

Threat to the point: improving the value of comparative extinction risk analysis for conservation action

KRIS A. MURRAY*, LUIS D. VERDE ARREGOITIA†, ANA DAVIDSON‡, MORENO DI MARCO§ and MARTINA M. I. DI FONZO†¶

*EcoHealth Alliance, 460 West 34th Street, New York, NY, USA, †School of Biological Sciences, University of Queensland, Brisbane, QLD 4072, Australia, ‡Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY, USA, §Global Mammal Assessment program, Department of Biology and Biotechnology, Sapienza University of Rome, Viale dell' Università 32, I-00185 Rome, Italy, ¶ARC Centre of Excellence for Environmental Decisions, the NERP Environmental Decisions Hub, Centre for Biodiversity & Conservation Science, University of Queensland, Brisbane, QLD 4072, Australia

Abstract

Comparative extinction risk analysis is a common approach for assessing the relative plight of biodiversity and making conservation recommendations. However, the usefulness of such analyses for conservation practice has been questioned. One reason for underperformance may be that threats arising from global environmental changes (e.g., habitat loss, invasive species, climate change) are often overlooked, despite being widely regarded as proximal drivers of species' endangerment. We explore this problem by (i) reviewing the use of threats in this field and (ii) quantitatively investigating the effects of threat exclusion on the interpretation and potential application of extinction risk model results. We show that threat variables are routinely (59%) identified as significant predictors of extinction risk, yet while most studies (78%) include extrinsic factors of some kind (e.g., geographic or bioclimatic information), the majority (63%) do not include threats. Despite low overall usage, studies are increasingly employing threats to explain patterns of extinction risk. However, most continue to employ methods developed for the analysis of heritable traits (e.g., body size, fecundity), which may be poorly suited to the treatment of nonheritable predictors including threats. In our global mammal and continental amphibian extinction risk case studies, omitting threats reduced model predictive performance, but more importantly (i) reduced mechanistic information relevant to management; (ii) resulted in considerable disagreement in species classifications (12% and 5% for amphibians and mammals, respectively, translating to dozens and hundreds of species); and (iii) caused even greater disagreement (20–60%) in a downstream conservation application (species ranking). We conclude that the use of threats in comparative extinction risk analysis is important and increasing but currently in the early stages of development. Priorities for future studies include improving uptake, availability, quality and quantification of threat data, and developing analytical methods that yield more robust, relevant and tangible products for conservation applications.

Keywords: Biodiversity, declines, extrinsic traits, intrinsic traits, IUCN Red List, management, prediction, prioritization, threats

Received 28 May 2013 and accepted 13 August 2013

Introduction

Present rates of global species extinction are two to three orders of magnitude greater than background levels recorded in geologic history (Barnosky *et al.*, 2011; Pimm *et al.*, 1988, 1995). Around 20% of assessed vertebrate species are currently listed as threatened under the International Union for the Conservation of Nature (IUCN) Red List (Hoffmann *et al.*, 2010). Human impacts, such as agricultural expansion, logging, overexploitation, climate change and invasive species, are widely recognized as the major drivers of the current global extinction crisis (e.g., Davies *et al.*, 2006). Inadequate alleviation of such

threats is the key factor limiting the effectiveness of current conservation strategies aiming to reduce or reverse biodiversity loss (Hoffmann *et al.*, 2010; Tranquilli *et al.*, 2012).

The risk of a species' decline in abundance or extinction (often measured as a relative level of endangerment, e.g., as per the IUCN Red List) is nevertheless also strongly influenced by its intrinsic life-history and ecological traits, such as body size, fecundity or ecological versatility (Fisher *et al.*, 2003; Cardillo *et al.*, 2004; Purvis *et al.*, 2005; Lee & Jetz, 2011). For instance, relatively larger-bodied and longer-lived bird species are more likely to go extinct as a result of overhunting, whereas small-bodied species with high habitat specialization are more likely to decline in response to habitat loss (Owens & Bennett, 2000). Extinction risk is thus shaped by interactions that arise between species'

Correspondence: Kris A. Murray, tel. +1 347 475 9367; fax +1 212 380 4465, e-mail: murray@ecohealthalliance.org

intrinsic traits and the extrinsic factors including threats to which they may be exposed (Fig. 1).

Comparative extinction risk analysis has been one tool used to explore these complex interactions. By synthesizing global- or regional-scale information across large numbers of species, these macroecological analyses can yield important conservation recommendations by elucidating why some species are more vulnerable to extinction processes than others (e.g., Purvis *et al.*, 2000; Jones *et al.*, 2003; Koh *et al.*, 2004; Cardillo *et al.*, 2006; Cooper *et al.*, 2008; Davidson *et al.*, 2009; Isaac *et al.*, 2009; Di Marco *et al.*, 2012; González-Suárez & Revilla, 2012).

In a recent review, however, Cardillo and Meijaard (2012) highlight a general lack of influence that comparative extinction risk analyses have had on conservation practice and policy (i.e. 'primarily academic exercises'). One reason for this underperformance may be that these studies seem to focus more heavily on species' intrinsic traits, reflecting general patterns of 'vulnerability' or 'extinction proneness' (Reynolds, 2003; Purvis *et al.*, 2005), than on their more immediate and potentially manageable causes of endangerment: extrinsic threats (Fisher *et al.*, 2003).

Although trait-based responses can sometimes reflect or help identify the nature of underlying or unknown threats (e.g., Williams & Hero, 1998), failing to explicitly consider threats in comparative extinction risk analyses could be limiting for several reasons. In models that employ intrinsic traits only as predictor variables, there is an implicit assumption that susceptibility to

decline or extinction is the result of trait-based vulnerability to some uniform, average or overarching threat (Fritz *et al.*, 2009). However, we cannot assume that all threats are equal, or that a species' response to one threat will be correlated with its response to others.

For example, in addition to interactions that might arise between extrinsic threats and intrinsic traits (Fig. 1), threats often vary spatially and/or temporally in their presence and magnitude (Myers, 1988; Wilcove *et al.*, 1998; Harcourt & Parks, 2003; Davies *et al.*, 2006), and their prevalence can vary significantly between taxonomic groups (Mace & Balmford, 2000). Threats could also influence the decline in a population at multiple spatial or temporal scales (Wilcove *et al.*, 1998). Different threats may also cause different types of population responses, depending on distinctions in the rate at which they cause mortality over time (Mace *et al.*, 2008; Di Fonzo *et al.*, 2013), and multiple threats may impact a species interactively or additively (e.g., Hof *et al.*, 2011). If adequately quantified, these factors should explain additional variation in extinction risk patterns among species, beyond the variation that might be attributable to the mediating effects of intrinsic traits alone.

Due to the correlative nature of comparative extinction risk analyses, intrinsic trait-only models must implicitly include the above characteristics and other nuances related to threats (analogous to e.g., species interactions in correlative species distribution models; Pearson & Dawson, 2003). As such, while performance of trait-based extinction risk analyses might be reasonable for a given case study (e.g., Davidson *et al.* (2009) was able to classify threat listings in mammals globally with >80% accuracy based solely on intrinsic trait data), models failing to explicitly include threats may be poorly suited to extrapolation or have limited transferability into different regions, taxa or timeframes (e.g., future projections). For instance, trait-based models of extinction risk in farmland birds showed poor predictive ability among different regions (Pocock, 2011), perhaps due to varying patterns of key threats. Similarly, Fritz *et al.* (2009) showed that considerable geographic variation in mammalian extinction risk derived from trait-based models could be explained by considering varying patterns of past anthropogenic impacts.

