A systematic review of the relation between species traits and extinction risk

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ABSTRACT

Biodiversity is shrinking rapidly, and despite our efforts only a small part of it has been assessed for extinction risk. Identifying the traits that make species vulnerable might help us to predict the outcome for those less known. We gathered information on the relations of traits to extinction risk from 173 publications, across all taxa, spatial scales and biogeographical regions, in what we think is the most comprehensive compilation to date. The Palaearctic is the most represented biogeographical realm in extinction risk studies, but the other realms are also well sampled for all vertebrate groups. Other taxa are less well represented and there are gaps for some biogeographical realms. Many traits have been suggested to be good predictors of extinction risk. Among these, our meta-analyses were successful in identifying two as potentially useful in assessing risk for the lesser-known species: regardless of the taxon, species with small range and habitat breadth – two of the three classic dimensions of rarity – are more vulnerable to extinction. On the other hand, body size (the most studied trait) did not present a consistently positive or negative response. Large species

can be more, or less, threatened than their smaller counterparts, depending on the taxon and spatial setting. In line with recent research, we hypothesize that the relationship between body size and extinction risk is shaped by different aspects, namely body size is a proxy for different phenomena depending on the taxonomic group, and there might be relevant interactions between body size and the specific threat that a species faces. With implications across all traits, a particular focus in future studies should be given to the interaction between traits and threats. Furthermore, intraspecific variability of traits should be part of future studies whenever data is available. We also propose two complementary paths to better understand extinction risk dynamics: (i) the simulation of virtual species and settings for theoretical insights, and (ii) the use of comprehensive and comparable empirical data representative of all taxa and regions under a unified study.

Keywords: biological traits, functional diversity, IUCN, machine learning, meta-analysis, threat status.

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I. Introduction

The last annual checklist of the Catalogue of Life reports 1.7 million (eukaryote) species described on this planet (Roskov *et al.*, 2017). Describing the remaining estimated 7 million might still take 1,200 years if the rates of description, average number of new species described per taxonomist's career, and average cost to describe species remain constant (Mora *et al.*, 2011). This latency in describing species is put into a typical crisis context if, as predicted, 3,000 species fall into extinction every year (Wilson, 2003; González-Oreja, 2008), many of them undescribed.

The International Union for Conservation of Nature (IUCN) compiles and keeps updated a database with assessments of risk of extinction for species. As of August 2018, 26 197 (28%) of all 93 577 species in this list were either Critically Endangered, Endangered, or Vulnerable to extinction and 14 616 (16%) were Data Deficient (IUCN, 2018). Yet, species in the IUCN database mostly comprise well-known taxa (e.g. 67% of vertebrates have been assessed versus 0.8% of insects (IUCN, 2018)), and it will probably take decades until a reasonable proportion of many taxa, such as most invertebrates, are assessed (Cardoso *et al.*, 2011a, b, 2012). Increasing the number of species in the database to the point where we have an unbiased picture of extinction risk across all organisms during the next years seems highly unlikely, as is the Barometer of Life goal of assessing 160 000 species by 2020 (Stuart *et al.*, 2010). Moreover, extinction is taxonomically selective (e.g. 63% of cycads are assessed as threatened versus 'only' about 13% of bird species (IUCN, 2018)). The current proportions of endangered species might not represent the greater picture of species diversity. Therefore, alternative ways of predicting the risk of extinction of species are urgently needed.

Understanding which biological/ecological traits of species make them more vulnerable could help us predict their extinction risk and make species protection and conservation planning more efficient. This approach is not new. Some comparative studies can be traced back to the 19th century (see McKinney, 1997, for a thorough historical perspective), and since the beginning of the new millenium many new comparative studies have arisen on the topic, as well as discussions over their usefulness (Fisher & Owens, 2004; Cardillo & Meijaard, 2012; Murray *et al.*, 2014; Verde Arregoitia, 2016). Many traits have been tested across

hundreds of publications. Body size, for example, was found to be positively correlated with extinction risk across multiple taxa (Seibold *et al.*, 2015; Terzopoulou *et al.*, 2015; Verde Arregoitia, 2016), either through direct effects (e.g. larger species require more resources) or as a proxy for other traits (e.g. larger species have slower life cycles and therefore respond more slowly to change). Range size and population density, even after taking into account that they are often used to quantify extinction risk, have also been extensively tested and found to be relevant, at least for mammals (Purvis et al., 2000a; González-Suárez, Gómez & Revilla, 2013; Bland *et al.*, 2015; Verde Arregoitia, 2016). Traits related to exposure to human pressures have also been relevant in predicting threats to species (Cardillo, 2003), and recently Murray *et al.* (2014) have called for more studies explicitly incorporating threats and the interplay between traits and threats into the analyses. The inclusion of threat information in predicting extinction risk has indeed proved to increase the explanatory power of models (Murray *et al.*, 2014), and in some cases the same trait can bolster extinction risk or prevent it, depending on the threat (González-Suárez *et al.*, 2013).

Most of the studies to date have focused on mammals (e.g. Purvis *et al.*, 2000a; Cardillo *et al.*, 2008; González-Suárez *et al.*, 2013) and other vertebrates (e.g. Owens & Bennett, 2000; Luiz *et al.*, 2016), with relatively few on plants (e.g. Sodhi *et al.*, 2008; Powney *et al.*, 2014; Stefanaki *et al.*, 2015) and invertebrates (e.g. Sullivan *et al.*, 2000; Koh, Sodhi & Brook, 2004; Arbetman *et al.*, 2017). Each study was made on different spatial settings and scales, testing different traits (often according to availability of data), and employed different methods and response variables. While this is necessary and valuable information, making sense of the plethora of contrasting results is difficult, and perceiving general trends and trying to cover current gaps and bias are urgent. In this work we attempt to answer the following questions through a comprehensive bibliography search, data exploration and meta-analysis:

- Which traits have been studied more often?
- Which traits have been suggested as predictors of extinction risk?
- How generalizable are the past results?
- What directions should research take in the future to overcome the shortage and bias of data?

II. Material and Methods

In this review we undertook two sequential analyses of studies that examined the relation between traits of species and their estimated extinction risk: first, an exploratory analysis of the literature, to know which traits have been more studied and which were found to be most relevant, and second, multiple meta-analyses, in which we tried to use comparable data from a subset of the studies to understand and quantify trends across studies and taxa from all published data and to see whether any general conclusions can be made from existing literature.

(1) Bibliography selection

We were aiming to retrieve a list of all publications that have explicitly performed comparative studies of biological/ecological traits and extinction risk/decline of species and to identify which traits, extrinsic factors and taxa were used in each analysis and at which spatial scale. We searched in the Web of Science using the keywords 'trait*' and 'extinct*' in October 2016 and obtained a list of 2,616 manuscripts. To consider a given paper as relevant to our study, all of the following conditions had to be met:

- more than five species were involved in the study;
- for each species there was information on at least one biological trait;
- for each species there was some kind of quantification of its extinction risk;
- there was a statistical model linking the species traits (explanatory variables) to the extinction risk (response variables), assigning scores to each trait involved (not necessarily significance).

We considered as extinction risk measurements any of the following:

- recent (anthropogenic) extinctions versus extant species;
- any variable (continuous, ordinal, categorical or binary) directly indicating relative extinction risk, whether it was based on the IUCN Red List categories or not;
- population trend data, or a proxy of population trend data, in time;
- any other variables that indicated decline of species over time and/or risk of extinction.

On a first reading of a small part of the studies, we realized that most were not relevant to the study, as either traits or extinction were marginal to our questions (some were not even related to biology) or some of the minimum requirements were missing. Analysing 2,616 manuscripts would have been too time consuming when a relatively small fraction would be relevant. For this reason, we used an automated process to sort out relevant publications.

