universal predictors): narrow habitat specialization and geographical range (Chichorro et al., 2019). However, life-history and ecological theory suggest that additional universal traits exist. For example, extinction risk has been hypothesized to be related to slow life-history traits (Pimm et al., 1988; Purvis et al., 2000b), large body size (Purvis et al., 2000a), narrow habitat, diet, or climatic specialization (McKinney and Lockwood, 1999), poor dispersal ability (McCauley et al., 2014), high trophic level (Atwood et al., 2020; Purvis et al., 2000a), among others (Table 1). But their universality has not been so far properly examined because most studies linking the extinction risk of species to intrinsic and extrinsic factors have focused on few taxonomic groups or their scope is geographically narrow (Chichorro et al., 2019). Due to societal and knowledge biases (Cardoso et al., 2011; Etard et al., 2020; Verde Arregoitia, 2016), well-studied groups include vertebrates, namely mammals (Cardillo et al., 2008; Di Marco et al., 2018; Purvis et al., 2000a) and birds (Bennett and Owens, 1997; Gage et al., 2004; Richards et al., 2020) and the best-known region is the Palearctic realm (Chichorro et al., 2019; Nolte et al., 2019). Furthermore, the high volume of confounding effects and statistical approaches hampers synthesizing efforts across studies (Chichorro et al., 2019). In order to identify robust universal predictors, taxonomic groups with different ecological strategies ought to be selected and analysed with a standardized statistical approach at a global scale. In this study, we resolved the taxonomic and comparability issues and investigated whether several candidate traits could be used as universal, taxon-independent predictors of extinction risk.

2. Materials and methods

To investigate the relationship between traits and extinction risk, we first selected a set of candidate traits previously hypothesized to relate to extinction risk (Table 1) and quantified them for species within 15 taxa sampled from within three groups: vertebrates, invertebrates, and plants. Within each group and for each trait we fitted a generalized linear-mixed model to estimate the slope parameter of the regression between the trait and extinction risk. Generality was then investigated for each trait by running meta-analyses of the slope parameters obtained from each group.

2.1. Species selection and data

We restricted our analyses to vertebrates, invertebrates and plants, thus excluding major taxa such as the fungi due to the lack of extinction risk assessments available at the global scale (IUCN Red List of Threatened Species™ (IUCN, 2021)). As another aim was to select species using the same stratified sampling and analyses, we also restricted the analysis to terrestrial and freshwater realms: marine species would require different spatial sampling. The selection of taxa was nevertheless performed to capture a wide range of life-histories, geographical areas, and taxa, which thus provides robustness and universality to the analyses.

We chose five vertebrate, five invertebrate, and five plant taxa. Selection of groups at the same taxonomical level was difficult because species information is often collated at different levels across taxa. Vertebrate taxa comprised the major groups of terrestrial vertebrates: “Mammals” (Class: Mammalia), “Birds” (Class: Aves), “Reptiles” (Class: Reptilia), “Amphibians” (Class: Amphibia) and freshwater “Fishes” (Class: Actinopterygii). Many invertebrate taxa lack assessments at a global scale and thus it was not possible to obtain an exhaustive set of taxa of the terrestrial and freshwater diversity. The invertebrates

Table 1
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.	(Purvis et al., 2000a)
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.	(Purvis et al., 2000a)
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 a changing environment.	(Purvis et al., 2000a)
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.	(Purvis et al., 2000a)
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.	(Di Marco et al., 2015; González-Suárez et al., 2013)

(continued on next page)

Table 1 (continued)

Trait	Definition	Examples of traits	Hypothesis	References
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.	(Purvis et al., 2000a)
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.	(Bartonova et al., 2014; Bencotter et al., 2013; Parlato et al., 2015; Saar et al., 2012)
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 column due to loss of good quality substratum and benthic vegetation.	(Giam et al., 2011; Johnson and Isaac, 2009)
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	(Böhm et al., 2016)

Table 1 (continued)

Trait	Definition	Examples of traits	Hypothesis	References
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.	(Keane et al., 2005)

comprised “Dragonflies” (Order: Odonata, including damselflies), “Butterflies” (Suborder: Rhopalocera), “Grasshoppers” (Order: Orthoptera), “Spiders” (Order: Araneae), and land “Snails” (Class: Gastropoda). In the selection of plants we followed a recent baseline study (Brummitt et al., 2015), which includes species sampled from the five main phylogenetic branches of land plants (embryophytes): “bryophytes”, excluding hornworts (Divisions: Bryophyta and Marchantiophyta), “ferns” (Classes: Lycopodiopsida, Polypodiopsida), “Gymnosperms” (Classes: Pinopsida, Cycadopsida, Gnetopsida), “Monocots” (Class: Liliopsida), and finally the “Legumes” (Order: Fabales). “Legumes” served as a representative of the most diverse group of plants, eudicots, because they are the single family that best reflects both plant functional diversity as well as species richness of this large plant group (Nic Lughadha et al., 2005; Brummitt et al., 2015), with species reaching forest canopy heights as well as many small, herbaceous species.

To guarantee similar weights in the statistical analyses, we selected 60 species for each taxon. Given that threats are not homogeneously distributed in space (Harfoot et al., 2021), and to limit geographical biases in data (Etard et al., 2020) and to achieve global representativeness of the dataset, we selected, wherever possible, 10 species per taxon from each of six biogeographic realms (Table S1). To minimize knowledge biases, in which species selected for the study are those with more trait data, we randomly selected the species from within these taxa, provided each species were not Data-Deficient. Additionally, we selected equal numbers of threatened (one of each of Near Threatened, Vulnerable, Endangered, Critically Endangered, Extinct in the wild/ Extinct) and non-threatened (five Least Concern) species. Random selection was performed by ordering IUCN species based on random score using the rand() function in Microsoft Excel (2016).

As not all taxa have global coverage in the IUCN Red List, we had to restrict our dataset to smaller regions in the case of butterflies, grasshoppers, spiders, snails, and bryophytes. All species of spiders, snails and bryophytes were selected from Europe, due to a small number of assessments from other geographical realms. For grasshoppers, most assessments came from the Afrotropics and the Palearctic, and therefore 30 species were selected from each. In butterflies, no Nearctic species were included due to low availability of data from that group (IUCN, 2021), and very few from the Indo-Malay region were included. In total, our dataset included 872 species (Table S2).

