Review

A 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 status for those less known. We gathered information on the relationships between traits and extinction risk from 173 publications, across all taxa, spatial scales and biogeographical regions, in what we think it is the most comprehensive compilation to date. We aimed to identify (1) taxonomical and spatial biases, and (2) statistically robust and generalizable predictors of extinction risk through the use of meta-analyses. Vertebrates and the Palaearctic are the most studied taxon and region because of higher accumulation of data in these groups. Among the many traits that have been suggested to be predictors, only three had enough data for meta-analyses. Two of them are potentially useful in assessing risk for the lesser-known species: regardless of the taxon, species with small range and narrow habitat breadth are more vulnerable to extinction. Contrastingly, body size (the most studied trait) did not present a consistently positive or negative response. We hypothesize that the relationship between body size and extinction risk is shaped by different aspects, namely the phenomena represented by body size depending on the taxonomic group. To increase our understanding of the drivers of extinction, further studies should focus on understudied groups such as invertebrates and fungi and regions such as the tropics and expand the number of traits in comparative analyses that should avoid current biases.

1. Introduction

Extinction risk is the quantification of how likely a species is to disappear in the foreseeable future. The International Union for Conservation of Nature (IUCN) compiles and keeps updated a database with assessments of risk of extinction for species (IUCN Red-List, https://www.iucnredlist.org/). As of January 2019, 26,840 (28%) of all 96,951 species in this list were either Critically Endangered, Endangered, or Vulnerable to extinction and 15,055 (16%) were Data Deficient (IUCN, 2019). 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, 2019)), and it will probably take decades until a reasonable proportion of many taxa, such as most invertebrates, are assessed (Cardoso et al., 2011a, 2011b, 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, 2019)). 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 millennium many new comparative studies have arisen on the topic, as well as discussions over their usefulness (Fisher and Owens, 2004; Cardillo and 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), as a proxy for other traits (e.g. larger species have slower life cycles and therefore respond more slowly to change) or simply because larger species tend to be hunted more. Range size and population density, even after considering 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 et al., 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 and 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 et al., 2004; Arbetman et al., 2017). Each study focused on different spatial settings and scales, testing different traits (often according to availability of data), and employing 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?
- What are the taxonomical and spatial biases found in the literature?
- Which traits have been suggested as predictors of extinction risk?
- How generalizable are the past results, i.e., are there traits that have a consistent response across taxonomical groups and geographical settings?

2. 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. The first one was an exploratory analysis of the literature, that allowed us to identify the gaps and the traits have been more studied and which were found to be most relevant. The second analysis consisted of multiple meta-analyses, in which comparable data extracted from a subset of the studies were used to understand and quantify trends across studies and taxa from all published data and to see whether any general conclusions could be made from existing literature.

2.1. Bibliography selection

We were aiming to retrieve an extensive list of publications that 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. In doing so, we first retrieved a list of candidate publications, and then we considered them or not for this review based on them meeting a set of criteria. To assemble the candidate list, we searched Web of Science using the keywords 'trait*' and 'extinct*' until July 2018, and we checked the abstracts and titles for appropriateness. Additionally, we collected all papers from previous similar reviews (Murray et al., 2014; Verde Arregoitia, 2016), and included publications already known to us. To consider a given paper as relevant to our study, all 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 a measurement 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 measurements of extinction risk:

- 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.

While not all these were strict measurements of extinction risk, they provided some indication of the risk species face and where therefore used under the same framework.

2.2. Data collection

We assembled information on each comparative statistical test employed in each article. For each of these tests, we extracted

Table 1
Number of publications within each taxonomic group, response variables, statistical approach, and controlling phylogeny or not. Percentages are of the number of publications within each category divided by the total number of publications in the given taxonomic group. DT = decision tree; GEE = generalized estimating equation; GLM = generalized linear model; GLMM = generalized linear mixed model; LM = linear model; LMM = linear mixed model; PGCM = phylogenetic comparative method. **Control of phylogeny**: we distinguished absolute no control of phylogeny (no) from at least some control of phylogeny (yes, via using phylogenetic trees or a taxonomical higher group as a controlling or covariable in the analyses).

