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Quantifying extinction risk using multi-state Markov models

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Declaration

I declare that I have downloaded and collated all the data used in this study and that I have cited this appropriately. The data was then cleaned, prepared and analysed by me and where I have not written the computer code to do so myself I have acknowledged this and provided appropriate references. I declare that all ideas and materials which are not my own have been properly cited.

Throughout the preparation of this project, my supervisor has provided me with guidance on the methodology, analysis and presentation of my work.

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Abstract

Predicting future extinctions and identifying which species are most at risk is essential for conservation. A widely used source for such information is the IUCN Red List, which places species into discrete risk categories. Previous studies have struggled to convert these categories into probabilities of extinction, resulting in a wide range of possible extinction probabilities that are only weakly related to empirical measurements.

Here I develop a new approach to the problem using a multi-state Markov model, which is parameterised with extensive historic data from the IUCN showing transitions of species between Red List categories. The resulting probabilities predicted by the model are extremely robust producing consistent results, even when 75% of species data is discarded. The model predicts that 8% of mammals, 3% of birds, 23% of reptiles and 7% of amphibians currently included in Red List 'Threatened" categories will become extinct over the next 100 years.

I have quantified extinction risk as a function of Red List data and found a strong taxonomic bias. For example the probability of extinction within 100 years for a "Critically Endangered" bird is predicted to be lower than that for an "Endangered" mammal or a "Near Threatened" reptile. This suggests that caution is required when interpreting Red List data across taxa. This work will allow for ongoing analyses, which rely on values for extinction probabilities, to be informed by more data driven values than were used previously.

Keywords: *extinction risk, threatened species, IUCN Red List, Red List Index, multi-state Markov model*

Introduction

The loss of global biodiversity and associated extinction rates are of major concern and many studies have sought to quantify population declines and extinctions; see (Butchart et al., 2010), (Pereira et al., 2010) and (Ceballos et al., 2017), amongst others. This is of particular concern in the context of human destruction of habitats (Pimm et al., 2014) and the impact of biodiversity loss on how ecosystems function (Mendenhall et al., 2012).

The best known source of extinction risk data is the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species™ [1] (IUCN, b). This list places species into categories ranging from "Least Concern" through to "Extinct". These rankings are used as a fundamental part of many analyses, including those which seek to analyse and implement conservation efforts (Redford et al., 2011). As an example of this, the Zoological Society of London (ZSL) run the Edge of Existence programme (EDGE,) which aims to focus conservation resources to maintain diversity by identifying those species which are Evolutionarily Distinct and Globally Endangered (EDGE species). The latter of these criteria is entirely based on the IUCN Red List (IUCN, b).

The Red List Index (RLI) uses information from the Red List to review overall biodiversity trends within four taxonomic groups; mammals, birds, amphibians and corals (IUCN, c) (Figure 1). The RLI has been used in many studies to evaluate the impact of conservation. For example, Young et al. used RLIs to evaluate the impact of a Jersey based conservation organisation and concluded that RLIs a useful tool useful where conservation organisations target small numbers of species with restricted distributions (Young et al., 2014). Red List categories (IUCN, a) and RLIs (IUCN, c) have also been used in retrospective conservation studies, for example in studies of carnivores and ungulates (Di Marco et al., 2014).

There have been many suggested mappings of Red List categories (IUCN, a) to extinction probabilities within a range of future timescales. These predictions are required for conservation prioritisation and predicting extinctions across regions and taxa. The most commonly used mappings are those included in a paper published in 2008 (Mooers et al., 2008) (Table 1). Three of the suggested mappings are based on extrapolations from the limited quantitative guidelines provided by the IUCN (IUCN, a), one is inferred from Isaac et al. (Isaac et al., 2007) and one suggested by Mooers et al. (Mooers et al., 2008). The accuracy of this approach is doubtful and there is no region of uncertainty around the predications to give them context, Species are not all assessed under the same criteria and whilst the IUCN do provide some limited quantitative guidelines these do not

[1] From this point onwards referred to as the Red List.