2.2. Trait selection and data

As predictors, we selected traits of species whose relationship with extinction risk has been extensively hypothesized and often tested in previous studies (Table 1). These include traits related to pace of life-history (body size, relative offspring size, fecundity, generation length), traits related to specialization (habitat breadth, relative

altitudinal range as a proxy for climatic range and diet breadth), dispersal ability, trophic level, and microhabitat (measured as microhabitat verticality, from soil to canopy species). Despite of the fact that geographical range has been one of the traits hypothesized to be very important in the literature (Chichorro et al., 2019), we decided not to include this trait because Red List assessments are often based on range, making any inference circular (Munstermann et al., 2021).

Different taxa differ in their life-history and ecological strategies. Therefore, for each trait considered, we often selected different trait “proxies” (Tables S3, S4), which are analogous traits (Weiss and Ray, 2019), i.e., traits that indicate the same function across taxa but measured differently. The choice of proxies depended on the suitability of the trait as a proxy (e.g., body length is a better proxy of body size than body mass in birds, due to large variation within a migratory species between seasons (Scott et al., 1994)), and on the availability of data for that trait (e.g. dispersal ability is an ordinal trait reflecting the propensity to balloon in spiders and a continuous trait of seed size in plants).

Trait data were compiled from the literature, including existing trait databases and guides (Billerman et al., 2022; Froese and Pauly, 2022; IUCN, 2021; Meiri, 2018; Myhrvold et al., 2015; Oliveira et al., 2017; Tobias et al., 2022; Uetz and Hošek, 2022; Wilman et al., 2014), original species descriptions (BHL, 2022; Cigliano et al., 2022) and in some cases also measurements of photographs of pinned or herbarium specimens (usually the holotype or paratype of species) available online (BHL, 2022; Cigliano et al., 2022; Ryan, 2018). When no trait data were available for the species, we used either the value of a closely related species or the genus or family average; these latter approaches were used when values for other taxa were available in online trait databases. Average values at genus and family were not performed for binary data, habitat breadth, and altitudinal range, as these data cannot be accurately predicted between species of larger taxonomic entities. Only 1.6 % of the data in body size was imputed, contrasting with 45, 42, and 37 % in diet breadth, trophic level, and fecundity, respectively. Snails (30 %), Spiders (16 %), and Mammals (16 %) had the highest percentage of imputed data, and all plant taxa except bryophytes had no imputed data. Data were imputed most often by calculating average values at genus (64 %), or family (25 %) level, or for closely related species (10 %).

Some taxa lacked data completely for some traits, such as fecundity and offspring size for dragonflies and spiders, and diet breadth for reptiles and amphibians. To avoid extremely high error estimates in the statistical analyses, we also discarded taxa-traits with less than three data points for each level of the response variable (threat status), as well as binary traits which lacked observations for each combination of trait value and threat status.

Two traits, diet breadth and trophic level, were only studied in animal groups because they are invariant among plants. The trophic position resolution was fine in some taxa (fishes, (Froese and Pauly, 2022)), while for others it was an ordered factor consisting of two or three levels (herbivores, omnivores, or carnivores). Dragonflies, butterflies, and spiders were not considered for this trait as all species are either herbivorous or carnivorous.

Because offspring size is positively correlated with body size, we used a relative metric of offspring size instead: the residuals of a regression between $\log(\text{offspring size})$ and $\log(\text{body size})$ within all taxa. Because the altitudinal range is often related to the geographical range size of species, we used the residuals of a regression between $\log(\text{altitudinal range})$ and the $\log(\text{geographical range size})$. Extinction axiomatically leads to a non-existent range, so we incremented all species' geographical range size by 0.1, so that \log -transformation was possible. Likewise, the altitudinal range was incremented by 10 m for all species.

We \log -transformed count data (e.g. number of habitat types, number of diet types eaten), and continuous data (body length, number of offspring), except for the dispersal ability of dragonflies and bryophytes, and relative offspring size and altitudinal range, since these traits were already \log -transformed when estimating the values. This ensured that

the distribution of trait values followed a near-normal distribution without significant skewness and observations spread far away from the main density of trait values.

2.3. Statistical analyses

The goal was to understand if the relationship between 10 traits previously hypothesized to influence extinction risk is consistent across taxa or if some traits present contrasting signals dependent on taxon identity. The statistical analyses consisted of two parts: to calculate the relationship within taxa, and to summarize it across vertebrates, invertebrates, and plants. For each taxon and trait combination, we fitted a bivariate generalized linear mixed model (glmm) using the trait value as the independent variable, threat status as the response variable and taxonomy as random-intercept effect to account for phylogeny given the inexistence of phylogenies for most taxa. Multivariate analyses would have been impractical due to the very low number of species with available data across all traits. The response variable was binary (following (Atwood et al., 2020; Payne et al., 2016; Ripple et al., 2017)): whether a species was threatened (1, including Near-Threatened, Vulnerable, Endangered, Critically Endangered and Extinct species), or not (0, including Least Concern only), and therefore the model was constructed using the Bernoulli distribution and logit link function. Traits were z -transformed before running the models, so that the slope terms could be compared across taxa and thus be used as effect sizes in the posterior analyses. As random grouping variables, we used the family level for all taxonomic groups.

To analyse consistency of trait responses across groups, we ran fixed-effects meta-analyses using the extracted effect sizes from each taxonomic group. This meta-analytic approach has the advantage of taking into consideration the magnitude of effects and not only whether signals from linear models were positive or not. For each trait we calculated three effect sizes (using the slope parameters) and their confidence intervals (calculated from standard errors of the slope terms, at a significance level of 0.05): across vertebrate, invertebrate and plant groups.

We inspected the influence of imputed data, choice of sample size and differences in the number of available data among taxa in the model results. To test the influence of imputed data, we repeated the analyses excluding all imputed data and compared results with and without imputation. To test the influence of differences in species numbers among taxa we created 100 bootstrap datasets with 60 observations per trait*taxa and run the meta-analyses with the median value of the slope and standard error parameter across all 100 datasets. To test the choice of sample size, we collated a dataset with greatly increased sample size for mammals and birds, in the range of 1408–4851 and 1275–10,221 observations per trait, respectively, and inspected whether effect sizes changed in these taxa. Mammals and birds were selected for this because they have comprehensive trait data easily available (Myhrvold et al., 2015; Soria et al., 2021; Tobias et al., 2022) with relatively low taxonomical and geographical biases (Etard et al., 2020). All statistical analyses were performed in R version 4.2.0 (R Core Team, 2022). Generalized linear mixed models were performed with package glmmTMB (Brooks et al., 2017) and meta-analyses with package metafor (Viechtbauer, 2010).

