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Life history predicts risk of species decline in a stochastic world

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Understanding what traits determine the extinction risk of species has been a long-standing challenge. Natural populations increasingly experience reductions in habitat and population size concurrent with increasing novel environmental variation owing to anthropogenic disturbance and climate change. Recent studies show that a species risk of decline towards extinction is often non-random across species with different life histories. We propose that species with life histories in which all stage-specific vital rates are more evenly important to population growth rate may be less likely to decline towards extinction under these pressures. To test our prediction, we modelled declines in population growth rates under simulated stochastic disturbance to the vital rates of 105 species taken from the literature. Populations with more equally important vital rates, determined using elasticity analysis, declined more slowly across a gradient of increasing simulated environmental variation. Furthermore, higher evenness of elasticity was significantly correlated with a reduced chance of listing as Threatened on the International Union for Conservation of Nature Red List. The relative importance of life-history traits of diverse species can help us infer how natural assemblages will be affected by novel anthropogenic and climatic disturbances.

Keywords: International Union for Conservation of Nature Red List; extinction; life history; stage-based; elasticity; stochasticity

1. INTRODUCTION

Under increasing anthropogenic pressure, the Earth's biodiversity is currently facing a rapid decline [1–5]. The ability to predict which species are most vulnerable to extinction is thus a critical goal of conservation biology. Studies of past and ongoing extinctions, and of extant species, have consistently shown non-random patterns of species loss [6–10] and extinction vulnerability [1–4,6–14]. Uncovering traits that affect species extinction risk could thus improve predictions of future declines and enhance effectiveness of our conservation efforts [15].

To examine what factors affect species' risk of extinction, current approaches either examine species on a case-by-case basis or attempt to find general covariates with extinction risk for larger taxonomic groups. Approaches to predict extinction risk across a variety of taxa usually focus on traits of species that are associated with increased likelihood of extinction or decline, such as range size [7,9,16], generation length [9], body size [7,12,17,18] or life-history specialization [7,14,16,19]. Of these, range size has typically been found as the best single predictor of extinction risk [9], and it is used as a metric to designate current species threats by the International Union for Conservation of Nature (IUCN) [20].

It is clear that human-induced deterministic threats such as habitat degradation and loss, over-exploitation, pollution and detrimental impacts of invasive species have caused reductions in population sizes to a point where stochastic factors become critical and can drive a species to final extinction [21]. There is also mounting evidence suggesting that natural populations are experiencing increasing environmental stochasticity in the form of climatic variation (more extreme temperatures and rainfall patterns) and increasing frequencies of extreme environmental events [22–24], which have been shown to have negative consequences for populations [25–27]. Thus, life-history traits that may buffer a population's response to stochastic perturbation may be critical for determining extinction proneness in a world of increasingly smaller populations and increasing levels of environmental variability.

Life-history theory and empirical evidence suggest that organisms respond to their stochastic environments by adapting to certain modes of variation within their life-history stages [28–31] (but see [32] for cautions in making these assumptions). These trade-offs between life history and the amount and type of environmental variability across habitats and ecosystems have resulted in a large variety of life-history strategies that differ in their sensitivity to stochastic variation [33–35]. Given this wide variation in life histories, how can we predict more accurately which species might be more prone to extinction under anthropogenic disturbance?

We propose that the overall structure of an organism's stage-based life history could provide insight into the likelihood of decline towards extinction for species exposed to anthropogenic disturbance. If life histories are matched to a regime of natural variation, and anthropogenic disturbance both enhances variation and decreases

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population sizes, making populations more sensitive to stochastic processes, then we should expect to see differential patterns of species decline with respect to the life histories of species affected by anthropogenic disturbance. Specifically, we hypothesize that species with greater variation in the importance of each life-history stage for population growth are more likely to decline in a world experiencing increasing stochastic environmental events and major landscape changes.

Here, we introduce a novel approach that uses stage-structured vital rates of a species to predict sensitivity to increased environmental variation and test whether this can also predict species' endangerment level. In particular, we examine evenness of elasticities, a holistic summary of how evenly important the vital rates of a species' stage-based life history are to population growth. We calculate evenness of elasticities using published data for a diverse group of 105 plant and animal species, and test whether it can predict decline under simulated stochastic variation. We ask the following questions. (i) Does evenness of elasticities predict the response of population growth under increased environmental variation? And (ii) does evenness of elasticities for a species correlate with current conservation status? We show that evenness of elasticities can predict the relative magnitude of decline under generalized stochastic disturbance and that it is significantly correlated with current IUCN Red List endangerment status. This relationship suggests that a single parameter statistic representing the life history of a species is associated with risk of a species' decline under increasing environmental variation, and could be a valuable tool for conservation and extinction theory.