We used a random forest algorithm trained to identify relevant from non-relevant publications. We first created two sets of 35 abstracts+titles, one with relevant and one with non-relevant papers (70 in total). As words with common roots (e.g. extinction and extinct) should be quantified together, we used the R software (R Core Team, 2018) and package SnowballC (Bouchet-Valat, 2014) to stem these words (e.g. all words in the 'extinct' family fall into the same stem). We also excluded hyphenation, punctuation and stopwords (Rajamaran & Ullman, 2011) using R packages SnowballC and tm (Feinerer *& Hornik,* 2008). Then, all the words and corresponding word counts of each abstract were used as variables in training the random forest model.

Decision trees were built with packages rpart (Therneau & Atkinson, 2015) and rpart.plot (Milborrow, 2018). The training of the random forest algorithm was run with 50 000 trees and 45 variables tried at each step (the suggested number of variables is the square root of the number of words, Liaw & Wiener, 2002) with R package randomForest (Liaw & Wiener, 2002). To validate the model, we assembled another set of abstracts (n = 76, test set) and calculated the sensitivity, specificity and the true skill statistic (TSS) of the model based on predictions on the test set. After training and validating the algorithm, we used it to classify the remaining 2,000+ abstracts. In order to further test for false negatives, i.e. papers incorrectly labelled as non-relevant leading to the loss of important studies, we randomly picked 100 abstracts labelled as non-relevant and checked them.

To update the full set of relevant papers, we performed another search using the same keywords in June 2018, retrieving new publications and obtaining 682 further studies from the Web of Knowledge. The trained algorithm was again used to filter potentially relevant publications from these. We finally added to the relevant set all papers of which we had prior knowledge by other means.

(2) Statistical analysis

(a) Data collection

We assembled information on each comparative statistical test employed in each article. For each of these tests, we extracted information on the following (see also Appendix S1, S2):

- **Taxonomic group**: mammals, birds, reptiles, amphibians, fishes, insects, molluscs, other invertebrates, plants and fungi.
- **Geographical realm**: Afrotropics, Antarctic, Australasia, Indo-Malaya, Nearctic, Neotropics, Oceania and Palaearctic (Olson *et al.*, 2001).
- **Traits**: continuous, ordinal, categorical or binary – units, the number of observations (usually species), and whether there was a significant response to extinction risk for that test. We grouped traits with similar biological meaning into the same unified trait (e.g. body length and body mass into 'body size'). Henceforth, trait refers to these unified traits. Finally, to identify meaningful groups of traits and facilitate analysis, we clustered these traits into meaningful classes (see next section).
- **Statistical methodology**: generalized linear models and linear models (including parametric tests of the generalized linear models' and linear models' families, Pearson correlations, G-tests, analysis of variance and analysis of covariance, chi-square statistics), generalized linear mixed models (GLMMs) and linear mixed models (parametric tests of the generalized mixed linear models' and linear mixed models' families), decision tree based (including random forests, boosted or non-boosted classification and regression trees), generalized estimating equations, phylogenetic comparative methods (PGCMs; which include phylogenetic independent contrasts and phylogenetic generalized least squares), non-parametric (Kruskal–Wallis, Spearman rank correlations, etc.), and other (including discriminant analysis, path analysis, randomization tests, skewness tests, structural equation modelling).

- **Phylogenetic control**: we distinguished absolute no control of phylogeny from at least some control of phylogeny (via using phylogenetic trees or a taxonomical higher group as a controlling or covariable in the analyses).
- **Proxy of extinction used**: IUCN based (where the response variable – ordinal or binary – is based upon IUCN assessments of species), other red lists (based on non-IUCN red lists), temporal trends (in which the trend can be the difference between population numbers, or geographical range size, between two time periods, or the slope of the variation in the population numbers over time), and everything else as others (recently extinct species versus extant species, extirpated versus non-extirpated, etc.).

(b) Trait classes

We named nine natural groups (or categories) of traits (Table 1). All these categories describe a property of a focal species, but they differ in the general type of such property:

- **Individual**: traits measurable at an individual level: morphological traits, traits related to reproductive output and life-cycle speed.
- **Population**: traits that describe a property of a whole population. Such properties can relate to how individuals of the populations of the focal species aggregate, whether they are social, or other traits only measurable at the population level, like population density or abundance.
- **Community**: in this category, traits describe the interactions between the focal species and other species in the community, whether this interaction is trophic or other, such as symbiosis, commensalism or pollination.
- **Evolution**: including traits related to how successful a species might be in adapting to change through evolution, as well as any other traits related to the evolutionary history of the species.
- **Space**: traits describing the current or past geographical distribution in space of the species or its ability to disperse.
- **Time**: traits that describe how species use time at different scales, such as daily or seasonal cycles.
- **Environmental niche**: traits mainly describing species interactions with their biotic or abiotic niche, such as habitat affinities and preferential climatic ranges.

- **Human influence**: traits that describe the interplay between species and humans, such as habitat loss due to anthropogenic causes and hunting or other uses of the species.
- **Taxonomy**: taxonomic affinity or hierarchy of the species.
- **Other**: traits that do not fit into any of the previous groups.

(c) Exploratory analysis

In the exploratory analysis we first compared the number of studies across taxa and combinations of taxa across biogeographical realms, proxy of extinction used, statistical methodology, and phylogeny. Next, we compared the number of studies in which each trait was used, and calculated the percentage of significant measurements of each trait. Statistical tests which did not assign significance levels to traits had to be excluded from this step (e.g. most decision tree methodologies).

(d) Meta-analysis

To understand whether traits were positively or negatively related to extinction risk across the multiple studies, we performed meta-analyses for each continuous trait. Meta-analyses are useful because they allow the comparison of outcomes from different studies by converting the outcomes to effect sizes. The use of Fisher's Z as the effect size has the advantage of allowing very diverse statistical methodologies into the same effect size measurement. Effect sizes were obtained by transforming the statistics reported in the manuscripts (F, z, X^2, t or r^2) into Pearson's product-moment correlation coefficients (r) by applying equations (1) to (5) (Rosenthal, 1991) and then transforming r into Fisher's Z using equation (6) using R package metafor (Viechtbauer, 2010):

$$r = \frac{z}{\sqrt{N}} \qquad (1)$$

$$r = \sqrt{\frac{t^2}{t^2+df}} \qquad (2)$$

$$r = \sqrt{\frac{F_{1,df}}{F_{1,df}+df}} \qquad (3)$$

$$r = \sqrt{\frac{X_1^2}{N}} \qquad (4)$$

$$r = \sqrt{r^2} \qquad (5)$$

$$Z = \frac{1}{2\ \ln\frac{1+r}{1-r}} \qquad (6)$$

To ensure that the outcomes would be comparable, we restricted the analyses to univariate tests. We followed two different methodologies to detect the overall effect size for each trait. We first performed a traditional random-effects meta-analytic model for each trait. Random-effect meta-analytic models assume that in addition to the sampling error within measurements, there is also another source of variation between measurements due to different methodologies being used. However, traditional meta-analytic methods lack a tool to control for the existence of multiple measurements within studies. Therefore, we also used linear mixed models, since these allow for more flexibility by controlling multiple measurements within studies (and hence non-independence of observations) through the use of random effects (see Prugh, 2009; Chaplin-Kramer *et al.*, 2011). Fisher's Z was the response variable and was weighted by the inverse of the sample sizes. Additionally, in the linear mixed models the response variable was tested against the intercept term only, with random effects being taxonomic group and study.