3. Results

3.1. Effective sample sizes

Data availability for each trait varied within and across the 15 taxa. Traits available for all the taxa included body size and habitat breadth, while all other traits were missing in at least one taxon: in these cases, data were either missing for all species or available only to a few species and thus not enough to be used in the statistical analyses. For example, trophic level, diet breadth, and fecundity were only considered for five, five, and six taxa, respectively (Table S2); the latter was almost

exclusively available for vertebrates only. On average, vertebrate taxa had data for 9.8 traits, invertebrates for 6.8 traits, and plants for 4.8 traits. Considering only the taxa for which a trait was evaluated, the average data completeness was highest for habitat breadth (99 %), and body size (97 %), and lowest for altitudinal range (45 %), generation length (75 %), and diet breadth (78 %). As a percentage of the available data, imputed data varied among traits (excluding altitudinal range and habitat breadth, for which imputation was not applied, see methods, Table S5).

3.2. Consistency of extinction risk prediction

Habitat breadth was the trait with the most consistent signal across groups, with both significant negative relationships within many taxa (i.e., the confidence intervals not overlapping zero, Fig. 1), and meta-analyses indicating significant overall negative effect sizes among vertebrate, invertebrate, and plant groups (Fig. 1).

Offspring size, fecundity and generation length showed significant or marginally significant overall effect sizes for either vertebrates, invertebrates, or plants. (Fig. 1). Offspring size was correlated positively to extinction risk across plants, and in invertebrates the sole taxon studied for this trait also showed a positive relationship, despite non-significant. In vertebrates, fecundity was marginally negatively correlated, and generation length significantly positively correlated to extinction risk (Fig. 1). Altitudinal range was marginally negatively related to

extinction risk in invertebrates and plants (Fig. 1).

Dispersal ability was negatively correlated with extinction risk among invertebrates (Fig. 1), and the sole plant taxon studied for this trait (bryophytes) also suggested a negative relationship, with no apparent effect observed among vertebrates.

None of the remaining traits showed any consistent response across either vertebrates, invertebrates, or plants (Fig. 1), although significant relationships were observed in within taxa comparisons for body size in birds and microhabitat in spiders (Fig. 1).

Excluding observations with imputed trait values resulted in similar results in overall effect sizes, except for dispersal ability, where the significant negative overall effect size disappears within invertebrates (Fig. S1). Balancing observation numbers across taxa with bootstrapping led to similar overall effect sizes (Fig. S2), except for generation length and altitudinal range, where the significance in vertebrates disappeared in the former, and the effect became significantly negative within invertebrate taxa in the latter. Furthermore, the overall effect size of diet breadth and of microhabitat in invertebrates became marginally positive, with species with a greater diet breadth and microhabitat more prone to extinction. Within mammals and birds, adding more observations led to much narrower confidence intervals, but the same signal (Fig. S3).