2. METHODS

(a) *Models and calculations*

The change in population size and structure over time can be represented as $\boldsymbol{n}_{t+1} = \boldsymbol{A} \times \boldsymbol{n}_t$, where $\boldsymbol{n}_t$ is a vector containing current population numbers for each life-history stage and $\boldsymbol{A}$ is the projection matrix in which the non-zero elements (vital rates) represent the fecundities, survivals and transition probabilities across life stages [36]. The projection matrix determines the long-term growth rate of the population and its dynamic responses to perturbations. Our model is derived from a similar equation by Tuljaparkur [37]. Tuljaparkur's model and the derivation to reach our model can be found in the electronic supplementary material, appendix S1. Using our model, the decline in population growth rate due to increased variation in vital rates can be found by:

$$a \cong \ln \lambda_0 - \frac{c^2}{2} \sum_{(ij)} \left(\frac{b_{ij}}{\lambda_0} \frac{\partial \lambda_0}{\partial b_{ij}} \right)^2, \qquad (2.1)$$

where a is the approximate stochastic growth rate of the population (i.e. $\ln(\lambda)$ with stochasticity), b_{ij} is a vital rate within the population projection matrix and $\ln(\lambda)$ is the instantaneous growth rate for the matrix without stochasticity. Elasticity is the proportional contribution of a vital rate to population growth ($b_{ij}/\lambda \times \partial\lambda/\partial b_{ij}$) such that all elasticity values for a matrix sum to one and indicate the relative importance of vital rates for changes in growth, $\ln(\lambda)$ [38]. We simulated five levels of environmental variation as standard deviations equalling constant proportions (c-values) of 0, 0.05, 0.1, 0.15 and 0.2 of the vital rate being modified. The advantage of this equation is that it uses elasticities that have many desirable characteristics, as we will show below.

Since the only part of the decline term in equation (2.1) that involves the growth rate or vital rates of the population is the elasticity term, the response of a population to increased variation in vital rates can be predicted by its elasticity values. Elasticities sum to one, so if one vital rate has a high elasticity, the others must be lower. In equation (2.1), the squared elasticities are summed, and a higher number results in a larger decline. Imagine a population matrix with only two vital rates (for simplicity); a matrix with elasticity values of 0.1 and 0.9 would generate a value of $0.1^2 + 0.9^2 = 0.82$, while a matrix with elasticities of 0.5 and 0.5 would generate a value of 0.5. All else being equal, a population with less even elasticity values will thus decline more quickly under stochastic variation in all vital rates. We calculated evenness of elasticities by taking the evenness of all elasticity values in a population matrix using the equation

$$\mathrm{EE} = \frac{H'}{H'_{\max}}, \quad H' = -\sum_{i=1}^{S} (p_i \ln p_i), \ H'_{\max} = \ln(S), \qquad (2.2)$$

where EE is evenness of elasticities, S is equal to the number of vital rates in the stage-based matrix and each vital rate's elasticity value is denoted by p_i. The set of elasticities in the second example above has an evenness value of 1, while the numbers in the first have an evenness of 0.47. This relationship indicates that evenness of elasticities should correlate negatively with how much population growth rate will decline under increased variation to vital rates.

To validate the theoretical predictions of equation (2.1), we additionally constructed simulation models of this scenario using the statistical language R [39]. In the model, we attached standard deviations equal to cb_{ij} to each vital rate for multiple matrix population models and then ran population growth simulations at each c level. The results obtained from our simulations are virtually identical to those from equation (2.1). See electronic supplementary material, appendix S2 for more details of the methods and results of our simulations.