III. Results

(1) Bibliography selection

The random forests classified 488 abstracts as relevant in the first literature search. The sensitivity, specificity and TSS on the test data were respectively 0.895, 0.868 and 0.763. A number of word roots were found to be of considerable importance in the abstract filtering, namely 'extinct', 'risk', 'speci' and 'vulner', all with a decrease in the Gini index above 0.7 (Appendix S3, Fig. S1), even if the most parsimonious tree used the words 'extinct', 'habitat' and 'caus' (Appendix S3, Fig. S2). The algorithm classified an additional 135 abstracts as relevant from the second literature search. After human filtering and the inclusion of a single false negative, the number of relevant publications decreased from 623 to 136. To these we added 37 papers found a priori to be relevant and not identified by the algorithm, for a total of 173 manuscripts fulfilling all criteria and included in this study (Appendix S1).

(2) Exploratory analysis

(a) Studies

The number of publications relating traits to extinction risk has increased steadily (Fig. 1). Mammals and birds have received the most attention over the years, followed by fishes, insects and plants. Most studies were conducted in the Palaearctic region (Fig. 2), particularly for insects and plants. Of particular note, amphibians, reptiles and mammals have been included in many studies focusing on the Australasian realm. Oceania and especially the Antarctic were the least represented biogeographical realms, with intermediate values in all the other regions.

Regarding the response variable, IUCN categories and temporal trends (including range size or population size contractions over time) were the most used (Table 2). IUCN categories were used mainly in studies assessing mammals and amphibians but much less so in insect studies. Temporal trends and other red-list types were mostly used in bird and insect studies.

Most studies used methodologies that take into consideration at least some degree of non-independence of species, namely GLMMs (by using taxonomic group as random effect) and PGCMs (Table 2). Among these, PGCMs require phylogenetic trees, often not available for many taxa, and hence they were mostly used in mammal studies for which a global tree was easy accessible (e.g. Bininda-Emonds *et al.*, 2007).

(b) Traits

The most commonly used trait categories were Individual, Space, and Environmental Niche (Fig. 3 and Table 1). Similarly, the Individual, Space, and Environmental Niche categories had the highest number of measurements, along with Human influence (Fig. 3).

Body size was by far the most studied trait both in the Individual category, as well as overall (Fig. 4), followed by geographical range size. After these, several traits appeared in a similar number of studies: habitat type, habitat breadth and fecundity (Fig. 4). The taxonomic group was used in some studies to control for phylogeny and often to guarantee the comparability of results across taxa. The compound metric trait was

in most cases a variable resulting from the first axis of principal component analysis of traits and their relationships, and therefore it contained a mix of traits from multiple groups.

Geographical range size was the trait with the greatest proportion of studies with not non-significant tests (almost three quarters) (Fig. 4). Among the traits that were present in at least 10% of the studies, several were not non-significant in at least 40% of the tests, half of them belonging to the Environmental Niche category (temperature, (micro)habitat type, habitat breadth) but also to the Individual (body size), Space (location) and Community (diet breadth) categories.

Even when used in at least 10% of studies, not all of these traits were studied across all taxa. Body size and geographical range size were the only traits that were studied for all taxa (except for fungi, since the only study focusing on fungi did not attribute significance levels to traits and thus this group was not included here) and were significant in at least one test for each taxon. The other 10 traits occurred in at least 7 out of 9 taxa. They belong to the Environmental Niche (altitude, temperature, temperature range, habitat breadth, habitat type, microhabitat type), Community (diet type), Space (location, motility), and Individual (offspring number per reproductive event) categories.

Despite occurring in less than 10% of the studies, many traits have been found to be good predictors of extinction risk for some taxa. A number of traits (see Appendix S4 for the significances of all tested traits within taxa) were tested in at least three studies and were significant at least once, even if for single taxa (torpor/hibernation and weaning age in mammals; duration of flight period in birds; temperature for breeding in fishes; overwintering stage in insects; pollen vector, reproduction type, dispersal agent, and seed size in plants).

(3) Meta-analysis

Geographical range size, habitat breadth, and body size were the only traits from which we could determine effect sizes and sample sizes from at least 10 studies including univariate tests – the minimum number that we considered reasonable in order to have confidence in the results of the meta-analyses. Effect sizes of geographical range size and body size mostly originated from mammal and bird studies but also from studies on reptiles, amphibians, fishes, insects, other invertebrates and plants (Appendix S5, Figs S14, S15). Effect

sizes of habitat breadth also originated mostly from mammal and bird studies, yet reptile, amphibian, other invertebrates and plant studies were included (Appendix S5, Fig. S16).

The random-effect meta-analytic model identified significant negative effect sizes for geographical range size and habitat breadth, and positive effect sizes for body size. However, these analyses failed to take into consideration the disproportionate number of effect sizes within studies (some studies with more tests drove the results) and the number of effect sizes per taxon (some taxa drove the results) in all three analyses (Appendix S5, Figs S14–S16). Due to the much better control of such bias allowed by the linear mixed model analyses, we henceforth focus on this.

For geographical range size and habitat breadth, the overall effect size was consistently and significantly negative across taxa and studies (Table 3, Appendix S5, Figs S14–15). Contrasting with the classic meta-analysis, the linear mixed model revealed an overall effect size not different from zero for body size (Table 3). Effect sizes of body size were either positive or negative (Appendix S5, Fig. S16), and while there was some tendency in mammals and birds for the effect sizes to be positive, in plants these were consistently negative.

IV. Discussion

Our review clearly reveals the increasing importance of the study of species traits on the understanding and prediction of extinction risk. The interest in the subject, even if relatively recent, is increasing exponentially and shows no signs of slowing down. Yet, we also found that past studies were biased in scope in terms of taxa, with vertebrates having the largest share, and spatial setting, with the Palaearctic dominating across taxa, although Australasia is much studied for mammals, reptiles and amphibians. Such biases should be mostly due to a large body of accumulated knowledge of these taxa and regions, to which a predominance of researchers in these areas continue to contribute. The special interest in the Australasian mammals may be

due to an ongoing debate on the role of body size in extinction risk in this particular region (Verde Arregoitia, 2016).

Despite being, to our knowledge, the largest review of the relation between traits and extinction risk to date, we are aware that this contribution might not include all relevant studies in this field. Using less restrictive rules for inclusion of studies would help to retrieve more publications (like the ones used in Verde Arregoitia, 2016, and Murray *et al.*, 2014) but would probably lead to a higher bias towards some better studied taxa (vertebrates). The proportion of non-vertebrate studies included in our study is larger than that of Murray *et al.* (2014), even though the bias is inevitable in any comprehensive study on this subject. Publication bias may also occur due to studies with non-significant terms being often less reported in the literature (Gurevitch *et al.*, 2018), which might cause changes in the magnitude of effect sizes. We are, however, confident that this review is thorough and as unbiased as possible with current data.

Herein we suggest a new way of grouping traits that works across taxa and is useful to better visualize trends when many traits are studied. Previous attempts of grouping traits by Verde Arregoitia (2016) followed functional groups: traits related to reproduction, morphology, ecology, behaviour, among others. Yet, this categorization was hard to do across taxa, as the same trait might reveal different phenomena of interest according to each study and in particular each taxon. That is the case, for example, with body size, which in mammals and invertebrates is often associated with reproductive speed (Purvis *et al.*, 2000a; Cardillo, 2003; Kotze & O'Hara, 2003; Bland, 2017) but with competitive ability and fitness in plants (Falster & Westoby, 2003; Walker & Preston, 2006; Laanisto *et al.*, 2015). Some traits in the Spatial category would fit equally well under Individual traits, but in those publications from where they were extracted they were used as proxy of dispersal ability (e.g. wing length and wing aspect ratio for bats, Safi & Kerth, 2004). Our trait classes, thus, are not functional classes in the typical sense, but rather follow a more complex set of rules related to how traits are measured and what they represent for the chance of survival of the species.