Studies that do not consider threats might also suffer from a lack of mechanistic information that may be of critical interest for implementing conservation action. For example, declines due to a waterborne disease might require very different management strategies to those caused by habitat loss along streams (e.g., Murray *et al.*, 2011), although they may be correlated with the same intrinsic traits (ecological specificity to streams, for example). The examples above underscore the

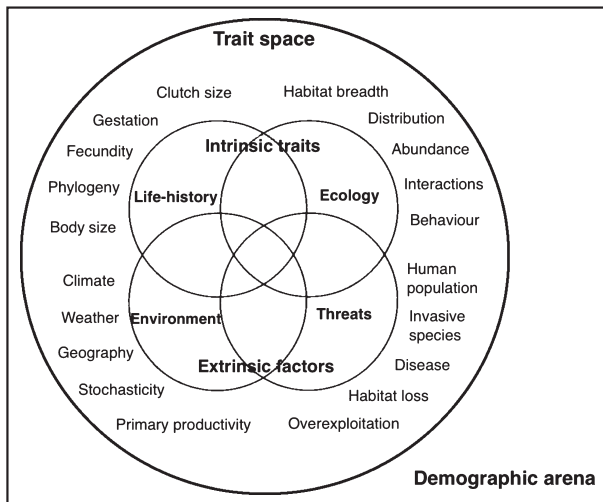


Fig. 1 Schematic of the interactions between intrinsic and extrinsic factors that drive variability in extinction risk. We consider these variables as existing and interacting in some 'trait space' for each species. The effects of these interactions on a species' distribution and/or abundance play out in that species' 'demographic arena', and culminate in variable extinction risk.

importance of considering both intrinsic and extrinsic factors together to obtain a more complete picture of extinction risk (Fisher *et al.*, 2003; Purvis *et al.*, 2005; Cardillo *et al.*, 2008) (Fig. 1).

With these considerations in mind, we aimed to take stock of the general use of threats in the comparative extinction risk literature and to investigate the potential effects of their exclusion on the interpretation and application of model results. First, we quantify the prevalence of threat variables as predictors of extinction risk in a large sample of published studies. We quantify the threat types considered in these studies, assess the range of methods that have been used for the quantification of threats to individual species and catalogue the model types that have been used to integrate threats into the study of extinction risk. Second, we present two case studies in which we directly compare extinction risk models developed with and without threats to highlight some of the key effects that threat omission may have for model interpretation and downstream end-uses in conservation management, such as species ranking on the basis of specific conservation need.

Materials and methods

The use of threats in comparative extinction risk studies

We reviewed 98 studies drawn from the ISI Web of Science that investigated the correlates of extinction risk across numerous taxonomic groups and geographic regions. Specifically, we compiled referenced literature from previous reviews on extinction risk (Fisher & Owens, 2004; Purvis, 2008; Reynolds, 2005; Bielby *et al.*, 2010; Cardillo and Meijaard, 2012) and all related studies published up to 2011, which were identified by the search terms 'extinction risk', 'extinction proneness', 'vulnerability + extinction', 'susceptibility + extinction', 'correlates + extinction', 'predictors + extinction' and 'drivers + extinction'. A list of the reviewed literature appears in Supplementary Information S1. All variables used in each study were recorded and classified into extrinsic or intrinsic factors (e.g., see Fig. 1), and subclassified into specific categories (e.g., extrinsic factors could be classified as either 'direct threats', such as habitat loss or human population density, or 'other extrinsic' variables, typically environmental or geographic factors such as temperature, rainfall, latitude or altitude). We then recorded the data source, the modelling framework, whether the extrinsic factors were spatially explicit or not, the taxon-specific quantification method and whether the variable was a significant predictor of extinction risk or not.

Modelling extinction risk with and without threats: two case studies

We evaluated the influence of considering threats on predictions of extinction risk using two model systems: (i) a global analysis of mammals (following the framework of Davidson

et al., 2009) and (ii) a continental analysis of Australian amphibians (following Murray *et al.*, 2011). These two study systems represent different taxa, spatial scales (global and continental) and threat data availability and resolution, providing typical scenarios encountered in extinction risk studies. While for mammals our analysis is global in scale and contains many species, the analysis was conducted at a fairly coarse resolution (1 degree, approx. 100 km) with relatively little information about threats (restricted to the human influence index (Sanderson *et al.*, 2002) and a measure of human population density (Jones *et al.*, 2009)). In contrast, our amphibian data set was geographically and taxonomically more restricted (continental), but we were able to utilize a larger number of key threats (disease, invasive species, habitat degradation) at better spatial resolutions (9 arc seconds, approx. 250 m).

Extinction risk models. For both systems, random-forest (RF) models were developed for the prediction of species' IUCN red list categories (Cutler *et al.*, 2007; Breiman & Cutler, 2011). RF is a nonparametric, tree-based, machine-learning approach suited to modelling extinction risk due to its limited assumptions about data types and properties, its high classification stability and performance, its ability to cope well with a large number of potentially correlated predictors and nonlinear responses and its useful variable importance probe and partial dependence plots that can be used for variable selection and response visualization (Davidson *et al.*, 2009; Murray *et al.*, 2011). We also built conditional inference trees for graphical depiction of the main quantitative relationships between predictor variables and the response. We used the *randomForest* (Liaw & Wiener, 2002) and *party* (Hothorn *et al.*, 2012) packages in R (R Development Core Team, 2012) for model development. Although models that do not account for the potential problem of pseudoreplication arising from phylogenetic relatedness among species have been criticized, we avoided such methods (e.g., PIC) because our models contained numerous nonheritable, nonevolving predictors (extrinsic traits and threats) with no conceivable phylogenetic underpinning, such that we would not understand the implications of forcing phylogenetic correction in this instance (see Discussion for more details).

For mammals, models with and without threats were developed for comparison on 4019 (of ca. 5400) terrestrial mammal species. We used a dichotomous response variable to represent extinction risk: species classified as Vulnerable, Endangered, or Critically Endangered by the IUCN were considered 'Threatened', and species listed as Near Threatened and Least Concern were considered "Non-Threatened" (IUCN, 2009). For amphibians, the model with threats was previously published as a standalone extinction risk analysis (Murray *et al.*, 2011), so here we replicated this model and then excluded threats for direct comparison. For amphibian models with and without threats, IUCN Red List 'Trend' classifications (Declining or Stable) were analysed for 198 Australian amphibian species with sufficient data (ca. 90% of all Australian amphibians). Although these dichotomous response variables may oversimplify the concept of extinction risk, we felt this was

appropriate here because it more simply illustrates the direct influence of threats across two study systems, minimizes assumptions and is consistent with previous studies. For both study systems, we used (for amphibians) or further developed (for mammals) previously published databases to provide information on predictor variables; both intrinsic species traits (e.g., body size, geographic range size, ecological mode, etc.) and numerous extrinsic factors and threats (e.g., human influence index, the distribution of disease, invasive species, habitat loss, etc.) that were hypothesized to be of interest for explaining the conservation status of mammal or amphibian species.

Model comparisons. For each study system, we compared a number of different model outcomes between models with and without threats to understand the way in which threats may affect the interpretation and use of results. We evaluated model predictive performance, the agreement between models with and without threats for species classifications, the contribution of threats to mechanistically understanding predicted IUCN classifications and the effect that threats have on one potential downstream effect relevant to conservation decision making, namely, species ranking on the basis of specific conservation need.