		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%)

information on the following (see also Table 1 and Appendix B, C):

- **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 that refer to the same attribute into a single unified trait. The unified traits serve two purposes: one is to standardize the names of traits that have the same biological meaning (e.g. body length and snout-vent-length, but not neonate body size as this has different implications). The other purpose is to group as many traits as possible from across all taxonomical groups, provided their biological meaning is similar to make analyses more robust and general. This is specially challenging when grouping organisms with very distinct survival strategies such as animals and plants (e.g. animal growth is deterministic, plant and fungal growth is opportunistic; the concept of individual is much easier to grasp in animals, but harder to grasp in plants and fungi due to lateral growth and cloning). We arranged traits in a way that minimized overlap between unified traits. In most cases, we were able to assemble unified traits that, at least theoretically, may occur in every taxonomical group studied and which have very clear biological meaning (e.g., body size, a measure of the potential biomass of a species; habitat type, the rough habitat type of a species; microhabitat type: abiotic preferences of a species at the sub-habitat level). In other cases, some traits were so specific to some taxonomical groups that it was deemed impossible to group them with others (e.g. chela size, characteristic only of some invertebrates). In those cases, we preferred to assemble unified traits that preserved biological meaning rather than taxonomical ubiquitousness. All original names and assigned unified traits are available in Table B.1 of Appendix B, and Appendix C. Henceforth, trait refers to these unified traits.

2.3. Exploratory analysis

In the exploratory analysis we first compared the yearly cumulative growth of the number publications included in the review with that of the field of biodiversity and conservation (Appendix A). Next, we compared the number of studies across taxa, biogeographical realms, proxy of extinction used, statistical methodology, and if phylogeny was controlled for (in comparative studies, phylogenetic relationships between species are often accounted for, so that species can be treated as independent observations from each other in statistical tests, which they are not due to shared evolutionary history, see Purvis et al., 2000a). Next, we compared the number of studies and the number of measurements (the number of measurements corresponds to the total number of statistical coefficients of each trait, usually corresponding to the number of statistical tests for that trait) in which each trait was used and calculated the percentage of significant measurements of each trait (based on reported *p*-values of those statistical coefficients). Statistical tests which did not assign significance levels to traits had to be excluded from this step (e.g. most classification and regression tree methodologies, random forests, but also some traditional generalized linear and phylogenetic generalized linear models).

2.4. 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 Eqs. (1) to (5) (Rosenthal, 1991) and then transforming r into Fisher's Z using Eq. (6) using R package meta for (Viechtbauer, 2010):

$$r = \frac{z}{\sqrt{N}} \tag{1}$$

$$r = \sqrt{\frac{t^2}{t^2 + df}} \tag{2}$$

$$r = \sqrt{\frac{F_{1,df}}{F_{1,df} + df}} \tag{3}$$

$$r = \sqrt{\frac{X_1^2}{N}} \tag{4}$$

$$r = \sqrt{r^2} \tag{5}$$

$$Z = \frac{1}{2 \ln \frac{1+r}{1-r}} \tag{6}$$

To ensure that the outcomes would be comparable, we only used effect sizes from univariate tests. To detect the overall effect size for each trait, we ran linear mixed models. In relation to more traditional analytic tools, mixed models can be more flexible in 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. The response variable was tested against the intercept term only, with random effects being taxonomic group and study.

Comparing the geographical range size of a species with its extinction risk is in some cases a circular exercise, since this trait is often used in IUCN red-list assessments to quantify the extinction risk of a species, namely through its criteria B and D2. Therefore, we excluded from the meta-analysis of this trait those effect sizes from studies that did not exclude species listed in the IUCN red list solely based under criteria B and D2.

3. Results

A total of 173 manuscripts fulfilled all criteria and were included in this study (Appendix S2).