(1) Relation between traits and extinction risk

Geographical range size was the best predictor of extinction risk overall. This is not surprising, since small geographical range is one of the values used in IUCN assessments (criteria B, D2), and these assessments are

the measure of extinction risk in many studies, which might lead to circular reasoning. However, even when excluding from the analyses all species considered threatened due to small range, range was still strongly associated with extinction risk (e.g. Purvis *et al.*, 2000a; Wang *et al.*, 2018). The mechanism behind this relationship is not entirely understood (Purvis *et al.*, 2000a), but geographical range size captures ecological and dispersal attributes of species that would require harder to obtain variables, such as overall abundance of species, which are important in understanding extinction risk (Polaina, Revilla & González-Suárez, 2016). The abundance–occupancy relationship is a well-known and thoroughly studied pattern, and many mechanisms relate abundance to extinction risk (Gaston *et al.*, 2002). Likewise, range size is related to the dispersal ability of species, determining the capacity of a species to occupy new areas to escape multiple pressures, and with habitat breadth, revealing the ability of a species to cope with habitat change or loss.

Among the studies we included in our analysis, species with greater habitat breadth (habitat generalists) were less prone to becoming extinct. Specialists have long been regarded as losers, and generalists as winners in the current extinction crisis (McKinney & Lockwood, 1999), and ecological niche theory predicts the worldwide decline in specialist species (Clavel, Julliard & Devictor, 2011). Whether this trend is due to the intrinsic specificity of the species or to geographical range size is, however, not trivial to discern. In the studies included in this review, most habitat breadth measures were derived from maps. Consequently, less widespread species have less sampling points and therefore might show smaller habitat breadth due to sampling bias alone (Burgman, 1989), when in reality we lack knowledge of whether they could thrive under different habitats. Despite this, one of the studies we analysed controlled for range size by using the residuals of a regression of range size by habitat breadth (Tingley, Hitchmough & Chapple, 2013) thus excluding the effect of range size from the variable of interest, and they still found a negative relationship of this trait with extinction risk in New Zealand lizard species. Furthermore, in a review on the topic, Slatyer, Hirst & Sexton (2013) showed that even after taking into consideration sampling bias, the relationship between habitat breadth and geographical range size remains significant across taxa. Irrespective of the putative causes or relations to other variables, species with larger habitat breadth do have more chances to escape from multiple pressure types and are consistently less threatened across taxa and spatial settings.

Although almost half of all measurements of body size were significant, the meta-analyses revealed that the relationship between body size and extinction risk is not unidirectional. The interplay between body size and threat type is one of the reasons for this phenomenon. Owens and Bennett (2000) showed that while larger bird species were threatened by overexploitation, habitat loss or degradation selected for smaller species. The same trend seems to apply at least to marine fishes (Olden, Hogan & Zanden, 2007) and mammals (González-Suárez *et al.*, 2013), taxa that are often targeted directly and selectively by man. Independently of threats, relationships may not even be linear. Threatened freshwater fishes are found both at the smaller and larger spectrum of body sizes (Olden *et al.*, 2007), and the same bimodal relationship is found when pooling all vertebrates together (Ripple *et al.*, 2017). In general, this bimodality seems to be derived from threat type, with different threats leading to increasing extinction risk of different body size classes.

Other traits for which we could not perform a quantitative analysis have also shown to be useful in predicting extinction risk under certain circumstances. Among the most studied traits in the Individual category are traits related to speed of life cycle and reproductive output: fecundity, egg/neonatal size, and generation length. These traits usually correlate with each other and with body size and longevity: bigger, longer-lived species often have lower fecundity, bigger egg/neonatal sizes and longer generation lengths. Threat status has been positively related to species with decreased fecundity (Cardillo, 2003; González-Suárez & Revilla, 2013; Böhm *et al.*, 2016; Ribeiro *et al.*, 2016; but see Pinsky & Byler, 2015; Sreekar *et al.*, 2015), larger egg/neonatal sizes (Cardillo *et al.*, 2005; Jones, Fielding & Sullivan, 2006; González-Suárez & Revilla, 2013; Pinsky & Byler, 2015) and longer generation lengths (Anderson *et al.*, 2011; Hanna & Cardillo, 2013; Jeppsson & Forslund, 2014; Comeros-Raynal *et al.*, 2016; but see Chessman, 2013). These traits reduce the capability of species to compensate for high mortality rates (Pimm, Jones & Diamond, 1988; Purvis *et al.*, 2000a; González-Suárez *et al.*, 2013), even if their longer longevities should make them more apt to resist at lower densities as they survive longer and might be able to overcome short-lived threats (Pimm *et al.*, 1988). When species are directly persecuted by man, they are often bigger, with larger fecundity and egg/neonatal sizes (Owens & Bennett, 2000; González-Suárez *et al.*, 2013), and longer longevity alone is not sufficient to compensate for the high mortality. But when the threat is habitat loss, which indirectly increases mortality

and/or reduces natality rates, the trend is non-existent or even reversed (Owens & Bennett, 2000; González-Suárez *et al.*, 2013), this being possibly due to the advantages of longer longevity alone.

Some traits related to Environmental Niche (besides habitat breadth) are commonly used across taxa and much data are available about them. Among those, temperature (optimal temperature or temperature of the species across its geographical range) and temperature range (range of temperatures tolerated by the species or range of temperatures found across its geographical range) were often important predictors in the studies that used them. Species with lower average temperatures within their range or narrower temperature ranges are especially at risk due to an increasingly warmer climate (Jiguet *et al.*, 2010; Grenouillet & Comte, 2014; Flousek *et al.*, 2015). In contrast, thriving under broad temperature ranges grants species the necessary flexibility to deal with environmental or climatic change and hence lower their extinction risk (Chessman, 2013; Lootvoet, Philippon & Bessa-Gomes, 2015). When exceptions were found, these were due to the correlation of temperature with the true causes of change in extinction risk. For example, tropical species of amphibians living in narrower temperature ranges were found to be less at risk, as the higher tropical temperatures possibly lead to higher fecundity and hence adaptability of the species (Cooper *et al.*, 2008).

Although the generality of the pattern could not be confirmed across studies, species depending on habitats more affected by human influence are often more threatened (Stefanaki *et al.*, 2015; Powney *et al.*, 2014). In Greece, flowering plants occurring in coastal or ruderal habitats, under pressure from urbanization and tourism, were more at risk than flowering plants occurring on cliffs or high-mountain vegetation, the latter habitats being under lower human pressure (Stefanaki *et al.*, 2015). British plant species with lower affinity to nitrogen-rich soils are declining due to the intensification of agriculture, which has led to increased inputs of nitrogen in otherwise nitrogen-poor soils (Powney *et al.*, 2014). Likewise, microhabitat type was a good predictor of extinction risk in some studies due to some microhabitats becoming more rare with increased human pressure (Parent & Schriml, 1995; Seibold *et al.*, 2015). A striking example is the decline of saproxylic beetles that use dead wood of large diameter in Germany, as forest management options often lead to the scarcity of such microhabitat (Seibold *et al.*, 2015). These observations give support to recent claims that predicting extinction risk requires taking into account the threat type and using different variables related to human use of species and habitats (Murray *et al.*, 2014).

Among all variables measured at the community level, both diet breadth and type were significant predictors across several studies. The diet of a species can be important in leading to and predicting extinction in two ways. Species restricted to fewer dietary options have shown to be more threatened (Basset *et al.*, 2015; Jeppsson & Forslund, 2014; González-Suárez *et al.*, 2013; Matsuzaki *et al.*, 2011; Mattila *et al.*, 2008), probably due to lower flexibility in switching to other options when the availability of their preferred food source decreases (Purvis, Jones, & Mace, 2000). On the other hand, diet type, namely the trophic position of a species, may be as important. Species at higher trophic levels tend to be more threatened (Chessman, 2013; Bender *et al.*, 2013; Cardillo *et al.*, 2004; Purvis *et al.*, 2000a) and often provide early warnings of extinction across the entire food chain (Cardoso *et al.*, 2010). The greater dependence on the densities and larger foraging areas of prey species may lead to such a pattern (Carbone & Gittleman, 2002), with synergistic effects between resource abundance and other factors contributing to the decline of, for example, predators. With the density of wildlife dwindling everywhere (e.g. Hallmann *et al.*, 2017), and everything else being equal, top predators are expected to be more at risk.