(b) *Dataset*

We obtained stage-based life-history models by searching two databases, Google Scholar and Web Of Science, using the terms 'elasticity', 'matrix', 'stage-structured', 'life table' and 'population viability analysis' by themselves and with the addition of the taxon names 'bird', 'amphibian', 'mammal', 'reptile', 'insect', 'invertebrate', 'fish' and 'plant'. Additionally, a number of published books on conservation biology or matrix population models were examined for usable data and citations that could be followed to journal articles containing the appropriate data (see electronic supplementary material, appendix S3 for sources). For each species, we determined a Red List status primarily using IUCN data [20]. In most analyses, we grouped species by 'Least Concern' and 'Threatened'; the latter category contains the IUCN categories 'Near Threatened', 'Vulnerable', 'Endangered' and 'Critically Endangered'. We primarily grouped Threatened species to create roughly equal and robust sample sizes for our two groups. We included Near Threatened with Threatened species a priori to our analyses since these species have been evaluated and are considered very close to or likely to qualify as more seriously threatened in the near future [20]. In our analyses, however, we also examined the scenarios of Near Threatened species included with Least Concern species or removed from the dataset to see if this changed our results. For details of the methods used to

collect population matrices for our dataset and how we determined their endangerment classification, see electronic supplementary material, appendix S4.

In total, 105 population matrices were suitable for analysis. Of these matrices, 87 were for animal species and 18 for plants. The matrices for animal species comprised 13 amphibians, 23 birds, 8 bony fish, 2 sharks, 5 invertebrates, 24 mammals and 12 reptiles. For plants, 14 angiosperms, 3 conifers and 1 cycad were represented. We used two pairs of mammal subspecies as each pair was isolated from its conspecific and an independent unit for conservation purposes. Additionally, one matrix used came from a source which provided elasticity values without the actual parameter values or population growth rates. This matrix for one mammal population was only used for our question on current endangerment status.

Previous studies suggest that geographical range size is one of the best predictors of extinction risk [9]. Thus, we also collected categorical data on the maximum native extent of occurrence (range extent) of each species during the last century. Data were of varied resolution, so this was expressed as a number between one and eight, where one = $x \times 10^1 \, km^2$ (i.e. less than $100 \, km^2$) and eight = $x \times 10^8 \, km^2$, and so on. We could find range extent using this notation for all but one of our species, a marine copepod. For analyses that included range extent, we removed species that were listed as threatened due to small range size by the IUCN to avoid circularity [9].

(c) Analyses
Using equations (2.1) and (2.2), we examined how evenness of elasticities is associated with decline in population growth rate due to increased environmental variation for 105 modelled species. To test how increasing environmental variation influences the decline of population growth rate, we first calculated the population growth rates for each level of variation (*c*-values above), and then fitted a linear regression model to the relationship between our five levels of variation and growth rates. This was repeated for each of the 105 species-specific projection matrixes. The slope of the regression for each species indicates the rate of decline of a species' long-term growth rate with increasing stochastic disturbance. While the elasticity values of vital rates are primarily important in determining evenness of elasticities, the number of vital rates determines how many elasticity values will be used in the equation. As a result, there could be a relationship between evenness of elasticities and the number of vital rates. As expected, evenness of elasticities is not entirely independent of the number of vital rates and showed a weak trend of decreasing as the number of vital rates increased (Spearman rank correlation $\rho = -0.219$, $p = 0.024$). The slopes of the declines for all population matrices were then examined using linear regression against evenness of elasticities with a covariate number of vital rates to correct for this non-independence.

To test whether evenness of elasticities correlated with known conservation status for our species, we assigned each population projection matrix a 'one' if the species was Least Concern and a 'zero' if it was Threatened. Species listed as 'Data Deficient' were excluded from these analyses [20]. We used a generalized linear model (GLM) with binomially distributed residuals to perform logistic regression of Red List status against evenness of elasticities with the number of vital rates as covariate to test whether populations

of Least Concern species had higher evenness of elasticity values than Threatened species. We removed non-significant ($p > 0.05$) interaction terms sequentially from all models, with higher-order interactions being removed first, and ran the analysis again until only significant interactions remained. Two of our population projection matrices exhibited evenness of elasticity values more than 3 s.d. below the mean of all matrices. To test whether these two outliers influenced the results, we ran the analysis with and without these matrices.

Because range size is a well-supported and currently used metric for predicting extinction risk, we ran a series of additional tests to examine whether including range extent categories improved the model and how it performed relative to evenness of elasticities. For these tests, species listed as threatened due to small range size were removed from our data to avoid circularity [9,20]. Thus, we performed another logistic regression of conservation status against evenness of elasticities, range extent and number of vital rates using a GLM with binomially distributed errors.