3.1. Exploratory analysis

3.1.1. Studies

The number of publications relating traits to extinction risk has increased steadily (Fig. 1). Compared to the growth in biodiversity and conservation studies in general, there was a disproportional increase in the number of studies relating traits to extinction risk in the early 2000s (Fig. 1), especially so in studies that based their response variables on red-list categories (Fig. A.1). Since the 2010s the number of studies has been decreasing when compared with the number of studies in conservation, and comparatively less red-list information is being used to build response variables (Fig. A.1). Mammals and birds have received the most attention over the years, followed by fishes, insects and plants (Table 1). Most studies were conducted in the Palaearctic region (Fig. 2), particularly for insects, which were barely studied outside of this realm. Of particular note, amphibians, reptiles and mammals have been included in many studies focusing on the Australasian realm. We only identified one study including fungi, and it was just in the Palaearctic realm.
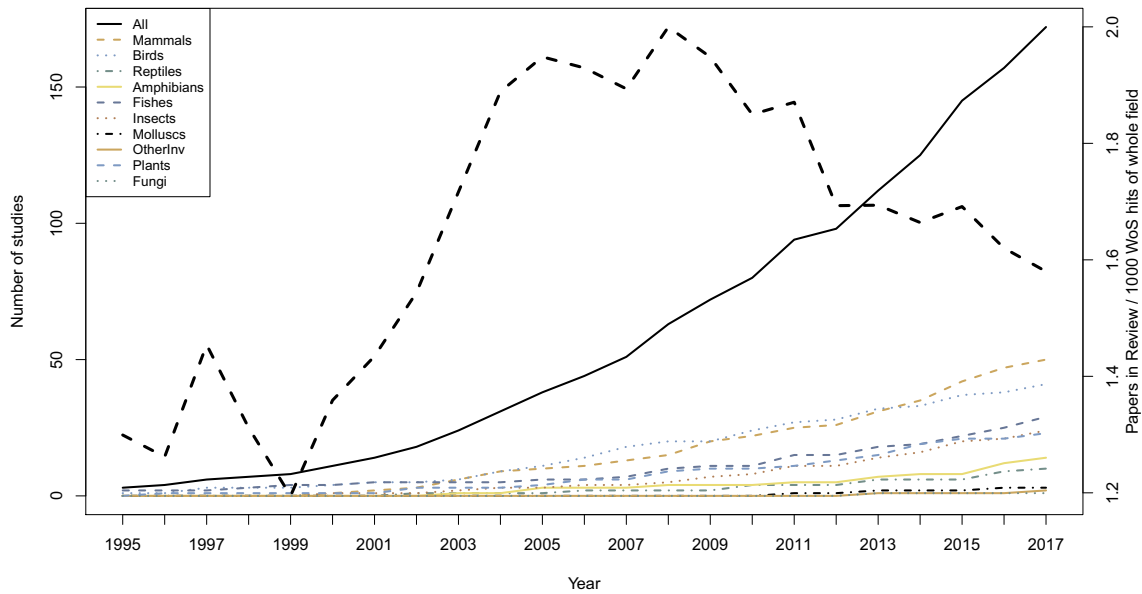
Fig. 1. This figure shows: the cumulative number of publications per taxon relating traits to extinction risk (left Y axis, all lines except dashed bold black line); and the cumulative number of publications included in the review per each 1000 publications published in biodiversity and nature conservation (right Y axis, dashed bold black line) at each year interval. Data from 2018 is not plotted here since at the time of our literature search the year 2018 was not yet complete.

3.1.2. Traits

Body size was by far the most studied trait (Fig. 3, Table B.2), followed by geographical range size and fecundity. Among the traits that were present in at least 10% of the studies, geographical range size was the trait with the greatest proportion of significant measurements (almost three quarters) (Fig. 3). Besides geographical range size, only location (the geographical setting of the study) was significant in at least half of the measurements, but many traits were significant in > 40% of the tests: body size, habitat type, diet breadth, habitat breadth, temperature and microhabitat type (Fig. 3). Fecundity, while among the most tested traits, was significant in only 27% of the measurements.

Even when used in at least 10% of studies, not all of these traits were studied across all taxa, but note that some traits are not meaningful or available in some groups. 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 (Appendix D, Fig. D.1 – D.4).