Within the Space category, location and migration distance were often tested and found to be important predictors. Location as a trait is very idiosyncratic, and it just informs that the geographical location where the species is found is a significant predictor of threat. As extinctions are not spatially random, and might even interact with some traits (see, for example, Fritz, Bininda-Emonds & Purvis, 2009), this is to be expected and relates more to the threat than to the species itself. Most studies on migration distance are of birds. Long distance migrants tend to be more at risk, which could be either due to phenological mismatch due to climate change (Amano & Yamaura, 2007; Jiguet *et al.*, 2010; Thaxter *et al.*, 2010; Flousek *et al.*, 2015), dependence on the good quality of at least two habitats or sites (Jiguet *et al.*, 2010; Flousek *et al.*, 2015), or to increased competition with resident species that, in temperate regions, survive through increasingly less severe winters (Jiguet *et al.*, 2010; Amano & Yamaura, 2007).

Finally, there are also traits that were found to be significant but only studied for one or two taxa. These include a wide array of morphological traits that are taxon specific. Some plant growth forms (e.g. herbaceous, bush or tree) are more threatened than others. Perennial growth forms can sustain populations through harsh times (Stefanaki *et al.*, 2015) but might be more affected by forest loss (Leão *et al.*, 2014).

Mammals going through a hibernating or torpor phase are less prone to becoming extinct, due to a greater capacity to avoid harsher seasonal conditions (Liow *et al.*, 2009). The life stage in which an insect overwinters (egg, larva, pupa or adult) influences vulnerability (e.g. Powney *et al.*, 2015; Jeppsson & Forslund, 2014; Mattila *et al.*, 2009). At least for some studies with particular applied relevance, Cardillo & Meijaard (2012) claim that 'researchers should adopt a somewhat "smaller picture" view by restricting the geographical and taxonomic scope of comparative analyses, and aiming for clearer, more focused outcomes on particular hypotheses'. We corroborate that restricting the studies in these two dimensions might prove useful when the goal goes beyond understanding the general pattern and requires true predictive power for species extinctions.

(2) Generalization

Given the inherent bias of past studies, any generalizations require critical consideration. Geographical range and habitat breadth seem to be very well supported across taxa and regions, even if most past studies using such traits were on vertebrates. Both are consistently negatively related to extinction risk and might be seen as representing a single phenomenon: the range or rarity of a species in two different dimensions (area and habitat). Species with larger ranges, be these spatial or biotic, have more chance of surviving in case of diminishing availability of resources, and the risk of their populations or the entire species vanishing is smaller. These traits can therefore be confidently used as predictors of extinction risk across taxa. Area and habitat are in fact two of the three dimensions of rarity preconized by Rabinowitz (1981): geographical range size, habitat breadth, and local abundance. The latter was seldom used probably due to the scarcity of abundance data for most taxa (the Prestonian shortfall, Cardoso *et al.*, 2011b) but is certainly crucial to fully understand the extinction phenomenon.

Body size, on the other hand, seems to be at least taxon dependent, probably because, as previously mentioned, it represents different ways in which species interact with their environment and therefore how they affect their risk of extinction (González-Suárez *et al.*, 2013; Ripple *et al.*, 2017). This trait is often studied as a proxy for traits that may be very hard to measure or are very abstract. This implies that the mechanisms behind the relation between body size and extinction risk are very much dependent on the traits that body size proxies. Therefore, what it really represents for the way the species copes with different

threats must be treated with caution. If for animals it usually is related to resource availability, as larger animals require more, often scarce, resources, being these space, food or other, for plants it represents competitive ability, with larger plants being able to better exploit, for example, the sun, by growing taller and overshadowing smaller species, or water and mineral resources found deeper underground. Many other traits were either seldom studied or rarely found to be relevant. We must emphasize, however, that we still lack a complete and unbiased picture of the relation between traits and extinction risk and that future studies could and should provide insights much beyond what is possible now.

(3) Next steps

Given the scarcity and/or lack of comparability of data, we were not able to test the importance of the vast majority of traits used in the past. Many of them might turn out to be crucial to the understanding of extinction mechanisms and their prediction across multiple taxa. Also important to emphasize, Murray *et al.* (2014) have already called for more papers that include human pressures as covariables in comparative studies of extinction risk. Here we further reinforce this need. Furthermore, and somewhat surprisingly given its perceived and demonstrated importance, not many studies included intraspecific variability of any trait. Higher intraspecific variability has shown to predispose species to adapt to changing conditions (González-Suárez & Revilla, 2013); however, morphological, physiological, genetic or behavioural variability have seldom been studied, probably due to a lack of data. Here we also emphasize the importance of including intraspecific variability in its different dimensions in future studies whenever data is available.

We propose two complementary paths for the future that will allow research in this area to be advanced further and eventually allow prediction of the extinction risk of species based on their traits: (1) simulations of virtual settings, threats and species using agent-based modelling, and (2) exhaustive sampling of unbiased data across taxa and regions.

Computer simulations, in the form of agent-based models (ABMs, Grimm *et al.*, 2010), offer a framework in which species, maps and interactions can be designed from scratch and which therefore can help us untangle the often complicated relationships between traits, threats and the extinction risk of species. Out of simple rules between interacting agents often emerge patterns not implicitly incorporated into the system (Grimm *et*

al., 2010). This is one of the main advantages of ABMs. By defining simple rules on how agents are created, get energy, reproduce and die, we can test how changing different aspects related to a functional trait, in interaction with a landscape, where threats are also modelled, will influence the outcome. Two approaches, with different objectives, are possible. In one approach, the objective is to understand the mechanisms behind extinction risk. In this approach, we simplify the system and simulate only the minimum required complexity to understand the underlying mechanisms under certain conditions. Such a procedure is not very common in biological sciences, but theoretical results are an important part of science and have proven crucial to moving science forward in some fields, such as physics (Goldstein, 2018). In a second approach, the objective is to use the models for prediction and therefore model complexity must be as much as is needed for robust and realistic predictions. These two approaches are complementary and much needed to complement the set of tools available to conservation biologists.

A strong predictor of extinction risk is important in a model when the amount of variation it explains is high even after introducing other traits into the analysis. However, because we analysed very diverse studies, focusing on multiple taxa and spatial settings, it was impossible to compare the performance of each trait while taking into consideration other traits, because no two studies compared exactly the same traits in a multivariable setting. The main idea behind this approach is to perform a single comparative study including many different taxa, in which species selection, trait data collection, and statistical analysis are performed in a congruent way thus allowing full comparability of taxa and traits.

V. Conclusions

(1) Most studies investigating drivers of extinction risk have focused on vertebrates, particularly mammals and birds, due to larger amounts of knowledge accumulated for these taxa. Likewise, many studies were restricted to certain regions, namely the Palaearctic, with other regions remaining understudied.

(2) Species with smaller ranges are more at risk of extinction irrespective of the taxon or geographical setting. The underlying mechanism is not entirely understood, yet species that occur in smaller ranges may have a particular set of traits, not captured in other commonly studied traits, that predispose them to elevated extinction risk such as reduced numbers and less dispersal ability.

(3) Species with narrow habitat breadth (habitat specialists) are also consistently more vulnerable to extinction across taxa and regions. When estimating the habitat breadth of a species, one may, however, find a spurious relationship between habitat breadth and extinction risk, due to the former being often correlated with geographical range size. Nonetheless, habitat breadth has been correlated with extinction risk, independently of geographical range. Like geographical range size, habitat breadth is a good predictor for less known species.