We compared performance between models with and without threats with a range of metrics, including overall classification accuracy (percentage of species correctly classified, PCC), sensitivity, specificity and Cohen's Kappa. We examined classification agreement by looking at which species had contrasting classifications from models with and without threats. We also correlated raw probability scores for each species from models with and without threats to assess overall model agreement. For amphibians, we also examined correlations within subclasses of species corresponding to an important intrinsic trait (ecological group) to examine the way interactions might influence disagreement between models with and without threats. For mammals, we used an internal RF variable importance probe to rank the influence of threats vs. intrinsic traits in the model that included threats. The same outputs for the amphibian model with threats are presented in Murray *et al.* (2011). By definition, models without threats

provide no information about them, so variable importance statistics and decision trees were not generated for these models.

Finally, we evaluated the agreement between species classifications made by RF models with and without threats for each study system as they would relate to a decision oriented, downstream end-use, species ranking. We constructed a simplistic, hypothetical situation in which only a certain percentage of species could be allocated conservation resources due to the ever-present constraint on conservation funding (Bottrill *et al.*, 2008; Rondinini *et al.*, 2011; Cullen & White, 2013). For this exercise, we deemed that funding should be allocated on the basis of our confidence that a species is at risk of extinction. In this hypothetical framework, we used model results to identify which species should receive resources by ranking them by the certainty that models had in classifying them as at risk of extinction (highest confidence in the prediction), then compared the membership of priority species lists derived from models with and without threats (note: we are not advocating this or any particular prioritization scheme in this study, but rather include this analysis for demonstrative purposes only to illustrate the potential influence of threat exclusion for a practical conservation oriented end-use).

Results

The use of threats in comparative extinction risk studies

How often are threats considered in extinction risk analyses?

Of 98 extinction risk studies, many (78%) included extrinsic factors of some kind (e.g., bioclimatic or geographic information). However, most (63%) did not include direct threats, such as habitat loss or overexploitation (Fig. 2a). Threat use has, however, increased in step with an overall increase in the number of studies published per year and with increasingly variable-rich models (Fig. 3). The mean number of predictor variables included in models across all 98 studies was 9.3, comprising an average of 6.3 intrinsic trait variables and 3.0 extrinsic variables. Among the 36 studies in

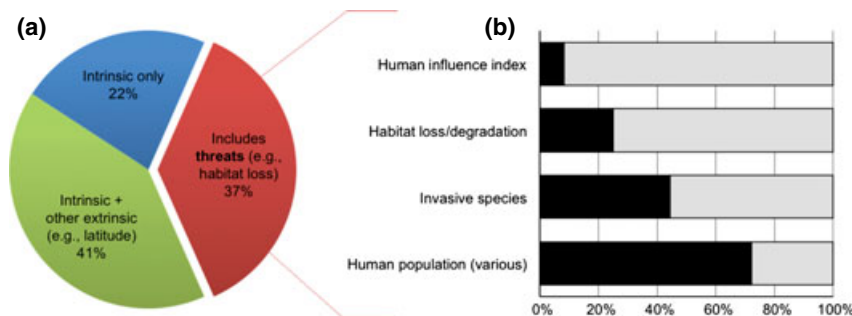


Fig. 2 (a) Composition of extinction risk studies that consider threats, other extrinsic traits and intrinsic traits ($N = 98$ studies), (b) The four most commonly considered threats and their proportional use in 36 extinction risk studies that considered threats. Many more threat variables appeared in only one or two studies. Overall, 59% of unique threat variables were significant predictors of extinction risk in at least one study.

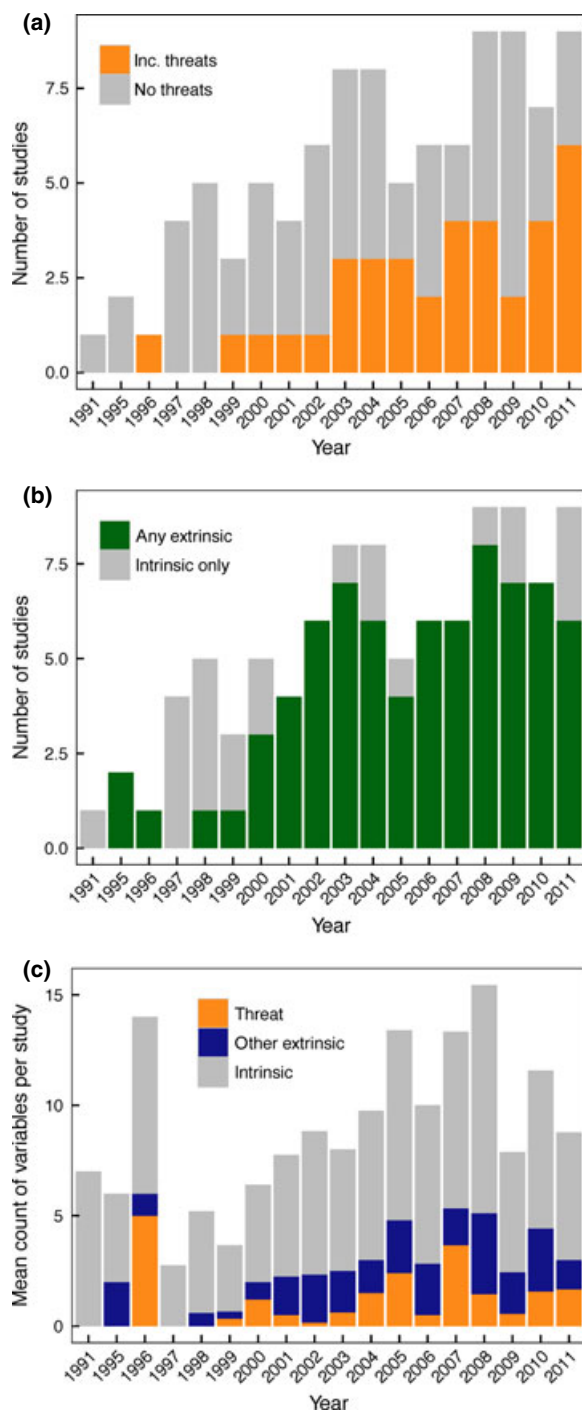


Fig. 3 Trends in extinction risk publications. (a) The proportion of studies considering threats has increased through time, against a background of more publications per year. (b) From 2000, most studies have considered some form of extrinsic predictor, including threats, environmental or geographic factors. (c) In step with more publications per year (a,b), models of extinction risk have also become more variable rich with fairly consistent inclusion of threat or other extrinsic factors since 2000; however, on average, models remain dominated by intrinsic trait variables.

which direct threats were considered, an average of 6.3 intrinsic traits, 3.1 direct threats and 2.5 other extrinsic factors (i.e. environmental or geographic factors) were used (Fig. 3c).

What are the most common threat variables? Among the 36 reviewed studies that considered threats, 70 different threat variables were used, with a few used in more than one study. The most frequently used threat variables were human population density, represented in a variety of metrics (26 studies), invasive species (16) and habitat loss or degradation (9) (Fig. 2b). The Human Influence Index, a compound spatial measure comprising eight metrics of human presence and activity (Sanderson *et al.*, 2002), appeared in three studies. Most threat variables appeared in just one (53 variables) or two (7 variables) studies. Overall, 41 (59%) of the 70 threat variables used were significant predictors of extinction risk in at least one study.