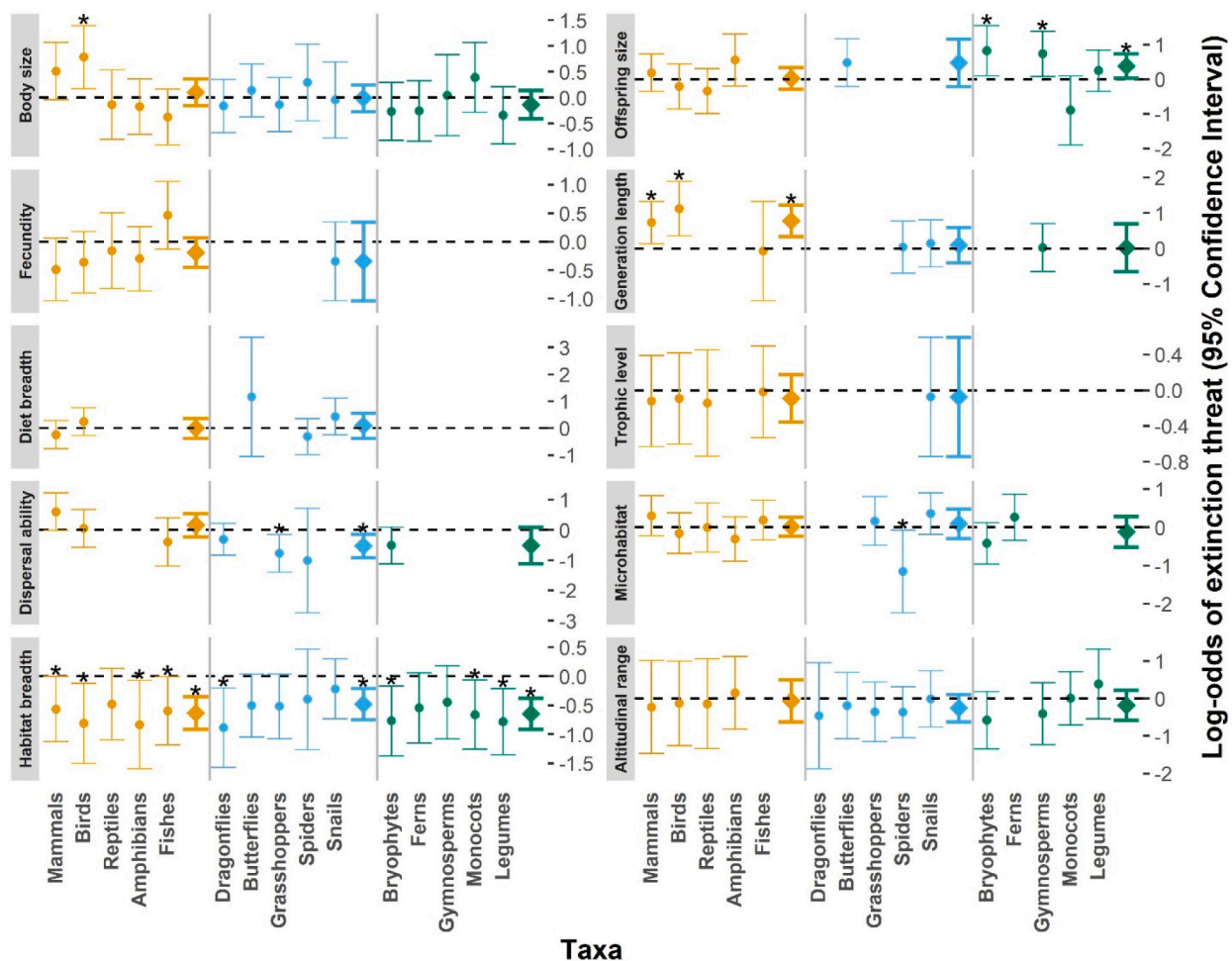


Fig. 1. Log-odds of extinction threat for each trait and within each taxon studied (glmms, thin dots and error bars), and among vertebrates, invertebrates, and plants (meta-analyses, bold diamond and error bars). Error bars represent lower and upper bound 95 % confidence intervals. Positive values indicate a positive relationship between the trait and extinction risk, and vice-versa. Confidence intervals not overlapping with 0 (marked with an asterisk *) indicate a smaller than 5 % probability that the slope of the relationship is zero.

4. Discussion

Our results show that many traits that have been shown to be significant predictors for some taxa cannot be used as general predictors across all groups. Based on their ability to predict extinction risk for many taxa, we can divide traits into four categories. The first category includes a single trait that can be confidently considered as universal, showing a similar relationship with extinction risk across all taxa (habitat breadth); the second category includes traits whose trends suggest that they may be universal, but additional data is needed to clarify this (slow life-history traits - offspring size, fecundity, generation length - and altitudinal range); the third category includes a single trait whose response is consistent across several but not all groups (dispersal ability); and the fourth category includes traits whose response is taxon-dependent (body size, diet breadth, trophic level, and microhabitat).

4.1. Universal predictors

We consider habitat breadth as the only universal predictor, with a consistent relationship with extinction across vertebrate, invertebrate, and plant groups. Species occurring in a narrow range of habitats have fewer opportunities to expand to and survive in alternative living conditions and are consequently more likely to be threatened (Böhm et al., 2016; Garcia-R and Di Marco, 2020; Slatyer et al., 2013). In fact, habitat breadth, together with geographical range size and abundance, is one of the three classical dimensions of rarity (Rabinowitz, 1981). In a previous meta-analysis (Chichorro et al., 2019), habitat breadth was the only factor, besides geographical range size, that was consistently found to correlate with extinction risk. This trait should be very relevant in the face of generalized natural ecosystem destruction with consequent habitat loss for numerous species. With increasing levels of habitat loss occurring across all biomes, species that are able to use alternative habitats will inevitably fare better.

4.2. Candidate universal predictors

We grouped in this category predictors which showed a significant or marginally significant overall effect size across vertebrates, invertebrates, and plants, but for which data are lacking for certain groups which prevent them from being considered universal predictors. In this category we find offspring size, fecundity, generation length, and altitudinal range. The former three are directly related to the r-K continuum of life-history strategies. r-strategists achieve maturity faster, live shorter, and produce many small offspring, whereas K-strategists achieve maturity later, live longer, and produce few, larger offspring per reproductive event. Populations of K-strategists are presumed to decline when they face demographic threats, due to their diminished capacity to compensate for higher mortality rates (Pimm et al., 1988). Despite the dominance of vertebrate data in these analyses, the trends seen in offspring size in plants and invertebrates, as well as marginal significance of fecundity in vertebrates and invertebrates suggest that slow life-history traits might be consistently related with extinction risk. Even if data were missing for some plant taxa, it is likely that species with lower fecundity are also more threatened (Saar et al., 2012). Species with higher reproductive output will probably fare better in the future independently of any particular threat.

The strong negative signal seen in the extended mammal and bird datasets, and the significance in invertebrates in the bootstrapped dataset suggests that altitudinal range may also be a universal trait. Here we consider altitudinal range to be a measure of climatic range. Species with lower range have fewer chances to exploit new habitats for survival, and thus confronting higher extinction risk (Botts et al., 2013). Furthermore, species with a greater altitudinal range may have a larger, continuous geographical distribution, thus providing better resilience against human impacts (Keane et al., 2005). This trait might become particularly relevant with the increasing levels of climate change, as it

might indicate which species will be able to adapt in the future to changing temperature and precipitation patterns.

4.3. Predictors at high taxonomic levels

Traits in this category also had significant overall effect sizes but showed inconsistencies in effects between different groups studied. Dispersal ability was a consistent predictor of risk among invertebrates and plants, but not among vertebrates. In the face of localised threats, species with a better capacity to colonize new areas have a lower risk of extinction (Benscoter et al., 2013; Reinhardt et al., 2005). Consequently, taxa with high dispersal capability, such as birds and dragonflies, often have a lower number of threatened species compared to other taxa (IUCN, 2021). In addition, shifts in distributions caused by climate change are likely to exacerbate the extinction of poor dispersers (MacLean and Beissinger, 2017; Mattila et al., 2011; Santini et al., 2016). This trait might be very relevant in predicting which species will be able to adapt to increasing levels of fragmentation of natural habitats. As fragmentation is one of the consequences of habitat loss, its effects are increasing at global scale, and having good dispersal ability might prove crucial to the survival of many species (Chichorro et al., 2022). High motility is also associated with lower extinction risk in the oceans (Knape et al., 2020; Payne et al., 2016). Dispersal ability may not be, however, as important for terrestrial vertebrates as it is for invertebrates and plants: most vertebrates are able to cross linear barriers such as roads, or to move much farther than many invertebrates or plants, for which even small fragmentation levels may pose a challenge (Bartonova et al., 2014; Saar et al., 2012).

4.4. Predictors at low taxonomic levels

This category includes all the other traits for which no general pattern was found. Despite non-significant overall predictors, they are useful predictors at lower taxonomic scales or for given threats. Large body size, for example, is an important predictor of extinction among mammals and birds (Cardillo et al., 2005; González-Suárez et al., 2013; Owens and Bennett, 2000), but the opposite pattern seems to show in amphibians (Cardillo, 2021). Furthermore, the importance of body size may depend on the biome considered (Fritz et al., 2009). Finally, species threatened by overexploitation may be larger than average (González-Suárez et al., 2013; Ruland and Jeschke, 2017), and species threatened by habitat specialization were hypothesized to be smaller than average due to their lower capacity to colonize new areas (Ripple et al., 2017).