(4) Body size, the most studied trait, is an important predictor of risk. However, bigger species may be more, or less, threatened than smaller species. The underlying mechanism is rather more complicated than for the two previous traits, which is explained both by body size being (i) a proxy for very contrasting, often abstract, and hard to quantify traits (e.g. reproductive output in animals, competitive ability in plants), and (ii) very dependent on the threats to each species.

(5) The relationship between the vast majority of species traits, threats and extinction risk remains elusive. Many traits were found to be important across studies but have seldom been studied or are relevant for only some taxa.

(6) Human pressure and other threats should be increasingly used as covariates in comparative studies of extinction risk. Furthermore, intraspecific variability of traits should be part of future studies whenever data is available.

(7) We propose two contrasting approaches for future work: simulations with strong theoretical background to understand the mechanisms behind the relation of traits to extinction risk, and performing a single comparative study, across taxa, in order to ensure comparability of results.

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VII. References

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VIII. Supporting Information

Appendix S1 – List of all studies and traits included in the analyses

Appendix S2 – Data-frames with all information on studies and traits collected.

Appendix S3 – Important words in the automated filtering of publications

Appendix S4 – Proportion of significant measurements by trait and taxon

Appendix S5 – Forest plots of the meta-analyses

Figures

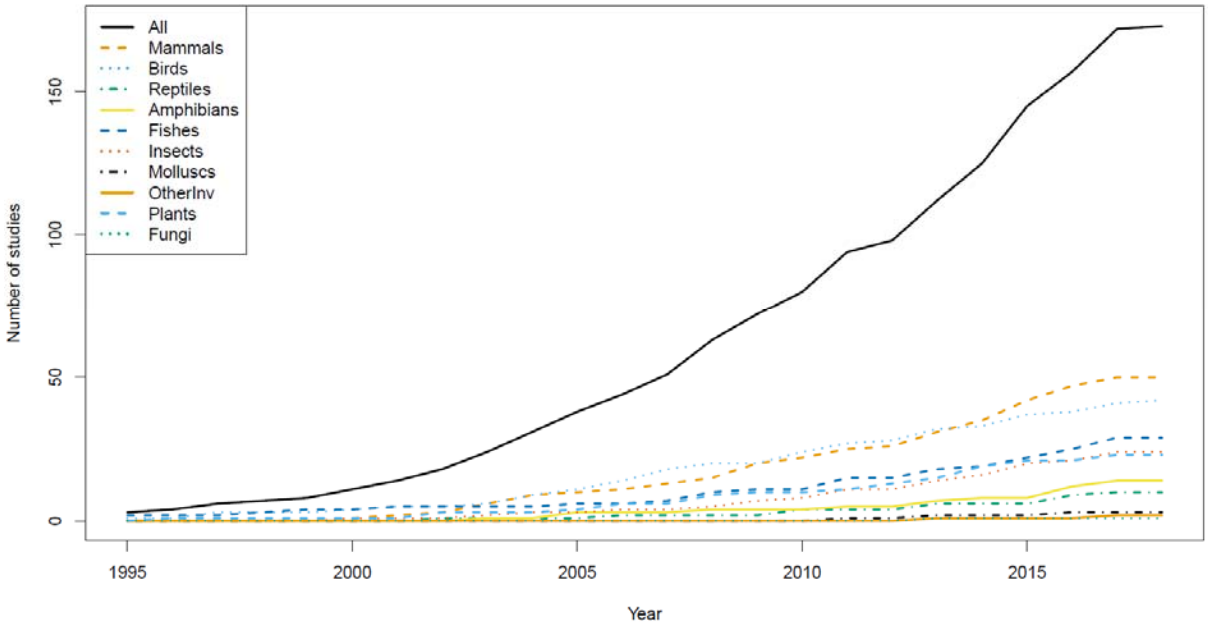

Figure 1: Cumulative number of publications per taxon relating traits to extinction risk.

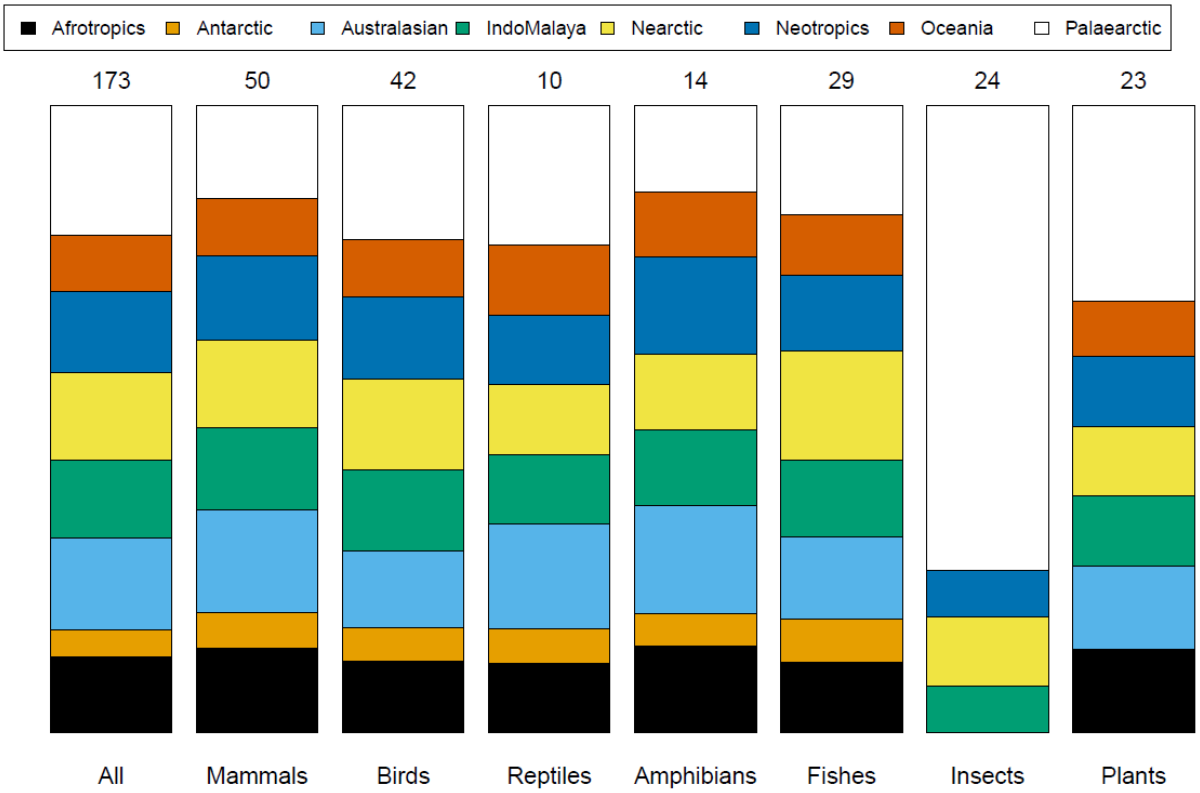

Figure 2: Proportion of manuscripts focusing on the different biogeographical regions by taxonomic group.