How are threats quantified at the species level? Only 21 studies (58% of 36 studies including threats, and 21% of all 98 reviewed) included threat variable measurements that were derived from spatially explicit threat and species occurrence data, each represented in a variety of ways. In these studies, quantification methods were diverse but predominantly based on spatial overlap between known threat locations and a species' geographic range (Table 1). No studies evaluated the potential variability in threat quantification associated with method of calculation (recently reviewed by Di Marco *et al.*, 2013). In a small number of cases, threats were assigned as categorical designations based on

Table 1 Quantification methods for species-specific threat values across a sample of 31 extinction risk studies that have considered threats quantitatively

Quantification Method	Abs. Frequency of Use
Area-weighted mean grid cell value across species' range	14
Proportion of species' range in threat area	8
Overlapping grid cell count (threat and species distribution)	7
Ranked categories derived from percentage overlap between polygons	5
Area-weighted mean by country	5
Average of values at occurrence points	4
Compound measure of external threat from cooccurrence with other threatened taxa	2
Percent of converted landscape area within species' range	1
Median grid cell value across species range	1

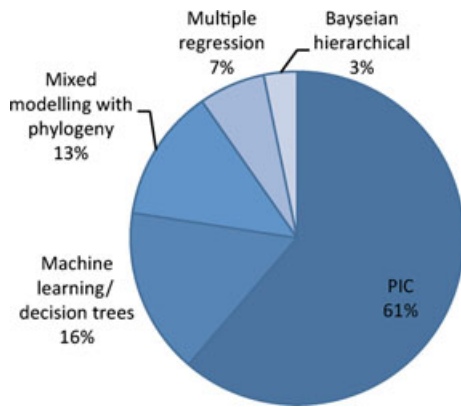


Fig. 4 Proportional use of model types for studying extinction risk when threats are considered quantitatively ($N = 31$ studies). PIC = phylogenetic independent contrasts, and is by far the most common method used. Given that threats (and other extrinsic factors) are nonphenotypic, nonevolving traits that may have no phylogenetic signal, the use of PIC in isolation for modelling extinction risk has been criticized (see text).

expert opinion and published accounts; for example, perceived threat from introduced competitors (Owens & Bennett, 2000) or imperilment by secondary biological interactions (Olden *et al.*, 2008).

How has extinction risk been modelled when including threats? Of the 31 comparative analyses of extinction risk that we reviewed in which threats have been included in a quantitative modelling framework, most modelled extinction risk using regression on phylogenetically independent contrasts (PIC; Purvis and Rambaut, 1995) (Fig. 4). Except for Lee & Jetz (2011), no study used more than one method and explicitly compared results or considered consensus, although Bielby *et al.* (2010) studied the relative performance of decision tree vs. PIC-based methods for modelling extinction risk across a range of taxa for which at least one threat (human population density) was considered.

Case studies – directly comparing models with and without threats

Overall performance statistics. The model comparisons indicated that threats modestly improved overall model predictive performance in terms of how well predicted threat categories agreed with original IUCN Red List classifications on which the models were built (Table 2). The effect of including threats was less apparent for mammals than it was for amphibians (Table 2). These improvements in overall classification accuracy translate to correct classifications for an additional 8 and 71 amphibian and mammal species respectively. For both systems, improvements in sensi-

tivity and specificity indicated that the models with threats were less likely to make both false-positive (predict a threatened species when it is not threatened) and false-negative (predict a nonthreatened species when it is threatened) trend classifications than the intrinsic trait-only models. Combined, this led to 12% and 5% increases in Kappa (an overall test of agreement between observed and predicted classes) for amphibians and mammals respectively (Table 2). Reasons for misclassification in each case study may be numerous (e.g., original misclassification by IUCN or genuine classification errors) and of potential interest but are not the focus of this study (see Davidson *et al.*, 2009; Murray *et al.*, 2011 for discussions of misclassification).

Classification agreement. Models with and without threats classified species in different ways. For amphibians, models with and without threats disagreed on the classification of 22 species (11.1% of 198) (Table 2). Ten (45.5%) of these were originally listed by the IUCN as having a 'Declining' Red List trend, a significantly higher proportion than the overall proportion of species with a declining trend status in the data set (24.7%; Fisher's exact test odds ratio = 2.52, 95% CI = 0.91–6.82, $P = 0.045$), indicating that disagreement between models with and without threats was disproportionately more likely for species considered at risk. In addition, the model that included threats correctly classified eight (80%) of these, whereas the model without threats correctly classified only two (20%; $P = 0.023$ Fisher's exact test), suggesting that threat information is able to better identify species at risk that cannot be predicted by intrinsic trait information alone. For mammals, models with and without threats disagreed on the classification of 219 species (5.4% of 4019), a smaller proportional difference (but translating to a higher number of species) than that seen in amphibians (Table 2). Again, species for which the models disagreed were disproportionately (34.4%) more likely to be threatened when compared to the background rate of threatened species (16.1%; Fisher's exact test odds ratio = 2.72, 95% CI = 1.91–3.83, $P < 0.001$). For mammals, the model that considered threats was more likely (55%) to detect threatened species (i.e. return a correct classification) than the intrinsic trait-only model (45%), but this difference was not significant ($P = 0.345$, Fisher's exact test).

Interactions and model agreement. Considering the strength of the classification prediction, models with and without threats were strongly correlated (mammals: overall $R^2 = 0.870$, $P < 0.001$; amphibians: overall $R^2 = 0.709$, $P < 0.001$) (Fig. 5a,b). However, when the

Table 2 Performance statistics for models predicting declining population trends in amphibians (continental) and threatened mammals (global), comparing intrinsic trait-only models with models that also incorporate threats

Metric	Australian amphibians (<i>n</i> = 198)		Global Mammals (<i>n</i> = 4019)	
	With threats	Intrinsic only	With threats	Intrinsic only
Out of bag error (OOB; overall classification error rate)	12.63%	16.67%	12.22%	13.98%
Species correctly classified	173	165	3528	3457
Percentage of species correctly classified (PCC)	87.37%	83.33%	87.78%	86.02%
Sensitivity (% of Threatened species correctly classified)	75.51%	63.27%	65.18%	63.63%
Specificity (% of Non-Threatened species correctly classified)	91.28%	89.93%	92.14%	90.32%
Cohen's Kappa (95% CI in brackets)	0.66 (0.54–0.79)	0.54 (0.40–0.69)	0.56 (0.52–0.60)	0.51 (0.47–0.55)
Disagreement in classification between models with and without threats	22 species (11.1%)		219 species (5.4%)	

Note: "Threats only" models were also tested for reference, and had PCC values of 81.46% and 79.29% for mammals and amphibians respectively. These models are not considered further here for brevity, but demonstrate that (i) threats may have inferior but still considerable ability to predict threatened species even in the absence of any intrinsic trait data and (ii) the addition of variables to models follows a pattern of diminishing returns in terms of overall performance (PCC). For management, the more interesting and significant differences between models are related to the disagreement in results for the classification of species that arises between available models (see main text).

correlations were exposed to the effects of other important factors (e.g., intrinsic traits), agreement between models with and without threats in some cases deteriorated. For example, an interaction between the threat overlap with a pathogen and the intrinsic trait ecological group meant that there was no discernible correlation between predictions from models with and without threats for amphibian species associated with permanent water (a key amphibian life-history factor) (Fig. 5b).