Surprisingly, diet breadth was an inconsistent predictor of risk unlike habitat breadth or altitudinal range (the other specialism-related traits studied here). The inconsistency may be due to two factors. First, it may be that this trait is truly inconsistent across taxa. For example, among mammals, diet specialists have been shown to be more at risk within bats (Boyles and Storm, 2007) but not within artiodactyls (Price and Gittleman, 2007). Alternatively, the data that were available for this trait was not the best proxy of dietary specialization. For almost all taxa considered, the proxy consisted of the number of diet types ingested by a species. Species A which has a value of two was thus considered less specialized than Species B that has a value of one, however, species A could in turn be more specialized than B if it requires both resource types to survive.

As for trophic level and microhabitat, their inconsistency as predictors was not surprising. Multiple trophic levels could be more at risk depending on the taxon considered, such as carnivores (Newbold et al., 2020; Purvis et al., 2000a), herbivores (Atwood et al., 2020), or even fungivores (Newbold et al., 2020). The microhabitat, and particularly the characteristics of the vertical microhabitat at which species occur, are highly variable across taxa due to many confounding factors that make it very unlikely for this trait to be used as a universal predictor of risk.

5. Conclusions

In this study we analysed for the first time the generality of trait-based prediction of extinction risk across terrestrial (including freshwater) vertebrates, invertebrates, and plants. We have shown that some pathways to extinction are common to all groups. Habitat specialists tend to be more threatened. Species with slow life-histories, through large offspring size (plants), low fecundity (vertebrates), or long generation length (vertebrates and plants), and species with narrow altitudinal ranges may also be more threatened with extinction across all taxa, but more data is needed to test these hypotheses. Species with poor dispersal ability are more threatened with extinction among invertebrates and plants, but vertebrate responses are not consistent. Other traits, such as body size, diet breadth, trophic level, and micro-habitat are important predictors of extinction but their importance and relationship with extinction risk varies with the taxon. This last set of traits should however be considered in some taxa, as they were all traits with a significant response in at least one taxon (Chichorro et al., 2019).

We identify two main implications of this study to species conservation. Firstly, even though habitat breadth has been identified as being universal, many seem only to be good predictors among lower taxonomic scales. Consequently, in order to have more accurate, predictive power of extinction risk, capable of being used confidently for species' conservation prioritization, studies should focus on narrower taxonomic scales. On the other hand, due to the cross-taxon consistency of universal and potentially universal traits, these may nevertheless be used confidently to inform assessments of risk in taxa lacking extinction risk assessments and to provide rapid, rough measures of relative extinction risk.

CRedit authorship contribution statement

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 wrote the first draft of the manuscript with suggestions from PC, and all authors read, and contributed with suggestions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The scripts and data supporting the manuscript are available in <https://doi.org/10.6084/m9.figshare.20391126>.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109738>.

References

- Atwood, T.B., Valentine, S.A., Hammill, E., McCauley, D.J., Madin, E.M.P., Beard, K.H., Pearse, W.D., 2020. Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Sci. Adv.* 6, eabb8458 <https://doi.org/10.1126/sciadv.abb8458>.
 Bartonova, A., Benes, J., Konvicka, M., 2014. Generalist-specialist continuum and life history traits of Central European butterflies (Lepidoptera) - are we missing a part of the picture? *Eur. J. Entomol.* <https://doi.org/10.14411/eje.2014.060>.