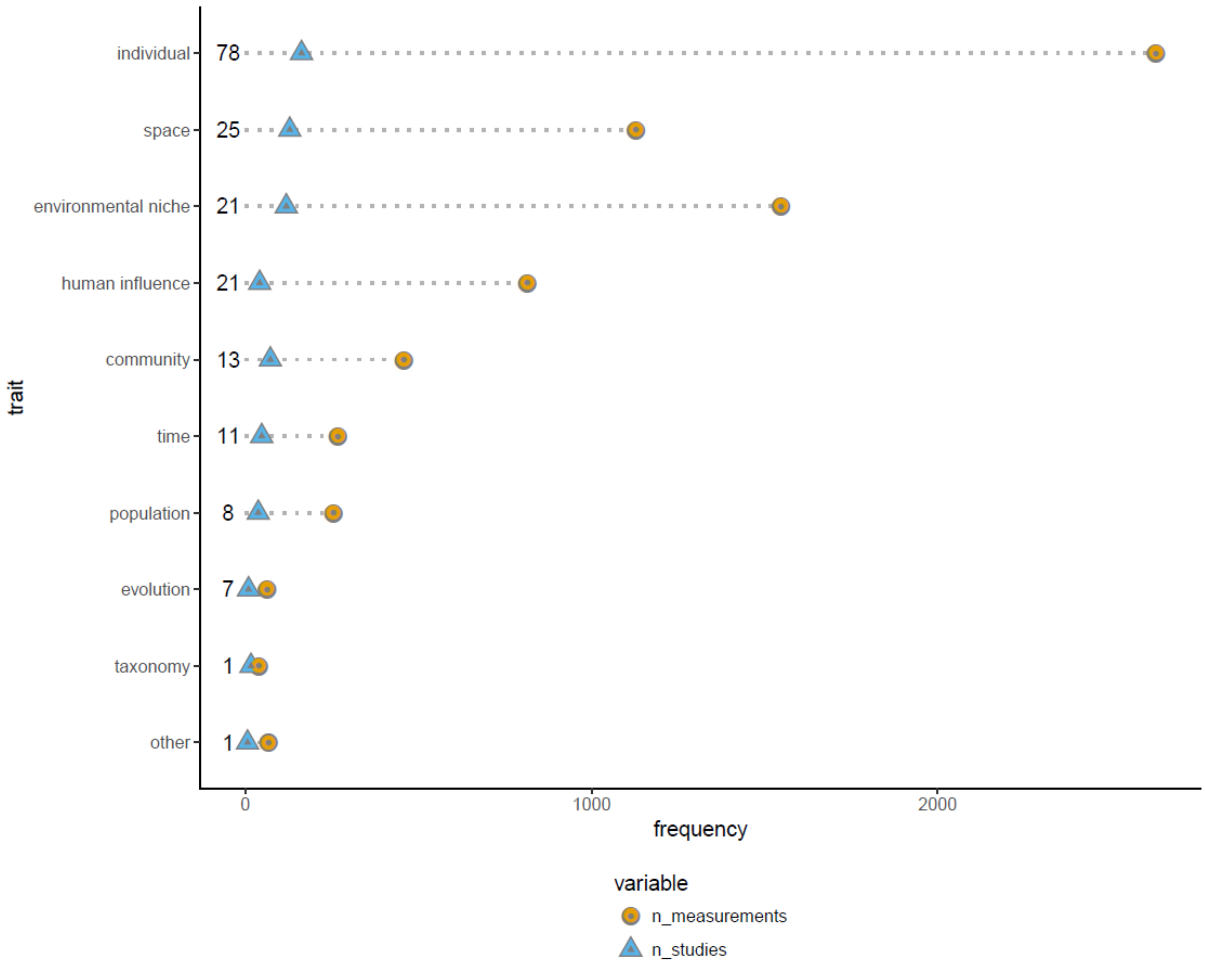

Figure 3: Number of studies and measurements per class of traits, as well as the number of unique traits in each major trait class (numbers before the dotted lines). **n_studies:** Number of studies in which the variable appears. **n_measurements:** total number of measurements for that variable.

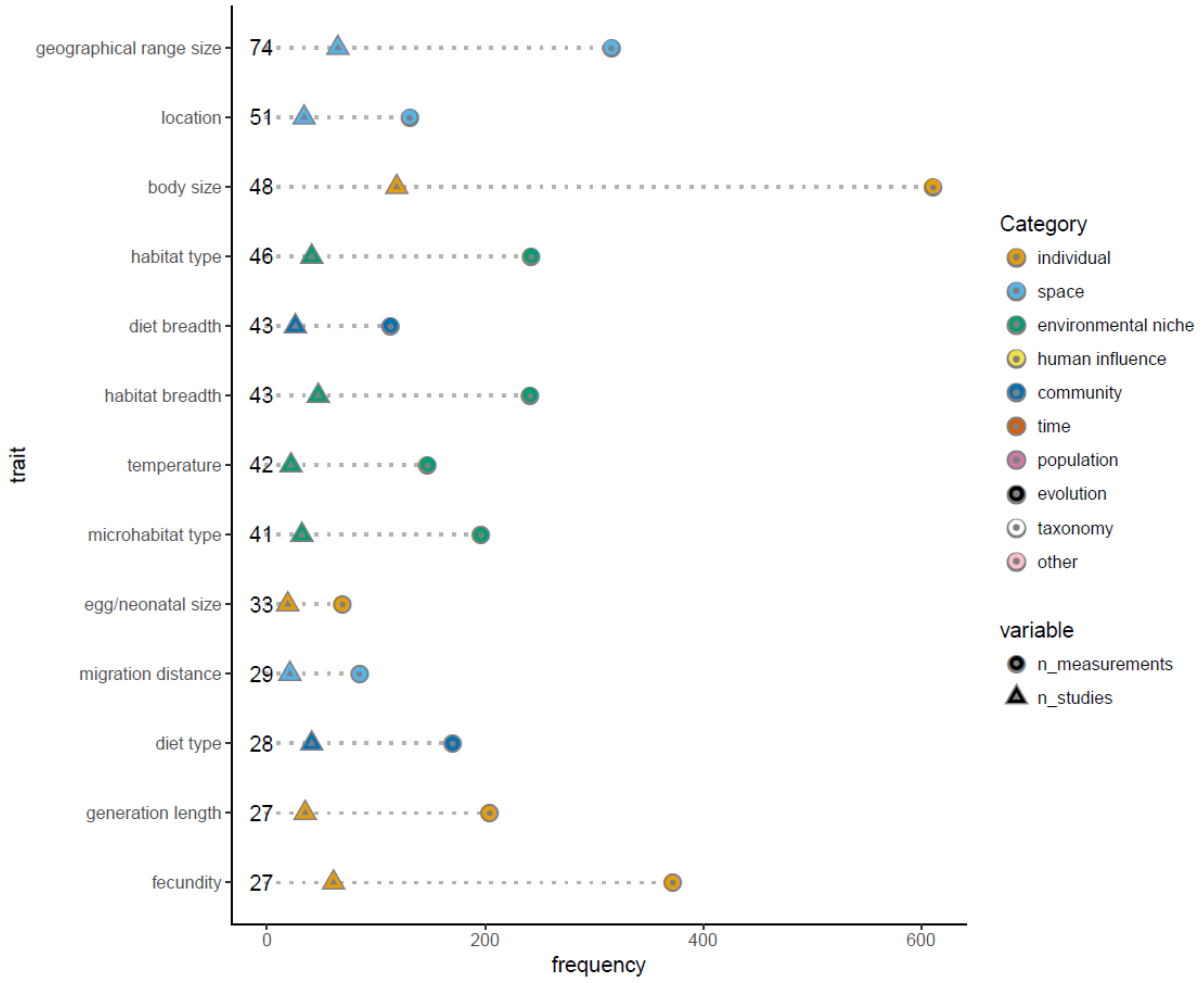

Figure 4: Summary information on variable use among all studies, depicting only variables included in at least 17 (10%) studies. The numbers before the dotted lines indicate the percentage of measurements in which the variable was significant. **n_studies**: number of studies in which the variable appears. **n_measurements**: total number of measurements for that variable.

Tables

Table 1: Traits and categories identified across the 173 studies analysed. The number of studies for each trait is shown in parentheses.