Despite occurring in < 10% of the studies, either due to being non-applicable, or due to being understudied, many traits have been found to be good predictors of extinction risk for some taxa. A number of traits
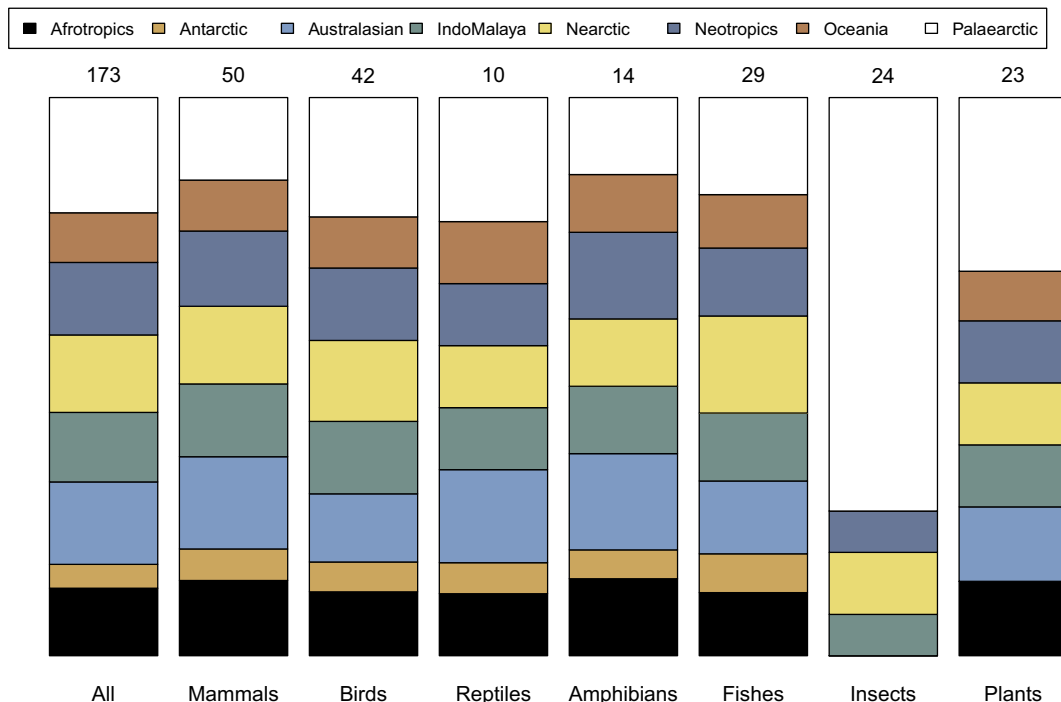

Fig. 2. Proportion of manuscripts focusing on the different biogeographical regions by taxonomic group. Numbers above columns are the total number of studies per taxon.
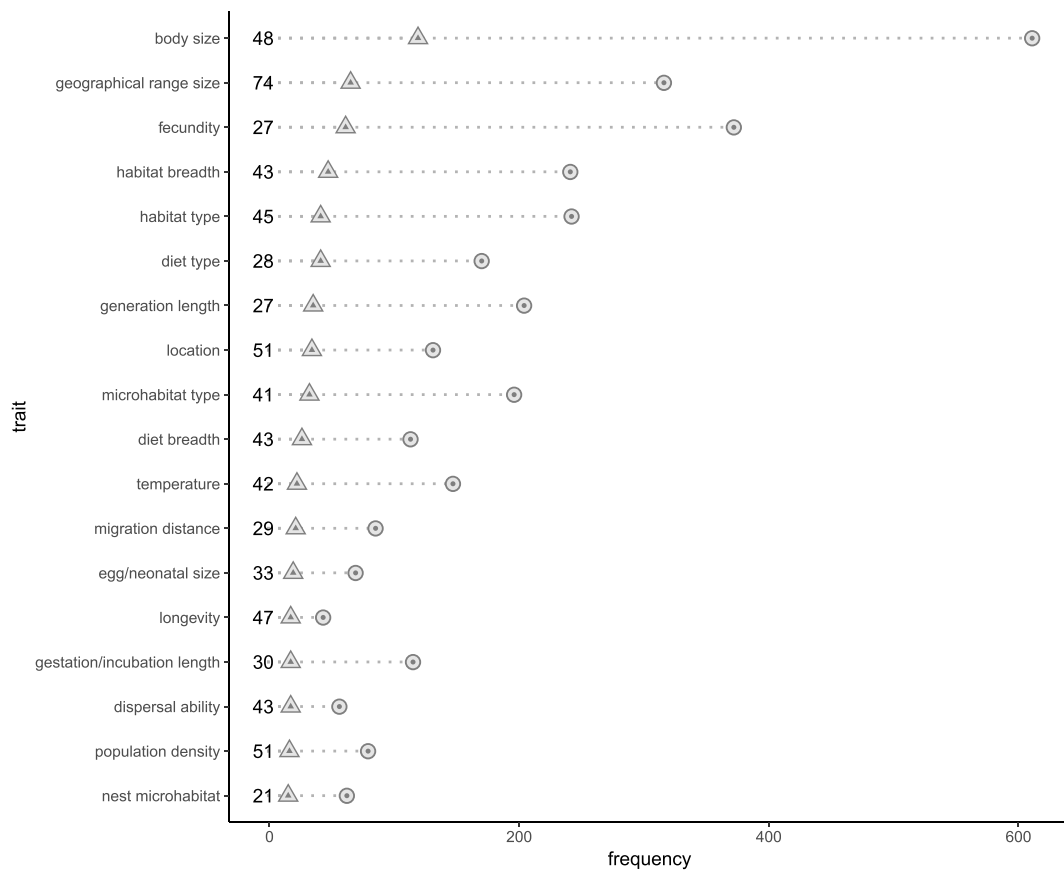
Fig. 3. Summary information on variable use among all studies, depicting only variables included in at least 17 (10%) studies. The numbers before the dotted lines indicate the percentage of measurements in which the variable was significant. **Triangles**: number of studies in which the variable appears. **Circles**: total number of measurements for that variable.