Variable importance. For mammals, the most important predictor variable was geographic range size, while the threat proxy human population density was a less influential but still important predictor variable. The Human Influence Index variable was a middle-range predictor (Supplementary Information Fig S2.1). For amphibians, the variable importance probe indicated that the most important single variable was ecological group, followed by two threat variables (distributional overlaps with a pathogen and an invasive species) (Murray *et al.*, 2011).

Mechanistic explanatory information. For mammals, the conditional inference tree with threats depicted significant threat variables interacting with intrinsic traits to explain patterns of extinction risk (Supplementary Information Fig. S2.2). Human impacts and human population density interacted with numerous intrinsic trait variables (e.g., mass specific production and

geographic range) to influence threat status. A similar result was evident for amphibians, with the threats of an invasive pathogen and an invasive species interacting with ecological group (Murray *et al.*, 2011). The presence of significant threats together with significant intrinsic traits in the tree, and clear interactions between them in some cases, provides additional mechanistic information over intrinsic trait-only models in both study systems that could be relevant for conservation management.

Species ranking. For both amphibians and mammals, our results indicated that agreement between priority lists was strongly dependent on the percentage of species selected. For amphibians, when selecting only the top 5% of species (*N* = 9 species), only four amphibian species appeared on both lists (56.6% disagreement). For mammals, when selecting the top 1% of species (*N* = 40) only 23 species appeared on both lists (42.5% disagreement). For both groups, this improved to around 20% disagreement between lists when the top 5% and 15% of species were prioritized for mammals and amphibians respectively. At higher proportions, amphibians tended towards greater disagreement while agreement between models for mammals slightly improved (Fig. 6) (Note: if we continued to increase the proportion of selected species indefinitely disagreement between species priority lists would eventually reach 0% as both priority lists would contain all species).

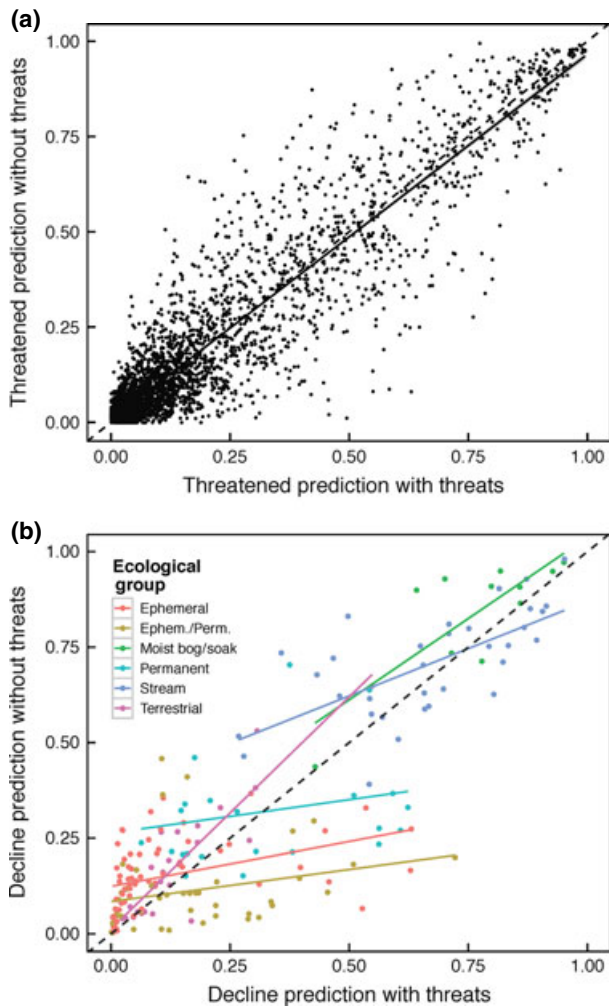


Fig. 5 Correlation between models with and without threats that predict whether a species is a) threatened (mammals, $N = 4019$, overall $R^2 = 0.870$, $P < 0.001$) or (b) in decline (amphibians, $N = 198$, overall $R^2 = 0.709$, $P < 0.001$). a, b) Probability values associated with each species' classification are plotted, dashed lines indicate perfect 1 : 1 agreement. (a) Black line indicates line of best fit. (b) Amphibian species are colour coded by their ecological group, with line of best fit shown for each group; R^2 (P value in brackets) for Ephemeral water associated = 0.164 (<0.001), Ephemeral/Permanent water associated = 0.067 (0.099), Moist bog/soak associated = 0.624 (0.004), Permanent water associated = 0.050 (0.307), Stream associated = 0.448 (<0.001), Terrestrial = 0.811 (<0.001), shows that while overall agreement is reasonable, the inclusion of threats can strongly affect classifications depending on additional factors, in this case ecological group.

Discussion

We show that threat variables are often significant predictors of extinction risk despite being irregularly considered in comparative extinction risk studies, exposing a disconnect between the drivers of biodiversity loss

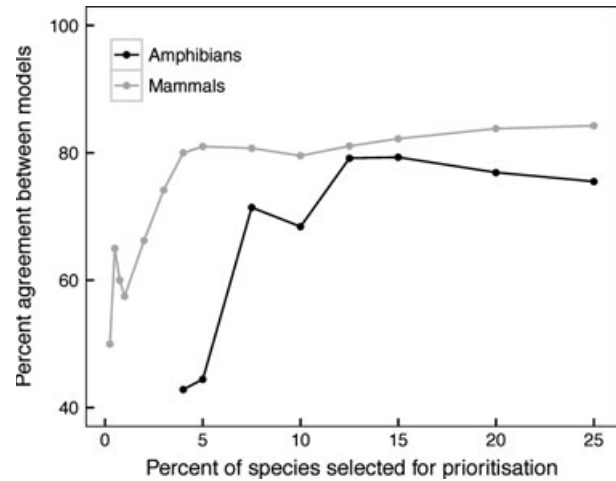


Fig. 6 Agreement (%) in the classification of threatened species between extinction risk models with and without threats as a function of the proportion of species selected for hypothetical prioritization (see text). Our two case studies, Australian amphibians and global mammals are shown. For both case studies, selecting shorter lists equated to greater disagreement between models with and without threats in which species ranked highest. Priority species lists were derived by selecting the top $x\%$ (range 0.25–25% for mammals; 4–25% for amphibians) of species when ranked by their probability of being classified as threatened or in decline (see text).

and our ability to interpret them for management. However, the use of threats is increasing in step with a greater number of studies published per year that are utilizing increasingly variable-rich models. This suggests that threat data availability and quality may be improving and that authors are increasingly cognizant of the potentially important role of threats in modelling extinction risk. Our quantitative analyses confirm that incorporating threats could both improve the predictive accuracy of extinction risk models and provide more tangible results that could be leveraged by managers to improve conservation outcomes. We also show that quantifying threats and integrating them into models nevertheless present a range of challenges, many of which could be addressed in future studies.

Current use of threats in comparative extinction risk studies

Across studies that have considered threats, the most common were various measures of human population impact, invasive species and habitat degradation or loss. A large number of other threat types have also been used, but most of these were restricted in use to just one or two studies. This threat specificity could indicate that either threats are indeed highly idiosyncratic and need to be evaluated on a case-by-case basis

to achieve explanatory power alongside intrinsic traits, or that there is a paucity of available information on the distribution and magnitude of threats relevant to a range of study systems and spatial scales. These issues reflect the practical difficulties involved in the threat quantification process, but suggest that threats should continue to receive increased attention in future studies.