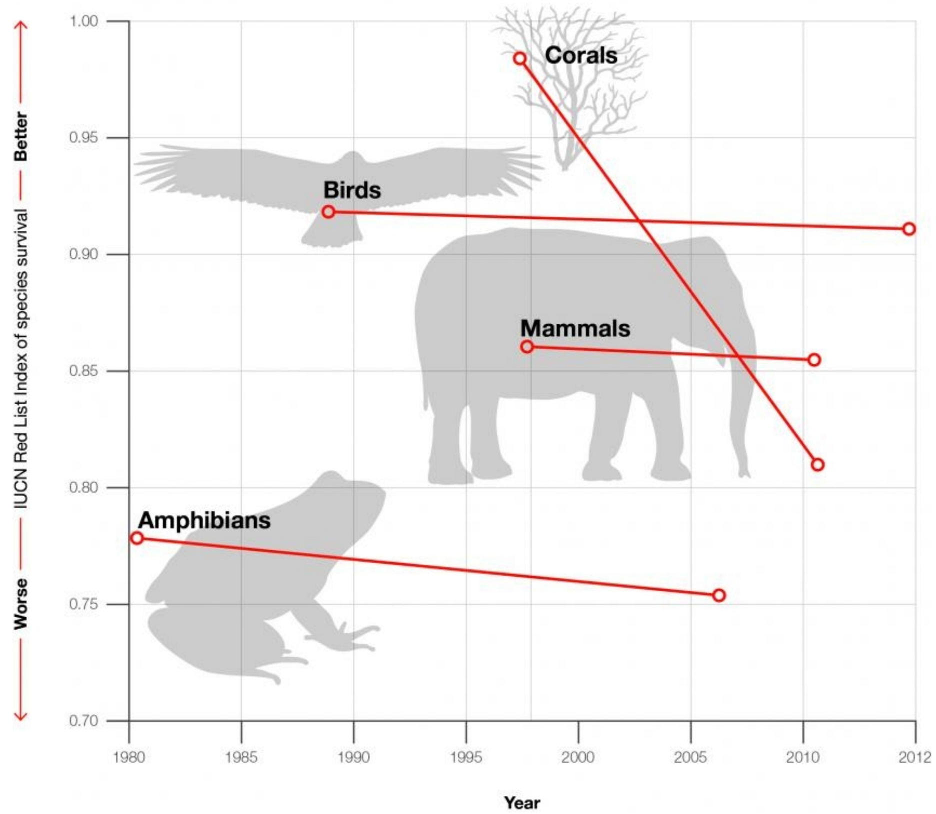


Figure 1: Red List Index (RLI), reproduced from the IUCN. The RLI shows the decline in major species groups between 1980 and 2012 and is based on the movement of species through Red List categories. An RLI of 1 indicates that all species are listed in the "Least Concern" category. An RLI of 0 indicates that all species have become "Extinct". The species included all show increasing rates of biodiversity loss, with Corals moving most quickly towards extinction (IUCN, c).

extend beyond the "Threatened" categories (IUCN, a). Isaac et al. treat the Red List categories (IUCN, a) as "intervals of extinction risk" and suggest that the difference between the categories represent a doubling of this risk (Isaac et al., 2007). This assumption is dubious since the category of "Least Concern" acts as a "catch-all" category where other categories are not appropriate.

There are currently 908 extinct species listed on the Red List [2]. In 2009 it was noted that only around 1,200 species had been recognised as having become extinct since 1600 (Stork, 2010). Indeed for the period from 1986 to 1990 only 33 animal species, including 15 vertebrates, were added to the extinction lists (Smith et al., 1993). To be shown as extinct, exhaustive surveys are required and there must be "no reasonable doubt that the last individual has died" (IUCN, a). Predicted

[2] Correct at 17 July 2018.

	Probabilities				
IUCN category	**Isaac**	**IUCN100**	**IUCN50**	**IUCN500**	**Pessimistic**
Least Concern	0.025	0.0001	0.00005	0.0005	0.2
Near Threatened	0.05	0.01	0.004	0.02	0.4
Vulnerable	0.1	0.1	0.05	0.39	0.8
Endangered	0.2	0.667	0.42	0.996	0.9
Critically Endangered	0.4	0.999	0.97	1	0.99

Table 1: Extinction rates extracted from Table 1 in Mooers et al. The figures in the Isaac column are inferred from Isaac et al, using a constant change of factor 2 and a probability of extinction from "Vulnerable" of 0.1 in 100 years (Isaac et al., 2007). The IUCN columns are based on IUCN probabilities (from "Critically Endangered" 0.5 in 10 years, from "Endangered" 0.2 in 20 years and from "Vulnerable" 0.1 in 100 years) (IUCN, a). Mooers et al. have suggested the figures in the Pessimistic column. (Mooers et al., 2008).

numbers of extinctions over different periods of time vary widely by taxa. In 1993, Smith et al. used the speed of status changes between Red List categories (as they were at that time) to estimate rates of extinction and calculated that in the case of birds and mammals it would take 200-300 years for 50% of species to become extinct (Smith et al., 1993). In 1994, Mace produced estimates for projected rates of extinction for 10 vertebrate taxa. These projections used the percentage of species in "Threatened" categories at that time (Mace, 1994). Estimates for extinction rates ranged from 6-50% over a 100 year period. Estimates of time taken until 50% extinction ranged from 101 to 1,168 years (Full details in the Supplementary Information section (Table 4).