We used Akaike information criterion (AIC) and evidence ratio ($E_{i,j}$) model selection to choose between significant models using all species and with our constrained set (species listed due to small range size removed) [40]. $E_{i,j}$ indicates the ratio of likelihood between the model with the most support and the model it is compared with [40]. The fit of well-supported models was evaluated with Nagelkerke r^2 for logistic multiple regression [41]. To check for biases within our dataset, we performed *t*-tests to find whether subsets of taxonomic classes or Red List status groups (i.e. Critically Endangered, Endangered, Vulnerable, Near Threatened and Least Concern) shared equal evenness of elasticities. See electronic supplementary material, §S5 for complete methods of how the dataset was divided in each case. We hypothesized that Least Concern species would have higher evenness of elasticities than all other groups and that this pattern should hold in most or all taxonomic classes. Splitting the dataset into multiple groups, however, reduced sample size in many cases, and thereby also reduced power to detect potentially significant results. All statistical tests were performed in the R statistical environment, and satisfied checks for heteroscedasticity and distributional requirements for residuals.

3. RESULTS
The 105 population projection matrices for real populations that we analysed had evenness of elasticities ranging from 0.279 to 0.999, with a group mean of 0.795. Matrices contained between 3 and 20 vital rates, with a mean of 8.23. As expected, increasing the stochastic variation in vital rates always decreased the overall long-run population growth rate. The average slope of decline in $\ln(\lambda)$ for a population with increasing vital rate variation differed by almost a factor of 10 across species (mean: -0.0287, min: -0.0814, max: -0.0084). See the electronic supplementary material for all species-specific results.

Overall, the final linear model, which included evenness of elasticities and number of vital rates, explained 91.4 per cent of the modelled decline in growth rates of species (figure 1 and table 1). Higher evenness of elasticities led to slower decline in growth rates under increasing vital rate variation (figure 1 and table 1). This effect was magnified when the number of vital rates was also high. In general, this indicates that species that are more balanced
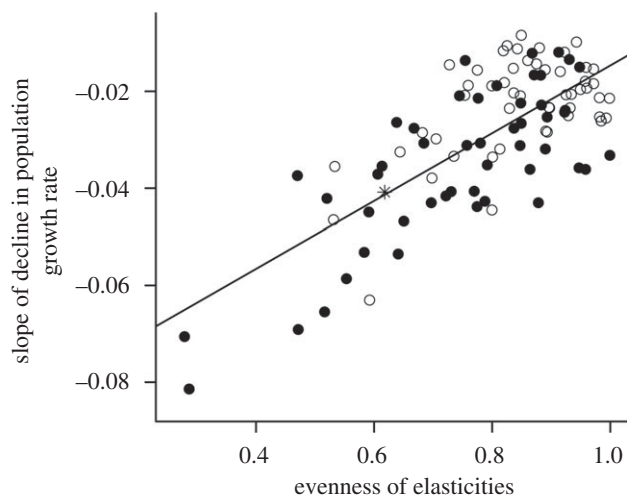
Figure 1. Slope of the decline in population growth across four levels of increasing vital rate variation against evenness of elasticities for stage-structured population matrices. Unfilled circles, Least Concern; filled circles, Threatened species; stars, Data Deficient species. Rate of decline decreases significantly with higher evenness of elasticity values. Most of the variation orthogonal to the trend line is explained by the number of vital rates in each matrix. $n = 104$. See §2 for calculations.

Table 1. Linear model of the relationship between evenness of elasticities (EE) and rate of decline in $\log(\lambda)$ with increasing simulated variation in vital rates.

	r^2	d.f.*	F	p-value
full model	0.914	2, 101	533.8	0.001
	coefficient	d.f.	t	p-value
EE	0.08	101	28.4	0.001
vital rates	0.002	101	20.98	0.001
intercept	−0.108	101	−42.81	0.001

*$p < 0.05$.

in their relative importance of life-history stages are also more resistant to decline when subjected to stochastic variation in their vital rates.