	Traits
Individual	Body size (141), fecundity (73), generation length (41), longevity (24), egg/neonatal size (21), nest microhabitat (20), gestation/incubation length (19), development type (13), plant growth form (13), interbirth interval (11), reproduction type (sexual or asexual) (11), parental care (10), sexual dimorphism (10), weaning age (10), pollen vector (9), fertilization mode (8), monogamy (7), brain size (6), population growth rate (6), gonad size (5), competitor richness (4), fledgling duration (4), age at eye opening (3), investment in reproduction (3), mass-specific metabolic rate (3), nest guarding (3), body shape (2), body size at weaning (2), colour detectability category (2), CSR ruderality (2), fecundity variability (2), nest vulnerability (2), vegetative resprouting capacity (2), body armour (1), body size variability (1), chela shape (1), chela size (1), chemical defence (1), clutch volume (1), colour pattern variability (1), CSR competitiveness (1), CSR strategy (1), CSR stress tolerance (1), egg-laying behaviour (1), egg adhesion (1), egg buoyancy (1), egg/neonatal size variability (1), endotherm (1), forearm length (1), forearm length variability (1), generation length variability (1), gestation/incubation length variability (1), incubating sex (1), interbirth interval variability (1), internal or external fertilization (1), larval body size (1), leaf length (1), leaf mass per unit area (1), leaf water content (1), male combat (1), male horn length (1), mouth brooding (1), niche uniqueness (1), number of reproductive years (1), number of teats (1), number of teats variability (1), plant coverage (1), ploidy (1), ploidy variability (1), plumage polymorphism (1), population juvenile ratio (1), population level sex ratio (1), sex change (1), specific leaf area (1), spire index (1), tail length (1), tongue length (1), weaning age variability (1)
Population	Population density (18), social group size (12), sociality (10), population abundance (6), spawning aggregation (2), survivability (2), population density variability (1), social group size variability (1)
Community	Diet type (49), diet breadth (35), floral colour (2), ambush predation (1), amount of floral reward (1), corolla segmentation (1), depending on symbioses (1), floral display (1), floral shape (1), floral size (1), functional reproductive unit (1), length of corolla tube (1), predator type (1)
Space	Geographical range size (81), location (39), migration distance (24), dispersal ability (21), home range size (17), insularity (13), wing size (13), dispersal agent (8), seed size (5), endemism (4), historical geographical range size (4), geographical range size change (3), wing shape (3), diaspore type (2), fruit dehiscence (2), geographic origin (2), location change (2), active dispersion (1), age at dispersal (1), air-breathing capability (1), altitudinal range shift (1), diaspore mass (1), geographical range size of host (1), home range size variability (1), reproductive area (1)
Time	Circadian period (17), overwintering stage (11), duration of reproductive season (10), timing of reproductive season (9), duration of flight period (8), torpor/hibernation (3), seasonality of reproduction (2), circadian range (1), flight period to adult life span (1), timing of migration (1), winter leaf carrying (1)
Evolution	Taxon age (5), evolutionary plasticity (2), rate of diversification (2), taxon richness (2), rate of climatic niche evolution (1), rate of habitat niche evolution (1), rate of trophic niche evolution (1)
Environmental niche	Habitat type (56), habitat breadth (54), microhabitat type (36), temperature (27), altitude (16), precipitation (16), temperature range (12), altitude range (7), evapotranspiration (6), precipitation range (6), productivity within range (6), nest habitat (5), temperature for breeding (3), climate range (2), annual productivity range (1), humidity (1), microhabitat breadth (1), shelter use (1), water balance within range (1), wingtip shape (1), wingtip size (1)
Human influence	Human population density (14), direct exploitation (13), land-use proportion (11), threat range (9), human footprint (7), threat type (7), land-use change (4), change in human population density (3), seed bank longevity (3), threat breadth (3), accessibility (2), gross domestic product (2), human resource intake (2), proportion of range protected (2), considered a pest (1), controlled by man (1), country responsible for management (1), economic value (1), human night-time lights (1), pollution tolerance (1), protection status (1)
Other	Compound metrics (6)
Taxonomy	Taxonomic group (16)

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Table 2: Number of publications within each taxonomic group, response variables, controlling phylogeny or not, and statistical approach. Percentages are of the number of publications within each category divided by the total number of publications in the given taxonomic group. GEE = generalized estimating equation; GLM = generalized linear model; GLMM = generalized linear mixed model; LM = linear model; LMM = linear mixed model; PGCM = phylogenetic comparative method.

		All	Mammals	Birds	Reptiles	Amphibians	Fishes	Insects	Plants
No. of studies		173	50	42	10	14	29	24	23
Response variable	IUCNcateg	76 (44%)	35 (70%)	14 (33%)	4 (40%)	10 (71%)	12 (41%)	3 (12%)	7 (30%)
	Temporal Trend	54 (31%)	9 (18%)	18 (43%)	0 (0%)	3 (21%)	6 (21%)	11 (46%)	8 (35%)
	Other Redlists	33 (19%)	7 (14%)	8 (19%)	6 (60%)	1 (7%)	6 (21%)	8 (33%)	6 (26%)
	Other	19 (11%)	1 (2%)	3 (7%)	0 (0%)	0 (0%)	7 (24%)	4 (17%)	3 (13%)
Approach	DT based	20 (12%)	7 (14%)	3 (7%)	1 (10%)	4 (29%)	6 (21%)	1 (4%)	4 (17%)
	GEE	5 (3%)	1 (2%)	2 (5%)	0 (0%)	0 (0%)	1 (3%)	0 (0%)	1 (4%)
	GLM&LM	82 (47%)	16 (32%)	19 (45%)	7 (70%)	5 (36%)	14 (48%)	13 (54%)	14 (61%)
	GLMM&LMM	21 (12%)	6 (12%)	5 (12%)	1 (10%)	2 (14%)	5 (17%)	3 (12%)	4 (17%)
	Non-parametric	18 (10%)	2 (4%)	4 (10%)	1 (10%)	1 (7%)	5 (17%)	3 (12%)	2 (9%)
	Other	9 (5%)	4 (8%)	2 (5%)	1 (10%)	2 (14%)	3 (10%)	1 (4%)	0 (0%)
	PGCMs	64 (37%)	30 (60%)	17 (40%)	4 (40%)	4 (29%)	3 (10%)	6 (25%)	3 (13%)
Control of phylogeny	yes	116 (67%)	41 (82%)	30 (71%)	8 (80%)	9 (64%)	16 (55%)	15 (62%)	13 (57%)
	no	94 (54%)	23 (46%)	22 (52%)	7 (70%)	7 (50%)	16 (55%)	15 (62%)	15 (65%)

Table 3: Results of the linear mixed-effect models relating extinction risk with body size, geographical range size and habitat breadth. ***df:*** Degrees of freedom, ***P:*** p value.

Model	Number of studies / measurements / different taxa	Taxa (number of studies/measurements)	Intercept estimate (standard error)	*df*	t value	*P*
Effect sizes of Geographical range size ~ (Intercept) + Random(Study) + Random(Taxon)	22/44/9	Mammals (6/10), Birds (6/15), Reptiles (3/3), Amphibians (3/4), Fishes (2/4), Vertebrates (1/2), Insects (2/4), Other Invertebrates (1/1), Plants (1/1)	−0.463 (0.112)	23.424	−4.137	0.0004
Effect sizes of body size ~ (Intercept) + Random(Study) + Random(Taxon)	30/84/9	Mammals (9/33), Birds (10/25), Reptiles (4/9), Amphibians (3/3), Fishes (3/7), Vertebrates (1/1), Insects (1/1), Other invertebrates (1/1), Plants (3/4)	0.126 (0.104)	11.503	1.205	0.2520
Effect sizes of Habitat breadth ~ (Intercept) + Random(Study) + Random(Taxon)	14/25/6	Mammals (2/6), Birds (6/11), Reptiles (2/3), Amphibians (2/3), Vertebrates (1/1), Other invertebrates (1/1), Plants (1/1)	−0.208 (0.040)	11.622	−5.162	0.0003