This project seeks to quantify probabilities of extinction by the application of a bi-directional multi-state Markov (MSM) model. Indeed, the probabilities I calculate here for the Kingdom Animalia, broadly support those of Isaac et al. (Isaac et al., 2007). The following questions will be addressed:

(i) How do the probabilities of extinction found here compare to the figures in general use at the moment?

(ii) Are these probabilities of extinction the same across major taxonomic groups?

(iii) How do my findings compare to existing work and can I support or refute previous studies?

Methods

The IUCN Red List

Transitions between IUCN Red List categories (IUCN, a) are used as a starting point for analysis here, and over the years many different categories have been applied. The "Guidelines for using the IUCN Red List Categories and Criteria" were first published in 1994 and revised in 2001 (IUCN, a). In this work I will use the most up to date IUCN categories (Figure 2).

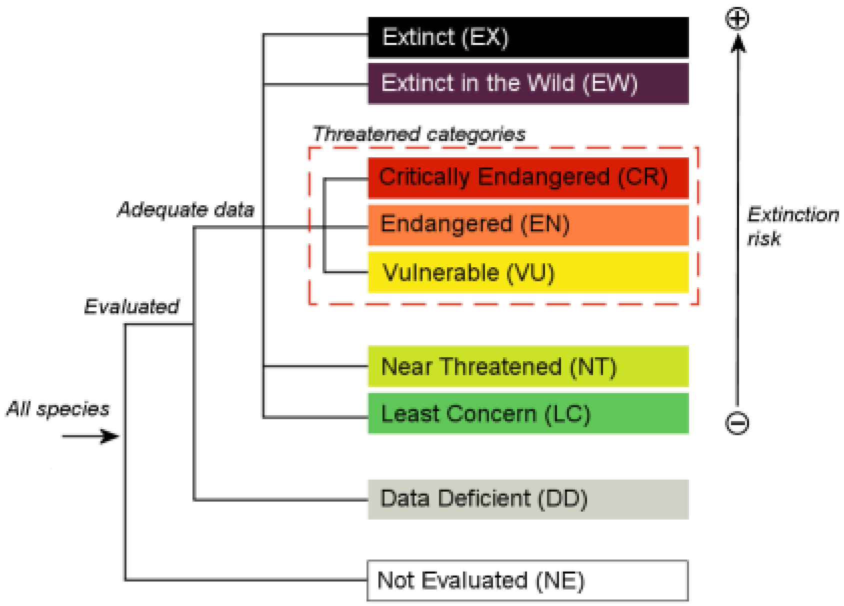


Figure 2: Currently used IUCN categories; reproduced from the IUCN website (IUCN, b)

The threatened categories are those of "Vulnerable", "Endangered" and "Critically Endangered". "Near Threatened" is used where a taxon is not currently threatened, but is close to qualifying. If a taxon is not close to qualifying, the category of "Least Concern" is applied. The difference between each of the categories is not equal, particularly with respect to "Least Concern" which, in effect, acts as a "catch-all" category. Direct mappings from one of these categories to a probability of extinction at some future time horizon is therefore not possible.

The five quantitative criteria used when applying these categories to a taxon are designated A to

E. These are set out in the Red List Guidelines and are reproduced below (IUCN, a):

A. Declining population (past, present and/or projected)
B. Geographic range size, and fragmentation, decline or fluctuations
C. Small population size and fragmentation, decline or fluctuations
D. Very small population or very restricted distribution
E. Quantitative analysis of extinction risk (e.g., Population Viability Analysis)

Whilst the application of these criteria is detailed in the Red List Guidelines (IUCN, a) there remain many issues with applying available data and many inherent biases. This is particularly the case where opportunistic data is used (Maes et al., 2015). Biases include, but are not limited to, preferences for certain taxonomic groups, and errors due to differences in the skills of observers. Collen et al. note that the the greatest variation in Red List assessments is due to differences in the assessor's risk tolerances (Collen et al., 2016). There is obviously a risk that species may have been placed into the wrong category, for whatever reason.

Of particular interest to this project is the application of Criterion E. Whilst Criteria A to D are concerned with population size and geographic range, Criterion E is based on a quantitative analysis, such as a Population Viability Analysis (PVA). This would be used to ascertain the probability of a taxon becoming extinct over a certain time period. For example, if a taxon is to be listed as "Critically Endangered" under Criterion E, there has to be a chance of extinction which is $\geqslant 50\%$ over 10 years or three generations, whichever is longer (up to a maximum of 100 years).

Whilst PVA predictions have been found to be accurate where data is adequate (Brook et al., 2000), there is a view that they are not best used for predicting absolute extinction risks (Mace et al., 2008); rather that they are better used for assessing management strategy benefits (Walsh et al., 1995), or in assessing relative rather than absolute extinction risk (Beissinger and Westphal, 1998). Mace et al. recommend using simple models rather than those with many assumptions for the purposes of Criterion E (Mace et al., 2008).