Mirroring our modelling results above, species with higher evenness of elasticities and number of vital rates were significantly less likely to be currently threatened (binomial regression model—evenness of elasticities: coefficient = 6.399, d.f. = 102, $z = 3.58$, $p = 0.001$; vital rates: coefficient = 0.111, d.f. = 102, $z = 2.21$, $p = 0.027$; intercept: coefficient = −6.012, d.f. = 102, $z = −3.64$, $p = 0.001$; table 2 [39]). Threatened species outnumbered Least Concern species by more than two to one within species, with an evenness of elasticities below 0.7 (figure 2). Above evenness of elasticities of 0.9, the opposite was true and Least Concern species outnumbered Threatened species by over two to one for our 54 Least Concern and 50 Threatened species (figure 2). Removing two Threatened statistical outliers (evenness of elasticities over 3 s.d. from the mean) did not alter the results. Placing Near Threatened species with Least Concern species or removing them from the dataset also

did not alter the results. The results of this test of real data are consistent with our modelled response to stochastic variation and indicate that species with life stages that are more similar in their relative importance are at a lower risk of becoming threatened.

Including range extent in our analysis resulted in a drop of vital rates from the model as it was no longer significant at $\alpha = 0.05$ (binomial regression model—evenness of elasticities: coefficient = 6.192, d.f. = 86, $z = 3.23$, $p = 0.001$; range extent: coefficient = 0.522, d.f. = 86, $z = 2.61$, $p = 0.009$; intercept: coefficient = −7.448, d.f. = 86, $z = −3.7$, $p = 0.001$; table 2). Range extent alone, even with 16 species categorized as Threatened owing to range size removed from our analysis, was still a significant predictor of conservation status. The range extent model was very unlikely compared against the full model, however ($E_{i,j} = 185.49$; table 2). Evenness of elasticities alone was supported much more than range extent, but still not well supported compared with the full model ($E_{i,j} = 19.31$; table 2).

Evenness of elasticities was higher for Least Concern species in four of six taxonomic classes where comparisons could be made (electronic supplementary material, figure A1). This difference was only significant for birds ($p = 0.012$, adjusted d.f. = 20.42, $n = 23$). Excluding birds and pooling all other classes still resulted in a significant difference in evenness of elasticities between Least Concern and Threatened species ($p = 0.037$, adjusted d.f. = 68.93, $n = 79$). Interestingly, reptiles and amphibians did not exhibit notable trends in evenness of elasticities between Least Concern and Threatened species (electronic supplementary material, figure A1). When grouped by Red List status, Least Concern species had higher evenness of elasticities than all Threatened groups, but, similar to taxonomic classes, only Endangered species had significantly lower evenness of elasticities (figure 3; $p = 0.007$, adjusted d.f. = 25.45, $n = 73$). No Red List groups of Threatened species differed significantly in their evenness of elasticities (all $p > 0.41$). Examining taxonomic and Red List status groups separately reveals that these subgroups show strikingly similar patterns to the group as whole.

4. DISCUSSION

Understanding what traits determine the extinction risk of species has been a long-standing challenge. Here, we show that a single predictor, evenness of elasticities, is highly correlated with population rate of decline under simulated increasing stochastic variation in vital rates. Furthermore, across 105 species from a diverse set of taxa, evenness of elasticities correlates significantly and negatively with current IUCN threatened status. Surprisingly, we found that evenness of elasticities was comparable with or better than a broad measure of species geographical extent for predicting current conservation status in our dataset. This not only emphasizes the importance of species' life-history traits for extinction risk, but also suggests that evenness of elasticities could be a useful indicator for predicting how species are likely to be affected by novel anthropogenic and climatic disturbances.

The relationship of evenness of elasticities to extinction risk may seem less obvious than metrics such as range size or population growth rate. However, evenness of elasticities

Table 2. Fit parameters for models examining the correlation between real species evenness of elasticity and conservation status (Threatened or Least Concern). Full dataset has 103 species; no range listed has 87 species, since those listed as endangered due to range size are removed. All full models except for vital rates are significant at $p < 0.01$. w_i is the model weight describing the proportion of likelihood support for each model in the group. $E_{i,j}$ is the evidence ratio describing the relative likelihood of the most well-supported model ($\Delta AIC = 0$) in each group against the less supported models [40].