(see Appendix D 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).

3.2. 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 (Figs. E.1, E.2). Effect sizes of habitat breadth also originated mostly from mammal and bird studies, yet reptile, amphibian, other invertebrates and plant studies were included (Fig. E.3).

For geographical range size and habitat breadth, the overall effect size was consistently and significantly negative across taxa and studies (Table 2, Figs. E.1, E.3). Contrastingly, the linear mixed model revealed an overall effect size not different from zero for body size (Table 2). Effect sizes of body size were either positive or negative (Fig. E.2), and while there was some tendency in mammals and birds for the effect sizes to be positive, although not consistently so, the effect sizes for plants and other invertebrates were strongly negative.

4. Discussion

We are aware that this contribution might not include all relevant studies in this field. It is, however, unique in two aspects. First, it investigates drivers of extinction risk across very diverse taxonomical groups and spatial settings, and therefore it identifies the current gaps in research. Secondly, not only does it narrate about traits studied in past studies, but also provides actual quantifications of their importance through true meta-analyses. The result is, to our knowledge, the largest and statistically better supported review of the relation between traits and extinction risk to date.

4.1. Taxonomical and spatial biases

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 accelerated in the beginning of the 2000s, probably fuelled by the fast increase in species assessments of extinction risk when the IUCN released their criteria version 3.1 (IUCN, 2001). It is clear then that informing the status of extinction of species has been relevant to understand its drivers. Yet, we also found that past studies were biased in scope in terms of taxa, with vertebrates having the largest share. Such biases should be mostly due to a large body of accumulated knowledge on these taxa, to which a predominance of researchers in these groups continue to contribute.

Comparative studies on vertebrate and plant studies have used in their analyses species from around the world, with a strong focus on the

Table 2
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)	21/47/9	Mammals (7/11), birds (7/17), reptiles (2/3), amphibians (3/4), fishes (2/4), vertebrates (1/2), insects (2/4), other invertebrates (1/1), plants (1/1)	−0.481 (0.117)	23.806	−4.108	0.0004
Effect sizes of body size ~ (Intercept) + Random(Study) + Random(Taxon)	31/85/9	Mammals (9/33), birds (11/26), reptiles (4/9), amphibians (3/3), fishes (3/7), vertebrates (1/1), insects (1/1), other invertebrates (1/1), plants (3/4)	0.130 (0.104)	11.000	1.251	0.237
Effect sizes of habitat breadth ~ (Intercept) + Random(Study) + Random(Taxon)	14/27/6	Mammals (2/6), birds (6/13), reptiles (2/3), amphibians (2/3), vertebrates (1/1), other invertebrates (1/1), plants (1/1)	−0.210 (0.041)	11.843	−5.112	0.0003

Palearctic realm (in plants) and the Australasian realm (some vertebrate groups, maybe due to an ongoing debate on the role of body size in extinction risk in this particular region, Verde Arregoitia (2016)). It is clear that this is also partly due to a large body of accumulated knowledge on these regions. However, if this were the single cause for this phenomenon, then why are insects so much more biased towards the Palearctic region than the other groups? We hypothesize that this bias could be due to both the lack of red list assessments for invertebrates across realms and the lack of publicly accessible trait databases at a global scale from where to extract standardized trait data for this group, unlike what happens with vertebrates and plants (e.g., AMNIOTE, Myhrvold et al., 2015; PANTHERIA, Jones et al., 2009 for vertebrates and TRY, Kattge et al., 2011 for plants). Therefore, extinction risk assessments (Cardoso et al., 2011a) and trait collection to overcome the Hutchinsonian shortfall (Cardoso et al., 2011b) should be a high priority for this group. Fortunately, initiatives both to standardize (Moretti et al., 2017; Kissling et al., 2018) and to curate trait data into global databases are slowly making their first steps in some invertebrate (not just insect) groups (e.g., CORALBASE, Madin et al., 2016; Carabids.org, Homburg et al., 2014; Globalants.org, Parr et al., 2017). The mega-diverse fungi are also notably understudied for the same reasons. Promising steps are being made in order to circumvent the difficulties in applying the IUCN criteria for fungi (Dahlberg and Mueller, 2011), but more basic research funding and databases of traits are still needed.