Data Collation

Full categorical listings histories for the 93,872 species held on the IUCN Red List were downloaded in February 2018 via the Red List API (IUCN, b) using the R (R Core Team, 2017) package "rredlist" (Chamberlain, 2017). Panel data are intermittent observations of a process in continuous-time, and the downloaded data were collated into panel data format used to build a Master dataset for this study.

A number of modifications were made to the downloaded data. Firstly, entries listed for years prior to 1994 were removed. This is when the categories used were first standardised and direct mappings of most statuses before that date are not possible. Listings for 1994 onwards were also removed where the categories could not easily be mapped to current standard categories (Figure 2). These comprised "Commercially Threatened", "Indeterminate", "Insufficiently Known", "Not Recognised" and "Rare". Each remaining category was then given a number from 0 to 7 for algorithmic purposes. These mappings are summarised in the Supplementary Information section (Table 5).

Where there were two listings for a species in one calender year, further exclusions were made where one of the entries was shown as "Data Deficient" or was an older-style listing. In the remaining cases, 6 months was randomly added to one of the entries and both listings retained.

Finally, species with only one entry remaining at this point were excluded. Single entries are not informative for the purposes of an MSM model based on panel data, since it a series of observations over a period of time are required.

Taking account of revisions and listing errors

Since 2007, the IUCN have published a table each year showing those species which had changes made to their Red List categories during that calender year (IUCN, b). This is called Table 7 and it specifies whether category revisions were made for genuine or non-genuine reasons. The former is defined as a "genuine improvement or deterioration in the species' status", the latter as "status changes due to new information, improved knowledge of the criteria, incorrect data used previously, taxonomic revisions etc" (IUCN, b).

Table 7 data for the years from 2007 to 2017 (inclusive) was comprehensively analysed and incorporated within the Master dataset. There were also over 2,000 status changes during this period which were not included within the appropriate Tables 7. The majority (nearly 80%) of these related to 2008, and for that year alone the relevant Table 7 only included genuine status changes. All of these missing status changes were incorporated within the main database as non-genuine changes. Many of those for years other than 2008 had a previous status of "Data-deficient" and a change from this status could only ever be a non-genuine change.

The post-2007 histories for each species were then reviewed by considering pairs of datapoints. Alterations were made to the data as follows:

(i) For a non-genuine change in a species listing, the previous listing was amended to that of the current status and the current status was, in turn accepted. The original ”mistaken” status was effectively ignored.

(ii) For a genuine change in a species listing, the statuses of the current and previous listing were accepted, based on the logic that the earlier status was re-examined and found to be reasonable as there was a genuine change in status.

(iii) Where there was no change between a pair of statuses, the status of the first was accepted on the basis that it had been looked at twice.

(iv) Where a listings history contained an “Extinct” listing, but at a later point was given a different listing (so the species “came back to life”), this was dealt with in the same way as for a non-genuine change detailed at (i) above. The incorrect “Extinct” listing was therefore effectively ignored.

Since the above alterations only took account of post-2007 listings, all the remaining pairs of datapoints prior to 2007 were also reviewed so that potential errors in categorisations could be taken account of.

As there is no Table 7 data for pre-2007 listings, an estimate for potentially incorrectly allocated states was based on the number of post-2007 transitions and the proportion of these that were non-genuine status changes during that time. Appropriate status changes based on these estimates were made on a random basis. These category changes are summarised in the Supplementary Information section (Table 6). Only transfers between states which might reasonably be considered to have been mis-categorised were considered. So, for example, if a species is currently listed as being “Endangered”, its true state could indeed be “Endangered”, but it may also be that its true state is “Vulnerable” or “Critically Endangered”. It will not be “Extinct” since it must have been observed, and it is unlikely to be of “Least Concern” or “Near Threatened”. This method also takes account of entries categorised as being “Data Deficient”.

The final listing for each species history was also considered, where that final listing did not come about because of a status change (these have already been taken into account at (i) and (ii) above). A proportion of these final listings were randomly re-categorised into appropriate different states in the same way as the pre-2007 listings, to account fairly for the fact that some of these categorisations will also be incorrect and will later be changed for non-genuine reasons.

These alterations resulted in the creation of a Master dataset for MSM modelling, with 25,782 species retained and 104,490 listings for these species (Figure 3).