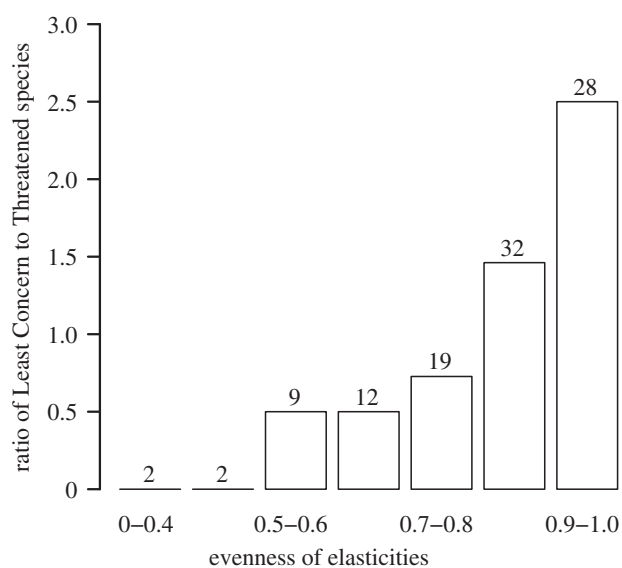| model parameters	dataset	ΔAIC	w_i	$E_{i,j}$	r^2
full model: EE* + vital rates*	full	0	0.842	—	0.226
EE*	full	3.35	0.157	5.36	0.167
vital rates (model not significant)	full	14.9	0.0005	1684	0.029
full model: EE* + range extent*	no range listed	0	0.946	—	0.330
EE*	no range listed	5.91	0.049	19.31	0.233
range extent*	no range listed	10.46	0.0051	185.49	0.172

*$p < 0.05$.

Figure 2. Ratios of the number of Least Concern to Threatened species as evenness of elasticities increases. Numbers above bars represent the sample size of species within that bin.
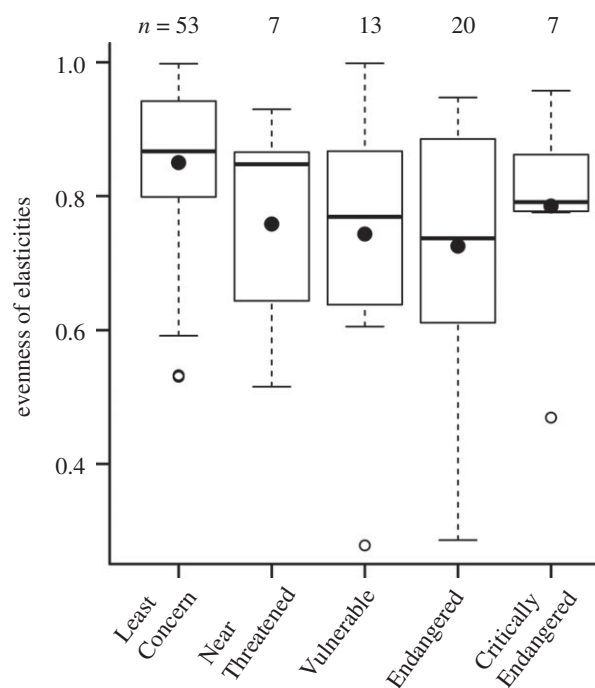

Figure 3. Comparison of evenness of elasticities between IUCN Red List threat level categories. Means are represented by filled dots. Bold dark lines in box represent medians, with box and whiskers representing quartiles from the median.

is a holistic, biologically meaningful metric that can affect how a population responds to environmental stochasticity. Evenness of elasticities is not a life-history trait, but like elasticity itself it represents a suite of important life-history traits that structure a species demographic dynamics. Species with very low evenness of elasticities have certain life stages that are disproportionally important to population growth. While such a strategy may be adaptive under past (or current) conditions [28–31], our results suggest that these species' populations are most likely to be negatively affected by novel environmental stochasticity (e.g. increased frequency of dramatic climatic events). This includes, for example, many large mammals, which tend to have relatively low evenness of elasticity due to the disproportionally high importance of long-lived reproductive adults. Recent work suggests that large mammals have always had higher extinction rates than many other clades [42] and many are currently included on the Red List by IUCN. On the other hand, species with well-balanced life histories (i.e. high evenness of elasticities) are affected less dramatically by changes in survival or fecundity owing to novel environmental variation. Some species with especially high evenness of elasticities, for example, are white-tailed deer (*Odocoileus virginianus*, 0.96) and garlic

mustard (*Alliaria petiolata*, 0.97). Both of these species thrive in moderately disturbed environments and are often abundant within their wide ranges.