- Bennett, P.M., Owens, I.P., 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc. R. Soc. Lond. B Biol. Sci.* 264, 401–408. <https://doi.org/10.1098/rspb.1997.0057>.
 Benscoter, A.M., Reece, J.S., Noss, R.F., Brandt, L.A., Mazzotti, F.J., Románach, S.S., Watling, J.L., 2013. Threatened and endangered subspecies with vulnerable ecological traits also have high susceptibility to sea level rise and habitat fragmentation. *PLoS ONE* 8, e70647. <https://doi.org/10.1371/journal.pone.0070647>.
 BHL, 2022. Biodiversity Heritage Library [WWW document]. URL: <https://www.biodiversitylibrary.org/>. (Accessed 18 May 2022).
 Billerman, S.M., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S., 2022. *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA.
 Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., Collen, B., 2016. Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. *Glob. Ecol. Biogeogr.* 25, 391–405. <https://doi.org/10.1111/geb.12419>.
 Botts, E.A., Erasmus, B.F.N., Alexander, G.J., 2013. Small range size and narrow niche breadth predict range contractions in south african frogs. *Glob. Ecol. Biogeogr.* 22, 567–576. <https://doi.org/10.1111/geb.12027>.
 Boyles, J.G., Storm, J.J., 2007. The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. *PLoS ONE* 2, e672. <https://doi.org/10.1371/journal.pone.0000672>.
 Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 378–400.
 Brummitt, N.A., Bachman, S.P., Griffiths-Lee, J., Lutz, M., Moat, J.F., Farjon, A., Donaldson, J.S., Hilton-Taylor, C., Meagher, T.R., Albuquerque, S., Aletrari, E., Andrews, A.K., Atchison, G., Baloch, E., Barlozzini, B., Brunazzi, A., Carretero, J., Celesti, M., Chadburn, H., Cianfoni, E., Cockel, C., Coldwell, V., Concetti, B., Contu, S., Crook, V., Dyson, P., Gardiner, L., Ghanim, N., Greene, H., Groom, A., Harker, R., Hopkins, D., Khela, S., Lakeman-Fraser, P., Lindon, H., Lockwood, H., Loftus, C., Lombri, D., Lopez-Poveda, L., Lyon, J., Malcolm-Tompkins, P., McGregor, K., Moreno, L., Murray, L., Nazari, K., Power, E., Tuijtelars, M.Q., Salter, R., Segrott, R., Thacker, H., Thomas, L.J., Tingvoll, S., Watkinson, G., Wojtaszkova, K., Lughadha, E.M.N., 2015. Green plants in the red: a baseline global assessment for the IUCN sampled red list index for plants. *PLOS ONE* 10, e0135152. <https://doi.org/10.1371/journal.pone.0135152>.
 Cardillo, M., 2021. Clarifying the relationship between body size and extinction risk in amphibians by complete mapping of model space. *Proc. R. Soc. B Biol. Sci.* 288, 20203011 <https://doi.org/10.1098/rspb.2020.3011>.
 Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309, 1239–1241. <https://doi.org/10.1126/science.1116030>.
 Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J., Purvis, A., 2008. The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. Lond. B Biol. Sci.* 275, 1441–1448. <https://doi.org/10.1098/rspb.2008.0179>.
 Cardoso, P., Erwin, T.L., Borges, P.A.V., New, T.R., 2011. The seven impediments in invertebrate conservation and how to overcome them. *Biol. Conserv.* 144, 2647–2655. <https://doi.org/10.1016/j.biocon.2011.07.024>.
 Carmona, C.P., Tamme, R., Pärtel, M., de Bello, F., Brosse, S., Capdevila, P., González-Suárez, M., Salguero-Gómez, R., Vázquez-Valderrama, M., Toussaint, A., González, M.R., 2021. Erosion of global functional diversity across the tree of life. *Sci. Adv.* 7, eabf2675 <https://doi.org/10.1126/sciadv.abf2675>.
 Chichorro, F., Juslén, A., Cardoso, P., 2019. A review of the relation between species traits and extinction risk. *Biol. Conserv.* 237, 220–229. <https://doi.org/10.1016/j.biocon.2019.07.001>.
 Chichorro, F., Correia, L., Cardoso, P., 2022. Biological traits interact with human threats to drive extinctions: a modelling study. *Eco. Inform.* 69, 101604 <https://doi.org/10.1016/j.ecoinf.2022.101604>.
 Cigliano, M.M., Braun, H., Eades, D.C., Otte, D., 2022. Orthoptera species file online [WWW document]. URL: <http://orthoptera.speciesfile.org/>. (Accessed 18 May 2022).
 Cowie, R.H., Bouchet, P., Fontaine, B., 2022. The sixth mass extinction: fact, fiction or speculation? *Biol. Rev.* 97, 640–663. <https://doi.org/10.1111/brv.12816>.
 De Vos, J.M., Joppa, L.N., Gittleman, J.L., Stephens, P.R., Pimm, S.L., 2015. Estimating the normal background rate of species extinction. *Conserv. Biol.* 29, 452–462. <https://doi.org/10.1111/cobi.12380>.
 Di Marco, M., Collen, B., Rondinini, C., Mace, G.M., 2015. Historical drivers of extinction risk: using past evidence to direct future monitoring. *Proc. R. Soc. B* 282, 20150928. <https://doi.org/10.1098/rspb.2015.0928>.
 Di Marco, M., Venter, O., Possingham, H.P., Watson, J.E.M., 2018. Changes in human footprint drive changes in species extinction risk. *Nat. Commun.* 9, 1–9. <https://doi.org/10.1038/s41467-018-07049-5>.
 Etard, A., Morrill, S., Newbold, T., 2020. Global gaps in trait data for terrestrial vertebrates. *Glob. Ecol. Biogeogr.* <https://doi.org/10.1111/geb.13184>.
 Fritz, S.A., Bininda-Emonds, O.R.P., Purvis, A., 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* 12, 538–549. <https://doi.org/10.1111/j.1461-0248.2009.01307.x>.
 Froese, R., Pauly, D., 2022. Fishbase [WWW document]. Fishbase (URL). <https://www.fishbase.org>. (Accessed 18 May 2022).
 Gage, G.S., Brooke, M.de L., Symonds, M.R.E., Wege, D., 2004. Ecological correlates of the threat of extinction in Neotropical bird species. *Anim. Conserv.* 7, 161–168. <https://doi.org/10.1017/S1367943004001246>.