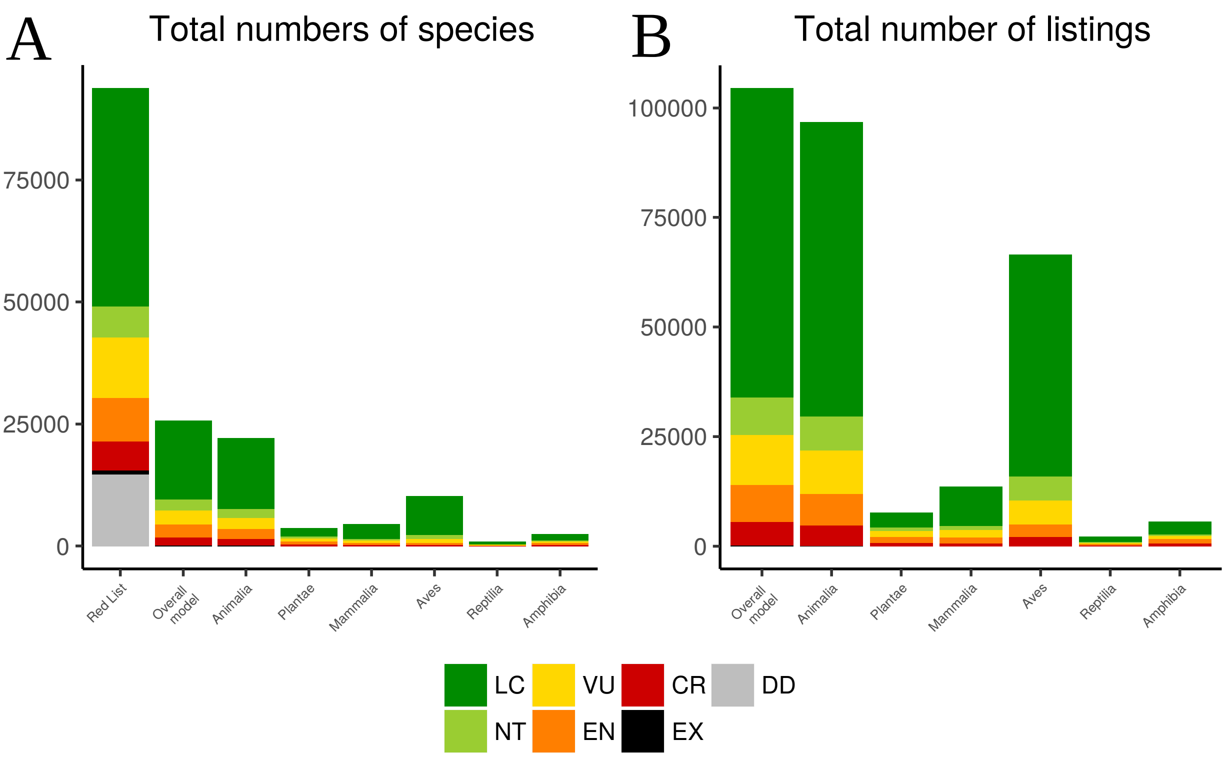


Figure 3: Species listed by the Red List and those retained in the overall model (A) and total numbers of listings for species retained in the overall model (B), broken down by major taxa and Red List category. Red List data downloaded throughout February 2018 (IUCN, b). The overall model comprises 25,782 species with 104,490 individual listings; 70,577 of these are "Least Concern" listings. There are 96,785 listings for 22,168 species of animals and 7,703 listings for 3,614 species of plants. The one remaining species of fungus has not been included. Chordates comprise almost 90% of animal species (19,815 in total) with 4,454 species of mammals, 10,280 species of birds, 987 species of reptiles and 2,450 species of amphibian.

The randomisation parts of the process described above were then repeated 100 times to produce 100 additional datasets on which to test the MSM model. Approximately 25,500 species were retained in each of the additional datasets; each species having a valid time series of transitions between categories (in the same way as the Master dataset).

Multi-state Markov model

Multi-state Markov (MSM) models are useful where there are a series of discrete states which are moved through in continuous time (Cox, 1965). The model used here follows that for disease progression and the state-space diagram is shown at Figure 4 with appropriate entries showing a progression in the severity of states from "Least Concern" through to "Extinct". So few species were included within the "Extinct in the Wild" category, that these were incorporated within "Critically Endangered" to avoid overcomplicating the model. "Extinction" is the absorbing state here (or death), and transitions are possible between adjacent states. Death is possible, although extremely unlikely, from any state.