The average number of threats considered in studies was modest (ca. 3 variables), at about half the average number of intrinsic species traits (ca. 6 variables) in models that combined both variable types. Previous species-based threat assessments suggest this may be inadequate. For example, on one continent where data were available (Australia), an average of about three threats per threatened species is listed, although this, as well as the composition of major threats, is highly variable across taxonomic groups and according to threat classification itself (Evans *et al.*, 2011). From another source, the average number of threats listed per species by the IUCN for assessed mammals is lower at 1.16 (IUCN, 2012a); however, threat listing is frequently empty for nonthreatened (Least Concern) species. This figure rises to an average of 2.84 major threats (i.e. level '0') per threatened species, and to 4.38 threats per species for those that are assessed with more detailed threat information (level 1 or level 2 IUCN threat categorization) (IUCN, 2012a). These figures suggest that there is considerable need to incorporate additional and a more diverse range of threats into future comparative studies.

Quantitative effects of ignoring threats in extinction risk analyses

Our case studies on mammals (global) and amphibians (continental) showed that the inclusion of threats could improve predictive accuracy of models, where even modest improvements in overall classification accuracy (12% and 5% improvements in Kappa for amphibians and mammals respectively) translated to better classifications for tens to hundreds of species. Furthermore, ignoring threats resulted in failure to detect threatened species and resulted in disagreements between models in the classification of species that were disproportionately likely for species at risk. Ignoring threats also had significant downstream effects relevant to conservation decisions. For example, priority species lists derived from models with and without threats showed considerable disagreement (20–60%) in the species that would receive conservation resources on the basis of model results in our hypothetical scheme, and that this disagreement was strongly dependent on the number of species that would be selected for prioritization.

Classifications may also strongly interact with other significant factors that drive variation in risk (e.g., intrinsic traits). This highlights the way that threats and other extrinsic factors can strongly interact with species' biological traits to create unique pathways to decline, and failing to incorporate such effects could lead to false inferences or poorly supported decisions. Given the costs of managing threatened species, more accurate, mechanism-oriented and species-specific results should help managers enact more focussed and effective conservation actions.

Our continental case study on amphibians proved more sensitive to the inclusion of threats than our global mammal analysis. The higher predictive value of threat information in our amphibian analysis could be explained by the difference in quality and specificity of the threat data, which is a side effect of the different scales between study systems. At finer spatial scales (continental), we were able to collect or derive threat information on a greater number of key threats and at better resolutions, whereas at global scales we relied on vague proxies (population density) or conglomerate indices (Human Influence Index) of threats. We have no way of knowing whether the relative unimportance of these threat variables observed when modelled alongside intrinsic traits in our global mammal analysis is due to a genuine lack of importance or simply inadequate representation of key threats. Our amphibian analysis and follow-up work improving threat representation for mammals (Di Marco *et al.* unpublished results) suggest the latter. It may be that some key intrinsic traits, such as range or body size, remain better proxies for the impact of threats up until the point that mechanistically more relevant or better quality threat data are included in models.

Future priorities: how can we better incorporate threats into extinction risk analysis?

Understanding threats impacting imperilled species has been one of the main goals of conservation and threatened species research (Pimm *et al.*, 1988; Wilcove *et al.*, 1998; Prugh *et al.*, 2010). This has naturally led to a strong bias in threat characterization across species (see e.g., IUCN threat listing statistics above). For comparative analysis, the difficulty of assigning threats to species is that most species lack information on 'potentially' threatening processes (i.e. threats that are present, regardless of perceived impact). Reducing this bias has already commenced with the development of some promising generic threat classification schemes (Balmford *et al.*, 2009; Harcourt & Parks, 2003; IUCN, 2012b; Salafsky *et al.*, 2008), and attention to species-independent threat mapping is increasing in availability,

quality and scale (e.g., IPCC, 2007; AfriPop, 2012; Microsoft, 2012; UCDP, 2012). Efforts such as these will continue to improve our ability to incorporate a more diverse range of threats of higher quality into comparative extinction risk studies.

More practically, it is challenging to meaningfully quantify extrinsic threats at the species level. In comparison with the already difficult task of quantifying intrinsic traits (González-Suárez *et al.*, 2012), the general heterogeneity among threat quantifications and their difficulty of measurement is likely ultimately related to the abstract nature of some of the threats themselves (e.g., climate change, hunting, invasive species). In addition, quantifying threats to species is confounded at its most fundamental level by difficulties in defining the geographic distribution of species (Rondinini *et al.*, 2006; Jetz *et al.*, 2008; Gaston & Fuller, 2009; Di Marco *et al.*, 2013). Indeed, well-defined, high-quality geographic maps of species ranges are lacking for the majority of species, even within well-studied taxonomic groups like mammals (Boitani *et al.*, 2011; Jetz *et al.*, 2012). Despite these challenges, we are optimistic that progress on threats for extinction risk analysis can be made. We propose several avenues that might lead to improved use of threat information and to more practical outcomes for conservation science.

Uptake. Our study provides some compelling reasons for researchers to continue the increasing trend of explicitly considering threats in future studies. The costs of thinking more critically about the role of threats and exploring available data on threats for extinction risk analyses seem minimal in comparison with enacting conservation measures. Including information on threats, whether spatially explicit or not, can only benefit models in terms of explanatory power and interpretability as uninformative threat data will simply be outcompeted at the modelling stage if other more informative predictors are in place. Costs (particularly financial or effort related) are conceivable where the collection or compilation of threat data requires more resources and comes at the direct expense of some other achievable conservation benefit. In these circumstances, cost-benefit analyses that examine the expected value of information or tolerance limits of uncertainty for management could be valuable (Regan *et al.*, 2005; Runge *et al.*, 2011).

Realism and data quality. In the context of a species-level analysis, it is important to have some idea about how realistically threats may be represented in order for their importance to be properly assessed in comparison with intrinsic traits. A poor representation of a threat may simply obscure its true importance in a modelling

exercise, which might then have implications for conservation management. Another priority should thus be to strive for better, more biologically meaningful, spatially relevant and verifiable quantification of threats. This could include a shift to more quantitative representations, better ground truthing of data, improved evaluation of species' distributions and a push towards characterizing exposure to potentially threatening processes for all species, not just for species that are perceived to be in trouble.

Threat quantification uncertainty. Most methods of species-level assignment currently assume some kind of an average value that is dependent not only on spatial information of threats but also species' distributions. Given the potential variability in threat quantification at the species level, Di Marco *et al.* (2013) find that it is important to consider how different methods might influence threat quantification. We extend this to suggest that it is also necessary to know how this variability might subsequently affect extinction risk model results. Considering sensitivity analyses to directly determine the influence of quantification variation should be a short-term priority. Similarly, trait variability itself has been recently integrated into an intrinsic trait-only model of extinction risk in mammals (González-Suárez & Revilla, 2012). We expect extrinsic factors in some cases could be quantified and tested in a similar way.

Scale: A trade-off in resolution and scale seems inevitable as macroecological studies approach continental and global scales. This trade-off implies that global threat quantification may be difficult, where local threat characterization may be more feasible (e.g. Karanth *et al.*, 2010). Problems may also arise when choosing between a potentially precise reflection of local dynamics (such as the patterns identified by Di Fonzo *et al.*, 2013), or a less direct and less precise inference about species-wide dynamics (Purvis *et al.*, 2005). Large-scale studies may thus miss distinctive drivers of decline that may be unique to particular geographic regions or taxonomic groups (Thomas *et al.*, 2006). We cannot discount that global analyses can be useful for local conservation but rather where issues such as these are anticipated, investigating the effect of scale directly or considering the development of finer scale analyses should be a priority.