- García-R, J.C., Di Marco, M., 2020. Drivers and trends in the extinction risk of New Zealand's endemic birds. *Biol. Conserv.* 249, 108730 <https://doi.org/10.1016/j.biocon.2020.108730>.
- Giam, X., Ng, T.H., Lok, A.F.S.L., Ng, H.H., 2011. Local geographic range predicts freshwater fish extinctions in Singapore: extinction correlates of tropical freshwater fish. *J. Appl. Ecol.* 48, 356–363. <https://doi.org/10.1111/j.1365-2664.2010.01953.x>.
- González-Suárez, M., Gómez, A., Revilla, E., 2013. Which intrinsic traits predict vulnerability to extinction depends on the actual threatening processes. *Ecosphere* 4, 1–16. <https://doi.org/10.1890/ES12-00380.1>.
- Harfoot, M.B.J., Johnston, A., Balmford, A., Burgess, N.D., Butchart, S.H.M., Dias, M.P., Hazin, C., Hilton-Taylor, C., Hoffmann, M., Isaac, N.J.B., Iversen, L.L., Outhwaite, C. L., Visconti, P., Geldmann, J., 2021. Using the IUCN red list to map threats to terrestrial vertebrates at global scale. *Nat. Ecol. Evol.* 5, 1510–1519. <https://doi.org/10.1038/s41559-021-01542-9>.
- IUCN, 2021. The IUCN Red List of Threatened Species. version 2021-3. [WWW document]. <http://www.iucnredlist.org>. (Accessed 18 May 2022).
- Johnson, C.N., Isaac, J.L., 2009. Body mass and extinction risk in Australian marsupials: the 'Critical weight range' revisited. *Austral Ecol.* 34, 35–40. <https://doi.org/10.1111/j.1442-9993.2008.01878.x>.
- Keane, A., Brooke, M.de L., McGowan, P.J.K., 2005. Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). *Biol. Conserv.* 126, 216–233. <https://doi.org/10.1016/j.biocon.2005.05.011>.
- Knape, M.L., Bush, A.M., Frishkoff, L.O., Heim, N.A., Payne, J.L., 2020. Ecologically diverse clades dominate the oceans via extinction resistance. *Science* 367, 1035–1038. <https://doi.org/10.1126/science.aax6398>.
- MacLean, S.A., Beissinger, S.R., 2017. Species' traits as predictors of range shifts under contemporary climate change: a review and meta-analysis. *Glob. Chang. Biol.* 23, 4094–4105. <https://doi.org/10.1111/gcb.13736>.
- Mattila, N., Kaitala, V., Komonen, A., Pälvinen, J., Kotiaho, J.S., 2011. Ecological correlates of distribution change and range shift in butterflies: distribution decline in butterflies. *Insect Conserv. Divers.* 4, 239–246. <https://doi.org/10.1111/j.1752-4598.2011.00141.x>.
- McCauley, S.J., Davis, C.J., Werner, E.E., Robeson, M.S., 2014. Dispersal, niche breadth and population extinction: colonization ratios predict range size in north American dragonflies. *J. Anim. Ecol.* 83, 858–865. <https://doi.org/10.1111/1365-2656.12181>.
- McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14, 450–453. [https://doi.org/10.1016/S0169-5347\(99\)01679-1](https://doi.org/10.1016/S0169-5347(99)01679-1).
- Meiri, S., 2018. Traits of lizards of the world: variation around a successful evolutionary design. *Glob. Ecol. Biogeogr.* 27, 1168–1172. <https://doi.org/10.1111/geb.12773>.
- Munstermann, M.J., Heim, N.A., McCauley, D.J., Payne, J.L., Upham, N.S., Wang, S.C., Knape, M.L., 2021. A global ecological signal of extinction risk in terrestrial vertebrates. *Conserv. Biol.* 1–13. <https://doi.org/10.1111/cobi.13852>.
- Murray, K.A., Verde Arregoitia, L.D., Davidson, A., Di Marco, M., Di Fonzo, M.M.I., 2014. Threat to the point: improving the value of comparative extinction risk analysis for conservation action. *Glob. Chang. Biol.* 20, 483–494. <https://doi.org/10.1111/gcb.12366>.
- Myhrvold, N.P., Baldrige, E., Chan, B., Sivam, D., Freeman, D.L., Ernest, S.K.M., 2015. An annuity life-history database to perform comparative analyses with birds, mammals, and reptiles. *Ecology* 96. <https://doi.org/10.1890/1548-8615.2015.96.3109>.
- Newbold, T., Bentley, L.F., Hill, S.L.L., Edgar, M.J., Horton, M., Su, G., Şekercioglu, Ç.H., Collen, B., Purvis, A., 2020. Global effects of land use on biodiversity differ among functional groups. *Funct. Ecol.* 34, 684–693. <https://doi.org/10.1111/1365-2435.13500>.
- Nic Lughadha, E., Baillie, J., Barthlott, W., Brummitt, N.A., Cheek, M.R., Farjon, A., Govaerts, R., Hardwick, K.A., Hilton-Taylor, C., Meagher, T.R., Moat, J., Mutke, J., Paton, A.J., Pleasants, L.J., Savolainen, V., Schatz, G.E., Smith, P., Turner, I., Wyse-Jackson, P., Crane, P.R., 2005. Measuring the fate of plant diversity: towards a foundation for future monitoring and opportunities for urgent action. *Philos. Trans. R. Soc.*, B 360 (1454), 359–372. <https://doi.org/10.1098/rstb.2004.1596>.
- Nolte, D., Boutaud, E., Kotze, D.J., Schuldt, A., Assmann, T., 2019. Habitat specialization, distribution range size and body size drive extinction risk in carabid beetles. *Biodivers. Conserv.* 28, 1267–1283. <https://doi.org/10.1007/s10531-019-01724-9>.
- Oliveira, B.F., São-Pedro, V.A., Santos-Barrera, G., Penone, C., Costa, G.C., 2017. AmphibiO, a global database for amphibian ecological traits. *Sci. Data* 4, 170123. <https://doi.org/10.1038/sdata.2017.123>.
- Owens, I.P.F., Bennett, P.M., 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *PNAS* 97, 12144–12148. <https://doi.org/10.1073/pnas.200223397>.
- Parlato, E.H., Armstrong, D.P., Innes, J.G., 2015. Traits influencing range contraction in New Zealand's endemic forest birds. *Oecologia* 179, 319–328. <https://doi.org/10.1007/s00442-015-3330-6>.
- Payne, J.L., Bush, A.M., Heim, N.A., Knape, M.L., McCauley, D.J., 2016. Ecological selectivity of the emerging mass extinction in the oceans. *Science*, aaf2416. <https://doi.org/10.1126/science.aaf2416>.
- Pimm, S.L., Jones, H.L., Diamond, J., 1988. On the risk of extinction. *Am. Nat.* 132, 757–785. <https://doi.org/10.1086/284889>.
- Price, S.A., Gittleman, J.L., 2007. Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in artiodactyls. *Proc. R. Soc. B Biol. Sci.* 274, 1845–1851. <https://doi.org/10.1098/rspb.2007.0505>.
- Purvis, A., Gittleman, J.L., Cowlshaw, G., Mace, G.M., 2000a. Predicting extinction risk in declining species. *Proc. R. Soc. Lond. B Biol. Sci.* 267, 1947–1952. <https://doi.org/10.1098/rspb.2000.1234>.