For a multi-state Markov model in continuous time, the movement between states and the time of that change is driven by transition intensities $q_{rs}(t, z(t))$ for each pair of states r and s. These can depend on time, t or on $z(t)$; time-varying explanatory variables (Jackson, 2011). The instantaneous movements from r to $s \neq r$ can be shown as follows:

$$q_{rs}(t, z(t)) = \lim_{\delta t \to 0} (\mathrm{P}(S(t + \delta t)) = s | S(t) = r) / \delta t \tag{0.1}$$

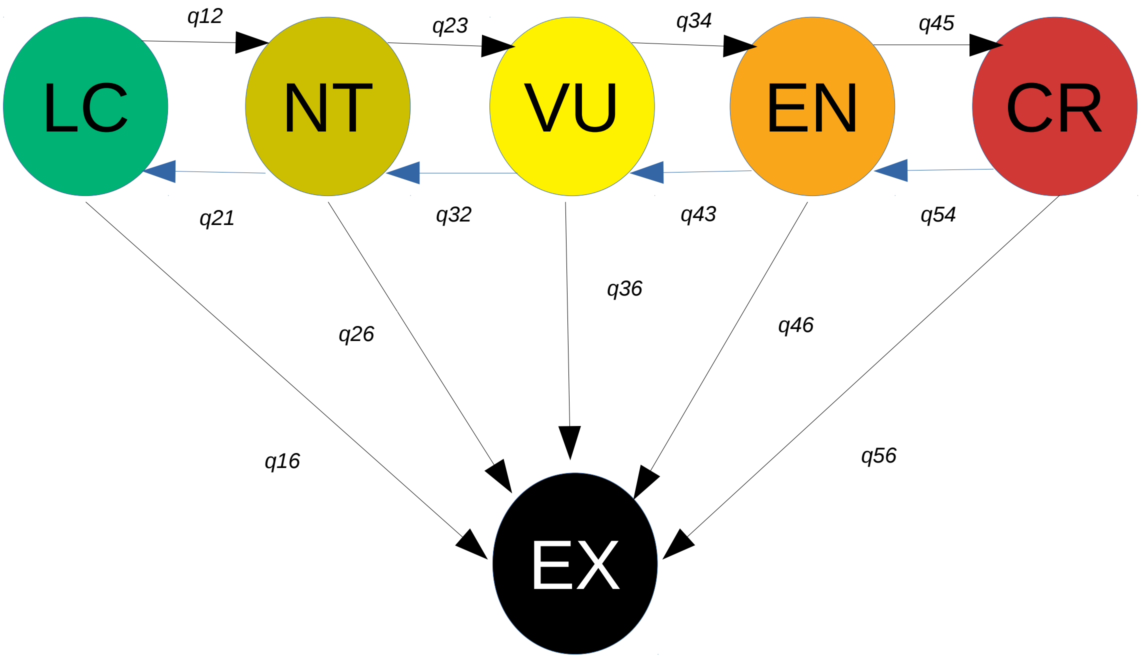
The Q matrix (Figure 4) is an $R \times R$ matrix with rows which add up to zero. It has diagonal entries where:

$$q_{rr} = -\Sigma_{s \neq r} q_{rs} \tag{0.2}$$

Each element in the Q matrix represents the rate at which transitions are made. The entry at q_{56}, for example, will represent the rate of transition from "Critically Endangered" to "Extinct".

We have panel data here where observations of the states of species have been made on two or more occasions through a period of time. As the process is in continuous time the MSM model relies on the Markov assumption that future states are independent of prior states; see (Cox, 1965), (Cook, 2018) and (Jackson, 2011) amongst others. The data may well show that a species has been observed on one occasion as being in a "Vulnerable" state and at the next observation as being "Critically Endangered". The Q matrix shows 0 for this entry as the underlying model specifies that the "Endangered" state must have been passed through even if it was unobserved. To take an example from the Master dataset, in the case of *Myiarchus semirufus*, there were six assessments made during the period from 1994 to 2016. In 1994, 2000 and 2004 the observed state was that of "Least Concern" [3]. In 2008, 2012 and 2016 the observed state was that of "Endangered". At some stage between the assessment in 2004 and that in 2008 the states of "Near Threatened" and

[3] More correctly, the first two of these observations were "Lower Risk/Least Concern" an old-style listing - see Table 5 in the Supplementary Information Section



$$Q = \begin{pmatrix} -(q_{12}+q_{16}) & q_{12} & 0 & 0 & 0 & q_{16} \\ q_{21} & -(q_{21}+q_{23}+q_{26}) & q_{23} & 0 & 0 & q_{26} \\ 0 & q_{32} & -(q_{32}+q_{34}+q_{66}) & q_{34} & 0 & q_{36} \\ 0 & 0 & q_{43} & -(q_{43}+q_{45}+q_{46}) & q_{45} & q_{46} \\ 0 & 0 & 0 & q_{54} & -(q_{54}+q_{56}) & q_{56} \\ 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

Figure 4: Illness death model with transition intensity matrix Q. This is a homogeneous continuous-time Markov process. The transition intensity martix Q defines the instantaneous transitions in the Markov process. The categories shown are the Red List categories of "Least Concern" (LC), "Near Threatened"(NT), "Vulnerable"(VU), "Endangered"(EN), "Critically Endangered"(CR) and "Extinct" (EX) (IUCN, a) and the colours of the states have been chosen to mirror those used by the IUCN (Figure 2). These colours and state abbreviations are used throughout the rest of this report for consistency.