Analysis frameworks. We found that phylogenetic independent contrasts (PIC) was the most commonly used modelling framework when incorporating threats into extinction risk analyses. The main argument for using phylogenetic methods is a perceived need to account for pseudoreplication when including variables that

have a phylogenetic signal, which may indicate that species are nonindependent units for analysis (Bielby *et al.*, 2010). However, several authors have questioned whether this makes sense in an extinction risk context because extinction risk itself and numerous other potential predictor variables often included in such models (e.g., bioclimate, geographic location, human population pressure) are not evolved traits (reviewed by Grandcolas *et al.*, 2011). To add to this debate, we found that most extinction risk analyses include extrinsic factors (including threats), perhaps rendering the use of phylogenetic comparative methods in isolation largely unsuitable.

As threats and other extrinsic factors continue to be quantified, mapped and integrated into models of extinction risk, we should be particularly wary of this methodological issue and strive towards the development of alternative analysis frameworks (see e.g., Grandcolas *et al.*, 2011 for some suggestions from the field of biogeography). Starting with a strongly biologically informed conceptual model and hypotheses that underpin and inform such correlative analyses is likely to be useful. Also, critical will be developing methods that can effectively quantify or capture meaningful categorical or continuous threat values (e.g., expert opinion), and have the capacity to effectively grapple with interactions and nonlinearities that are frequently encountered in studies of extinction risk. Finally, a shift from correlative to mechanistic or hybrid frameworks as seen in other fields, such as species distribution modelling (e.g., Kearney & Porter, 2009) and the prediction of biodiversity patterns (e.g., Gotelli *et al.*, 2009), is an exciting development (e.g., see Keith *et al.*, 2008; Fordham *et al.*, 2013).

References

- AfriPop (2012) AfriPop Project. Available at: <http://www.afripop.org>. (accessed 1 October 2012).
- Balmford A, Carey P, Kapos V, Manica A, Rodrigues ASL, Scharlemann JPW, Green RE (2009) Capturing the many dimensions of threat: comment on Salafsky *et al.* *Conservation Biology*, **23**, 482–487.
- Barnosky AD, Matzke N, Tomiya S *et al.* (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51–57.
- Bielby J, Cardillo M, Cooper N, Purvis A (2010) Modelling extinction risk in multispecies data sets: phylogenetically independent contrasts versus decision trees. *Biodiversity and Conservation*, **19**, 113–127.
- Boitani L, Maiorano L, Baisero D, Falcucci A, Visconti P, Rondinini C (2011) What spatial data do we need to develop global mammal conservation strategies? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2623–2632.
- Bottrill MC, Joseph LN, Carwardine J *et al.* (2008) Is conservation triage just smart decision making? *Trends in Ecology & Evolution*, **23**, 649–654.
- Breiman L, Cutler A (2011) Random Forests. Available at: http://www.stat.berkeley.edu/~breiman/RandomForests/cc_home.htm. (accessed 1 December 2011).
- Cardillo M, Meijaard E (2012) Are comparative studies of extinction risk useful for conservation? *Trends in Ecology and Evolution*, **27**, 167–171.
- Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM (2004) Human population density and extinction risk in the world's carnivores. *PLoS Biology*, **2**, 909–914.
- Cardillo M, Mace GM, Gittleman JL, Purvis A (2006) Latent extinction risk and the future battlegrounds of mammal conservation. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 4157–4161.
- Cardillo M, Mace GM, Gittleman JL, Jones KE, Bielby J, Purvis A (2008) The predictability of extinction: biological and external correlates of decline in mammals. *Proceedings of the Royal Society B-Biological Sciences*, **275**, 1441–1448.
- Cooper N, Bielby J, Thomas GH, Purvis A (2008) Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography*, **17**, 211–221.
- Cullen R, White PCL (2013) Prioritising and evaluating biodiversity projects. *Wildlife Research*, **40**, 91–93.
- Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ (2007) Random Forests for classification in ecology. *Ecology*, **88**, 2783–2792.
- Davidson AD, Hamilton MJ, Boyer AG, Brown JH, Ceballos G (2009) Multiple ecological pathways to extinction in mammals. *Proceedings of the National Academy of Sciences*, **106**, 10702–10705.
- Davies RG, Orme CDL, Olson V *et al.* (2006) Human impacts and the global distribution of extinction risk. *Proceedings of the Royal Society Biological Sciences Series B*, **273**, 2127–2133.
- Di Fonzo M, Collen B, Mace GM (2013) A new method for identifying rapid decline dynamics in wild vertebrate populations. *Ecology and Evolution*, **3**, 2378–2391.
- Di Marco M, Cardillo M, Possingham HP, Wilson KA, Blomberg SP, Boitani L, Rondinini C (2012) A novel approach for global mammal extinction risk reduction. *Conservation Letters*, **5**, 134–141.
- Di Marco M, Rondinini C, Boitani L, Murray KA (2013) Comparing multiple species distribution proxies and different quantifications of the Human Footprint map, implications for conservation. *Biological Conservation*, **165**, 203–211.
- Evans MC, Watson JEM, Fuller RA, Venter O, Simon CB, Marsack PR, Possingham HP (2011) The spatial distribution of threats to species in Australia. *BioScience*, **61**, 281–289.
- Fisher DO, Blomberg SP, Owens IPF (2003) Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 1801–1808.
- Fisher DO, Owens IPF (2004) The comparative method in conservation biology. *Trends in Ecology and Evolution*, **19**, 391–398.
- Fordham DA, Akçakaya HR, Araújo MB, Keith DA, Brook BW (2013) Tools for integrating range change, extinction risk and climate change information into conservation management. *Ecography*, doi:10.1111/j.1600-0587.2013.00147.x.
- Fritz SA, Bininda-Emonds ORP, Purvis A (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters*, **12**, 538–549.
- Gaston KJ, Fuller RA (2009) The sizes of species' geographic ranges. *Journal of Applied Ecology*, **46**, 1–9.
- González-Suárez M, Revilla E (2012) Variability in life-history and ecological traits is a buffer against extinction in mammals. *Ecology Letters*, **16**, 242–251.
- González-Suárez M, Lucas PM, Revilla E (2012) Biases in comparative analyses of extinction risk: mind the gap. *Journal of Animal Ecology*, **81**, 1211–1222.
- Gotelli NJ, Anderson MJ, Arita HT *et al.* (2009) Patterns and causes of species richness: a general simulation model for macroecology. *Ecology Letters*, **12**, 873–886.
- Grandcolas P, Nattier R, Legendre F, Pellens R (2011) Mapping extrinsic traits such as extinction risks or modelled bioclimatic niches on phylogenies: does it make sense at all? *Cladistics*, **27**, 181–185.
- Harcourt AH, Parks SA (2003) Threatened primates experience high human densities: adding an index of threat to the IUCN Red List criteria. *Biological Conservation*, **109**, 137–149.
- Hof C, Araújo MB, Jetz W, Rahbek C (2011) Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, **480**, 516–519.
- Hoffmann M, Hilton-Taylor C, Angulo A *et al.* (2010) The impact of conservation on the status of the world's vertebrates. *Science*, **330**, 1503–1509.
- Hothorn T, Hornik K, Strobl C, Zeileis A (2012) A laboratory for recursive partytioning V1.0-0. Available at: <http://cran.r-project.org/web/packages/party/vignettes/party.pdf>. (accessed 1 October 2012).
- IPCC (2007) Climate Change 2007: The Physical Science Basis. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL) Cambridge University Press, Cambridge, United Kingdom and New York, NY, US. Available at: http://www.ipcc.ch/publications_and_data/publications_ipcc_fourth_assessment_report_wg1_report_the_physical_science_basis.htm. (accessed 1 October 2012).
- Isaac JL, Vanderwal J, Johnson CN, Williams SE (2009) Resistance and resilience: quantifying relative extinction risk in a diverse assemblage of Australian tropical rainforest vertebrates. *Diversity and Distributions*, **15**, 280–288.