Besides the conceptual implications, our results also have important conservation applications. Previous studies have identified range size as one of the best predictors of species declines [9]. Optimally, evenness of elasticities and range size could be used together to include information about both geographical extent and life history. For instance, Purvis *et al.* [9] found that range size explained 24 per cent of the variation in the level of Red List status for carnivores and primates. Using a diverse list of taxa with over 100 species from two kingdoms, we found that combining estimates of range extent with evenness of elasticities improved our model and explained 33 per cent of the variation in Red List status. Combining independent measures of extinction risk can provide increased predictive power that neither measure of risk could determine alone [9,18].

As with many other metrics used to estimate extinction risks, there is often a lack of detailed information on the life

histories of species that are of potential conservation concern. However, in many situations the results of our study can still be applied to prioritizing conservation actions for species with limited life-history data. For example, Heppel *et al.* [43] found that a two-stage elasticity matrix with three vital rates (juvenile survival, adult survival and fecundity) can be constructed with estimates of earliest age at first reproduction, annual adult survival and population growth rate (λ). These simple elasticity matrices, constructed for mammals with many different life histories, were strikingly similar to matrices constructed using complete life tables [43]. Thus, while complete life tables may be difficult to obtain for some taxa, only partial information may be required to generate approximate elasticity matrices and calculate evenness of elasticity. In this study, the number of vital rates in a matrix is only marginally important for predicting whether a species is endangered or not, despite a wide variety in the dimensions of our species' matrices and their number of vital rates. In addition, we often know life histories of related species that we can use to infer whether a species is likely to have disproportionally important stages, and thus a low or high evenness of elasticities. In such scenarios, our results can still provide a simple 'rule of thumb' to make qualitative estimates on whether species are likely to have a high risk of decline. The utility of a life-history matrix is limited, of course, by the quality of information used to generate it. Evenness of elasticity should in any case be approached more qualitatively than quantitatively as in other sorts of elasticity analysis [43–45]. The use of life-history data to understand extinction risk will nonetheless be greatly improved with increased life-history data for more species, allowing for datasets with increased coverage of more diverse taxa.

Common caveats in the use of elasticity analysis are that the effects of large changes to vital rates may not linearly correspond to elasticities, and that changes to one vital rate will affect the elasticity of all vital rates [44,45]. We did not model large changes to our species' vital rates. Covariances between vital rates were not included in our model, since these were often not available. Species with complex trade-offs and interactions between life stages such as survival and fecundity, or different life-stage densities, could respond differently to variation in life-history parameters than we were able to model as a result. It would be interesting to examine how different levels of covariance between vital rates could change the model predictions. Despite this caveat, our results suggest that our approach is robust under less than ideal conditions.

One caveat specific to our analysis is that amphibian and reptile species in our dataset have nearly identical mean evenness of elasticities. Random sampling of a fairly small number of species (13 amphibians and 12 reptiles) could mean that this lack of a pattern is spurious, though it deviates from the pattern for every other group in this analysis. There are two other reasons that amphibians and reptiles could show this pattern. One is that the covariances between life-history stages for one or both groups may present difficulties for our methods, which use a 'snapshot' image of a species life history. Many amphibians, for example, are well known to have highly plastic phenotypes and life histories with high correlations between stages for traits related to survival or fecundity rates [46–48]. Another is that current reasons for decline in these groups could be somehow largely

independent of the life-history traits summarized by evenness of elasticities. Amphibians and reptiles are both declining worldwide owing to massive losses in wetlands and other habitats, as well as emerging diseases [49]. Impacts to species such as the emergence of amphibian chytrid fungus or massive habitat loss may affect most or all vital rates concurrently and strongly. The balance of importance of life-history vital rates may only be predictive when declines are not extreme across a life history.

Natural systems harbour a large range of species that differ in many aspects of their biology and life-history traits, but what traits determine a species' extinction risk? Here, we provide a new technique to holistically simplify life-history information and help predict species' response to increased variability in vital rates due to factors such as changing climates or habitat destruction. This approach could help to screen for species at higher risk of rapid decline to more quickly and accurately prioritize conservation actions [50]. We show that species' life-history traits, even in a summarized form, are important across wide taxonomic groups in determining and understanding risk of decline in this time of increasing worldwide change and loss of species diversity.

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