"Vulnerable" must have been passed through, even though these states were unobserved.

The "msm" package (Jackson, 2011) in R (R Core Team, 2017) was used to fit bi-directional MSM models to the longitudinal panel data. Observation times were assumed to be ignorable. This is the case where observation times are fixed in advance, or where they are random, or where the current state informs the timing of the next observation. Gruger et al. provide a summary of non-informative and informative sampling time (Gruger et al., 1991). In essence if an individual were a patient under the care of a Doctor, an informative sampling time would be one where that patient referred themselves for the next "observation". This will obviously not be the case here.

Kalbfleisch and Lawless described a continuous time Markov model for the analysis of panel data where sampling times are not informative (Kalbfleisch and Lawless, 1985). The "msm" package uses Kolmogorov differential equations to calculate a transition probability matrix *P(t)* from the transition intensity matrix Q and the matrix exponential $P(t) = exp(tQ)$ (Jackson, 2011) using eigensystem decomposition (Cox, 1965). To determine the eigenvalues of an R x R matrix, such as Q, the characteristic equation at 0.3 has to be solved, where I is an $N\ x\ N$ identity matrix and λ is the eigenvalue.

$$det(Q - \lambda I) = 0 \tag{0.3}$$

If there are repeated eigenvalues the "msm" package (Jackson, 2011) uses a method based on Padé approximants with scaling and squaring, as described by (Moler and Van Loan, 2003).

The "msm" package uses Maximum Likelihood Estimation (MLE) to calculate the unknown parameters in the model (Jackson, 2011). $L(Q)$ is the full likelihood and is the product of the transition probabilities between all species and observation times. It is dependent upon Q, which was used to determine *P(t)*. The MSM model was run repeatedly with many Q matrices to ensure that the true maximum likelihood estimates (MLEs) had been found. The MLEs calculated using the range of Q matrices were all very close to that calculated for the overall model, and gave no cause for concern.

95% confidence intervals were calculated for the transition matrices, using the "msm" package which drew random samples (of size 1,000) from the assumed multivariate normal distribution of the MLEs and the covariance matrix (Jackson, 2011). Uncertainty was also estimated using non-parametric bootstrap refitting which simulates datasets by resampling transitions from the data, with replacement, and then repeatedly refitting the model (Jackson, 2011). This is a slower process as the model has to be refitted for each resampled dataset, but it is a more accurate way of calculating uncertainty; see (Cook, 2018), (Jackson, 2011) and (Efron, 1993). A dataset containing panel data from M individuals is rearranged as $\sum_{i=1}^{M}(n_i - 1)$ where there are $\sum_{i=1}^{M} n_i$ serially correlated transitions. There were 100 bootstrap replicates for each transition matrix.

The sensitivity of the model was tested by applying it to the 100 additional datasets created for this purpose. For each of these additional 100 datasets, a random sample of 25% of the species histories was taken 100 times. The MSM model was then applied to the 100 samples of 25% from each of the 100 datasets to produce ten thousand 100 year transition matrices. The dataset was also split by taxa and the MSM model applied to see if there is any homogeneity of rates between major taxanomic groups.

The majority of the computer code to analyse the data and produce the graphics in this report has been within R (R Core Team, 2017). A full list of the packages used is included in the Supplementary Information section. Python was used for project workflow and wordcounts (Rossum, 1995).

Results

Projected probabilities of extinction for the overall model based on all taxa show that at the 100 year point none of the confidence intervals overlap (Table 2). The 100 year probabilities of extinction for Animalia, Mammalia, Aves, Reptilia and Amphibia do show differences (Table 3). Aves is a noticeable outlier here with lower probabilities than the other taxa from all initial states. Animalia and Reptilia have broadly similar probabilities to each other. Mammalia and Amphibia are also broadly similar to each other. The sensitivity analysis shows that the predicted probabilities for the overall model on all taxa are robust, even when 75% of the data is discarded (Figure 6).

Current state	**100 year P(Ext)**	**Lower CI**	**Upper CI**
Least Concern	0.007323	0.005997	0.008613
Near Threatened	0.04135	0.03361	0.04714
Vulnerable	0.09353	0.07810	0.1085
Endangered	0.1563	0.1308	0.1805
Critically Endangered	0.2562	0.2124	0.2927

Table 2: Projected probabilities of extinction over the next 100 years from current Red List categories (IUCN, b) for all taxa (to 4 significant figures). Uncertainty has been calculated using non-parametric bootstrap refitting. At the 100 year point, none of the confidence intervals overlap.