- IUCN (2009) The International Union for the Conservation of Nature Red List of Threatened Species. Available at: <http://www.iucnredlist.org/>. (accessed 1 July 2009).
- IUCN (2012a) The International Union for the Conservation of Nature Red List of Threatened Species. Version 20104 2008: Version 2012.1. Available at: <http://www.iucnredlist.org/>. (accessed 1 October 2012).
- IUCN (2012b) The International Union for the Conservation of Nature Threats Classification Scheme (Version 3.2). Available at: <http://www.iucnredlist.org/technical-documents/classification-schemes/threats-classification-scheme>. (accessed 1 October 2012).
- Jetz W, Sekercioglu CH, Watson JEM (2008) Ecological correlates and conservation implications of overestimating species geographic ranges. *Conservation Biology*, **22**, 110–119.
- Jetz W, McPherson JM, Guralnick RP (2012) Integrating biodiversity distribution knowledge: toward a global map of life. *Trends in Ecology & Evolution*, **27**, 151–159.
- Jones KE, Purvis A, Gittleman JL (2003) Biological correlates of extinction risk in bats. *The American Naturalist*, **161**, 601–614.
- Jones KE, Bielby J, Cardillo M *et al.* (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, **90**, 2648.
- Karanth KK, Nichols JD, Karanth KU, Hines JE, Christensen NL (2010) The shrinking ark: patterns of large mammal extinctions in India. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1971–1979.
- Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.
- Keith DA, Akçakaya HR, Thuiller W *et al.* (2008) Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters*, **4**, 560–563.
- Koh LP, Sodhi NS, Brook BW (2004) Ecological correlates of extinction proneness in Tropical butterflies. *Conservation Biology*, **18**, 1571–1578.
- Lee TM, Jetz W (2011) Unravelling the structure of species extinction risk for predictive conservation science. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 1329–1338.
- Liaw A, Wiener M (2002) The randomForest package *R News*, **2**, 18–22.
- Mace GM, Balmford A (2000) Patterns and processes in contemporary mammalian extinction. In: *Priorities for the conservation of mammalian diversity. Has the panda had its day?* (eds Entwistle A, Dunstone N). pp 27–52. Cambridge, Cambridge University Press.
- Mace GM, Collar NJ, Gaston KJ *et al.* (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, **22**, 1424–1442.
- Microsoft (2012) Mapping Threats to Biodiversity. Available at: <http://research.microsoft.com/en-us/projects/threatmapping/>. (accessed 1 October 2012).
- Murray KA, Rosauer D, McCallum H, Skerratt LF (2011) Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 1515–1523.
- Myers N (1988) Threatened biotas: "Hot spots" in tropical forests. *Environmentalist*, **8**, 187–208.
- Olden JD, Poff NL, Bestgen KR (2008) Trait synergisms and the rarity, extirpation, and extinction risk of desert fishes. *Ecology*, **89**, 847–856.
- Owens IPF, Bennett PM (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences*, **97**, 12144–12148.
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Pimm SL, Jones HL, Diamond J (1988) On the risk of extinction. *American Naturalist*, **132**, 757–785.
- Pimm SL, Russell GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. *Science*, **269**, 347–350.
- Pocock MJO (2011) Can traits predict species' vulnerability? A test with farmland passerines in two continents. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 1532–1538.
- Prugh LR, Sinclair ARE, Hodges KE, Jacob AL, Wilcove DS (2010) Reducing threats to species: threat reversibility and links to industry. *Conservation Letters*, **3**, 267–276.
- Purvis A (2008) Phylogenetic approaches to the study of extinction. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 301–319.
- Purvis A, Gittleman JL, Cowlshaw G, Mace GM (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 1947–1952.
- Purvis A, Cardillo M, Grenyer R, Collen B (2005) Correlates of extinction risk: phylogeny, biology, threat and scale. *Phylogeny and Conservation*, **8**, 295–316.
- Purvis A, Rambaut A (1995) Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer applications in the biosciences: CABIOS*, **11**, 247–251.
- R Development Core Team (2012) *R: A language and environment for statistical computing*. Available at: <http://www.r-project.org/>. Updated Jan 2012.
- Regan HM, Ben-Haim Y, Langford B, Wilson WG, Lundberg P, Andelman SJ, Burgman MA (2005) Robust decision-making under severe uncertainty for conservation management. *Ecological Applications*, **15**, 1471–1477.
- Reynolds JD (2003) Life histories and extinction risk. In: *Macroecology*. (eds Blackburn TM, Gaston KJ). pp 195–217. Oxford, Blackwell Publishing.
- Reynolds JD, Dulvy NK, Goodwin NB, Hutchings JA (2005) Biology of extinction risk in marine fishes. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 2337–2344.
- Rondinini C, Wilson KA, Boitani L, Grantham H, Possingham HP (2006) Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters*, **9**, 1136–1145.
- Rondinini C, Boitani L, Rodrigues ASL *et al.* (2011) Reconciling global mammal prioritization schemes into a strategy. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2722–2728.
- Runge MC, Converse SJ, Lyons JE (2011) Which uncertainty? Using expert elicitation and expected value of information to design an adaptive program. *Biological Conservation*, **144**, 1214–1223.
- Salafsky N, Salzer D, Stattersfield AJ *et al.* (2008) A standard lexicon for biodiversity conservation: Unified classifications of threats and actions. *Conservation Biology*, **22**, 897–911.
- Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The Human Footprint and the Last of the Wild. *BioScience*, **52**, 891–904.
- Thomas GH, Lanctot RB, Székely T (2006) Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis. *Animal Conservation*, **9**, 252–258.
- Tranquilli S, Abedi-Lartey M, Amsini F *et al.* (2012) Lack of conservation effort rapidly increases African great ape extinction risk. *Conservation Letters*, **5**, 48–55.
- UCDP (2012) The Uppsala Conflict Data Program (UCDP). Uppsala University. Available at: <http://www.pcr.uu.se/research/ucdp/datasets/>. (accessed 1 Oct 2012).
- Wilcove DS, Rothstein D, Jason D, Phillips A, Losos E (1998) Quantifying Threats to Imperiled Species in the United States. *BioScience*, **48**, 607–615.
- Williams SE, Hero JM (1998) Rainforest frogs of the Australian Wet Tropics: guild classification and the ecological similarity of declining species. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**, 597–602.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. References included in the literature review (p2–8).

Data S2. Comparing extinction risk models with and without threats (p9–12).

Figure S2.1 Variable importance plot from Random Forest indicating the rank order of importance of the different predictors included in the analyses.

Figure S2.2 Conditional inference tree showing interaction of intrinsic species' traits, environmental variables, and human threats in determining extinction risk in mammals. + sign indicates higher or larger predictor value, and – sign indicates lower or smaller predictor value.