- Purvis, A., Jones, K.E., Mace, G.M., 2000. Extinction. *Bioessays* 22, 1123–1133. [https://doi.org/10.1002/1521-1878\(200012\)22:12<1123::AID-BIES10>3.0.CO;2-C](https://doi.org/10.1002/1521-1878(200012)22:12<1123::AID-BIES10>3.0.CO;2-C).
- Purvis, Andy, Cardillo, M., Grenyer, R., Collen, B., 2005. Correlates of extinction risk: phylogeny, biology, threat and scale. In: Purvis, Andrew, Gittleman, J.L., Brooks, T. (Eds.), *Phylogeny and Conservation, Conservation Biology*. Cambridge University Press, Cambridge, pp. 295–316. <https://doi.org/10.1017/CBO9780511614927.013>.
- R Core Team, 2022. *R: A Language and Environment for Statistical Computing*. Vienna, Austria.
- Rabinowitz, D., 1981. *Seven forms of rarity*. In: *Biological Aspects of Rare Plant Conservation*. John Wiley & Sons Ltd., New York, pp. 205–217.
- Reinhardt, K., Köhler, G., Maas, S., Detzel, P., 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the orthoptera of Germany. *Ecography* 28, 593–602. <https://doi.org/10.1111/j.2005.0906-7590.04285.x>.
- Richards, C., Cooke, R.S.C., Bates, A.E., 2020. Biological Traits of Seabirds Predict Extinction Risk and Vulnerability to Anthropogenic Threats. *bioRxiv*. <https://doi.org/10.1101/2020.09.30.321513>, 2020.09.30.321513.
- Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J., McCauley, D.J., 2017. Extinction risk is most acute for the world's largest and smallest vertebrates. *PNAS*, 201702078. <https://doi.org/10.1073/pnas.1702078114>.
- Ruland, F., Jeschke, J.M., 2017. Threat-dependent traits of endangered frogs. *Biol. Conserv.* 206, 310–313. <https://doi.org/10.1016/j.biocon.2016.11.027>.
- Ryan, D., 2018. Global plants: a model of international collaboration. *Biodivers. Inf. Sci. Stand.* 2, e28233 <https://doi.org/10.3897/biss.2.28233>.
- Saar, L., Takkis, K., Pärtel, M., Helm, A., 2012. Which plant traits predict species loss in calcareous grasslands with extinction debt? *Divers. Distrib.* 18, 808–817. <https://doi.org/10.1111/j.1472-4642.2012.00885.x>.
- Santini, L., Cornulier, T., Bullock, J.M., Palmer, S.C.F., White, S.M., Hodgson, J.A., Bocedi, G., Travis, J.M.J., 2016. A trait-based approach for predicting species responses to environmental change from sparse data: how well might terrestrial mammals track climate change? *Glob. Chang. Biol.* 22, 2415–2424. <https://doi.org/10.1111/gcb.13271>.
- Scott, I., Mitchell, P.I., Evans, P.R., 1994. Seasonal changes in body mass, body composition and food requirements in wild migratory birds. *Proc. Nutr. Soc.* 53, 521–531. <https://doi.org/10.1079/PNS19940062>.
- Secretariat of the Convention on Biological Diversity, 2020. *Global Biodiversity Outlook 5*. Montreal.
- Slatyer, R.A., Hirst, M., Sexton, J.P., 2013. Niche breadth predicts geographical range size: a general ecological pattern. *Ecol. Lett.* 16, 1104–1114. <https://doi.org/10.1111/ele.12140>.
- Soria, C.D., Pacifici, M., Di Marco, M., Stephen, S.M., Rondinini, C., 2021. COMBINE: a coalesced mammal database of intrinsic and extrinsic traits. *Ecology* 102, e03344. <https://doi.org/10.1002/ecy.3344>.
- Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J.M., Yang, J., Sayol, F., Neate-Clegg, M. H.C., Alioravainen, N., Weeks, T.L., Barber, R.A., Walkden, P.A., MacGregor, H.E.A., Jones, S.E.I., Vincent, C., Phillips, A.G., Marples, N.M., Montañón-Centelles, F.A., Leandro-Silva, V., Claramunt, S., Darski, B., Freeman, B.G., Bregman, T.P., Cooney, C.R., Hughes, E.C., Capp, E.J.R., Varley, Z.K., Friedman, N.R., Korntheuer, H., Corrales-Vargas, A., Trisos, C.H., Weeks, B.C., Hanz, D.M., Töpfer, T., Bravo, G.A., Remes, V., Nowak, L., Carneiro, L.S., Moncada, R., A.J. Matyskiová, B., Baldassarre, D.T., Martínez-Salinas, A., Wolfe, J.D., Chapman, P.M., Daly, B.G., Sorensen, M.C., Neu, A., Ford, M.A., Mayhew, R.J., Fabio Silveira, L., Kelly, D.J., Annorbah, N.N.D., Pollock, H.S., Grabowski-Zhang, A.M., McEntee, J.P., Carlos, T., Gonzalez, J., Meneses, G.G., Muñoz, M.C., Powell, L.L., Jamie, G.A., Matthews, T.J., Johnson, O., Brito, C.G.R., Zyskowski, K., Crates, R., Harvey, M.G., Jurado Zevallos, M., Hosner, P.A., Bradford-Lawrence, T., Maley, J.M., Stiles, F.G., Lima, H.S., Provost, K.L., Chibesa, M., Mashao, M., Howard, J.T., Mlamba, E., Chua, M.A.H., Li, B., Gómez, M.I., García, N.C., Päckert, M., Fuchs, J., Ali, J.R., Deryberry, E.P., Carlson, M.L., Urriza, R.C., Brzeski, K.E., Prawiradilaga, D.M., Rayner, M.J., Miller, E.T., Bowie, R.C.K., Lafontaine, R.-M., Scofield, R.P., Lou, Y., Somarathna, L., Lepage, D., Illif, M., Neuschulz, E.L., Templin, M., Dehling, D.M., Cooper, J.A., Pauwels, O.S.G., Analuddin, K., Fjeldså, J., Seddon, N., Sweet, P.R., DeClerck, F.A.J., Naka, L.N., Brawn, J.D., Aleixo, A., Böhning-Gaese, K., Rahbek, C., Fritz, S.A., Thomas, G.H., Schleuning, M., 2022. AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.* 25, 581–597. <https://doi.org/10.1111/ele.13898>.
- Toussaint, A., Brosse, S., Bueno, C.G., Pärtel, M., Tamme, R., Carmona, C.P., 2021. Extinction of threatened vertebrates will lead to idiosyncratic changes in functional diversity across the world. *Nat. Commun.* 12, 5162. <https://doi.org/10.1038/s41467-021-25293-0>.
- Uetz, P., Hošek, J., 2022. Reptile database [WWW document]. URL <http://www.reptile-database.org/>. (Accessed 18 May 2022).
- Verde Arregoitia, L.D., 2016. Biases, gaps, and opportunities in mammalian extinction risk research. *Mammal Rev.* 46, 17–29. <https://doi.org/10.1111/mam.12049>.
- Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* 36, 1–48. <https://doi.org/10.18637/jss.v036.i03>.
- Weiss, K.C.B., Ray, C.A., 2019. Unifying functional trait approaches to understand the assemblage of ecological communities: synthesizing taxonomic divides. *Ecography* 42, 2012–2020. <https://doi.org/10.1111/ecog.04387>.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., Jetz, W., 2014. EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology* 95. <https://doi.org/10.1890/13-1917.1>, 2027–2027.