4.2. Relation between traits and extinction risk

Geographical range size was the best predictor of extinction risk overall. 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 et al., 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 and Lockwood, 1999; Clavel et al., 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. Nonetheless, Slatyer et al. (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. While larger bird species are threatened by overexploitation, smaller bird species are threatened by habitat loss or degradation (Owens and Bennett, 2000). The same trend seems to apply at least to marine fishes (Olden et al., 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, such as those traits related to speed of life cycle and reproductive output. Threat status has been positively related to species with decreased fecundity (Cardillo, 2003; González-Suárez and Revilla, 2013; Böhm et al., 2016; Ribeiro et al., 2016; but see Pinsky and Byler, 2015; Sreekar et al., 2015), larger egg/neonatal sizes (Cardillo et al., 2005; Jones et al., 2006; González-Suárez and Revilla, 2013; Pinsky and Byler, 2015) and longer generation lengths (Anderson et al., 2011; Hanna and Cardillo, 2013; Jeppsson and Forslund, 2014; Comeros-Raynal et al., 2016; but see Chessman, 2013). 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. These traits reduce the capability of species to compensate for high mortality rates (Pimm et al., 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 and 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 and Bennett, 2000; González-Suárez et al., 2013), this being possibly due to the advantages of longer longevity alone.

Traits indicating preference towards specific environmental niches are commonly used across taxa and many 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 and 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 et al., 2015). When exceptions were found, these were due to the correlation of temperature with the true causes of change in extinction risk (e.g. 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 (Powney et al., 2014; Stefanaki et al., 2015). 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 rarer with increased human pressure (Parent and 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 considering the threat type and using different variables related to human use of species and habitats (Murray et al., 2014).

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 (Mattila et al., 2008; Matsuzaki et al., 2011; González-Suárez et al., 2013; Jeppsson and Forslund, 2014; Basset et al., 2015), probably due to lower flexibility in switching to other options when the availability of their preferred food source decreases (Purvis et al., 2000b). 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 (Purvis et al., 2000a; Cardillo et al., 2004; Bender et al., 2013; Chessman, 2013) 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 and 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.

Migration distance was often tested and found to be an important predictor. 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 and 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 (Amano and Yamaura, 2007; Jiguet et al., 2010).

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. Mattila et al., 2008; Jeppsson and Forslund, 2014; Powney et al., 2015). At least for some studies with applied relevance, Cardillo and 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.

4.3. 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). Recently, a model was developed in which range size was used to estimate population density, which together with habitat breadth and dispersion ability were able to predict very accurately the threat status of mammals and birds (Santini et al., 2019). 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. 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.

5. Conclusions

In this review, we present the state of the art of the relationship between traits and extinction risk. Vertebrate and plant studies cover all main biogeographical regions, but invertebrates and fungi are remarkably underrepresented outside of the Palearctic region, probably due to being understudied, having relatively few species assessed for their extinction risk, and the lack of publicly available global databases with standardized trait data. Our meta-analyses reinforced the notion that species with smaller ranges, and those with narrow habitat breadths are more at risk than others, regardless of the taxon or geographic distribution. We must emphasize, however, that we still lack a complete and unbiased picture of the relation between traits and extinction risk. Future studies could and should provide insights much beyond what is possible now. Many traits were found to be important across studies but have seldom been studied or are relevant for only some taxa. In order to represent more accurately the extent of the biological diversity, conditions must be created for the understudied groups to be included in comparative studies (through more IUCN assessments of species, curation of trait databases, and funding of basic science). Not only that, but the intricate links between e.g. body size and extinctions provide reason for further studies to focus not only on the threat status of a species, but also on the underlying threat (whether it be human persecution, habitat degradation, climate change, or invasive species).

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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.2019.07.001.

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