	Probabilities				
Current state	**Animalia**	**Mammalia**	**Aves**	**Reptilia**	**Amphibia**
Least Concern	0.008	0.005	0.0007	0.022	0.004
Near Threatened	0.050	0.025	0.006	0.135	0.021
Vulnerable	0.119	0.045	0.018	0.176	0.042
Endangered	0.201	0.082	0.035	0.232	0.070
Critically Endangered	0.318	0.144	0.077	0.306	0.117

Table 3: Projected probabilities of extinction over the next 100 years from current Red List categories (IUCN, b) for for Animalia, Mammalia, Aves, Reptilia and Amphibia (mostly to 3 decimal places). Reptilia and Animalia are broadly similar as are Amphibia and Mammalia. Aves is a noticeable outlier with much lower probabilities in all categories.

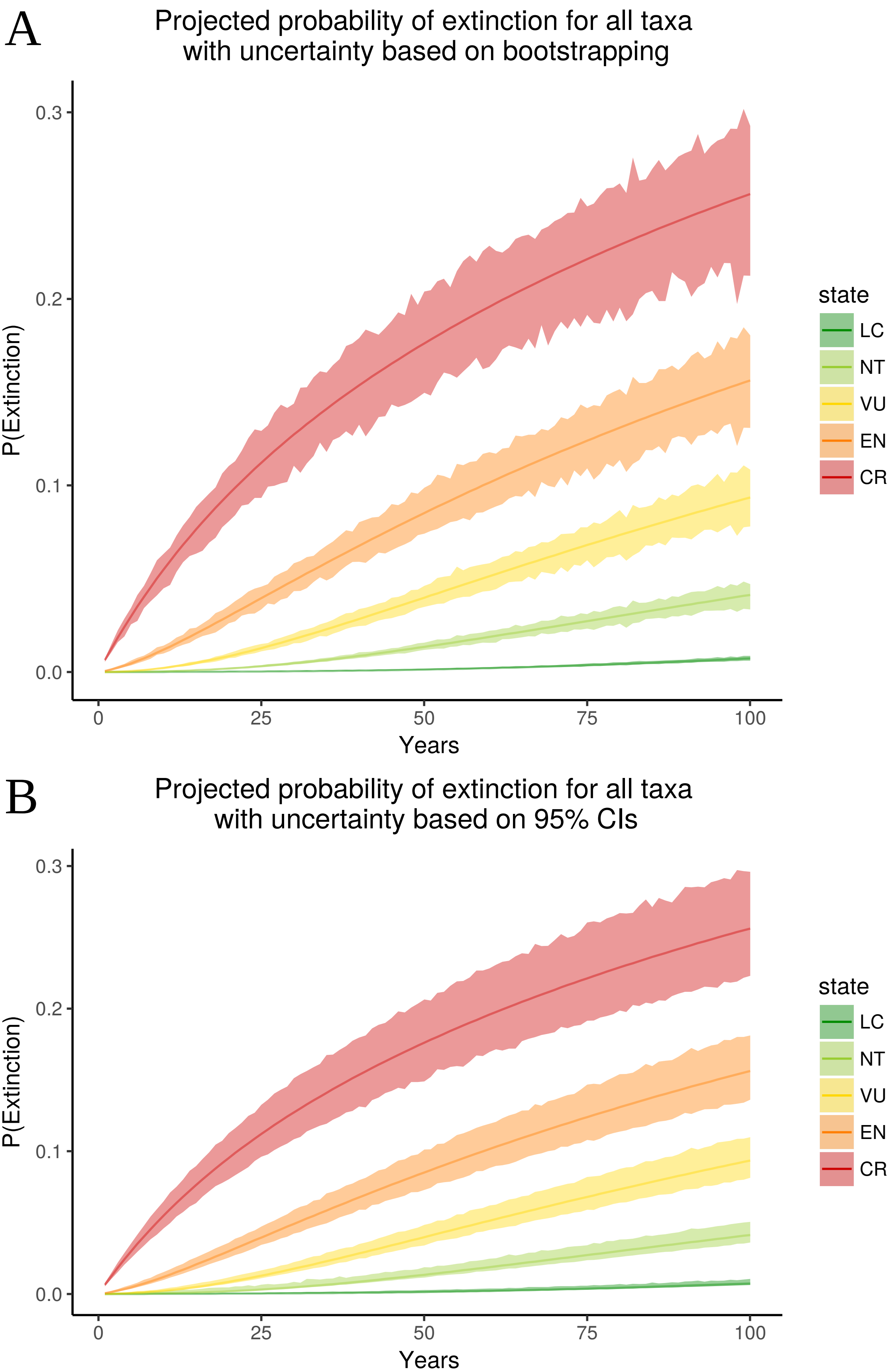


Figure 5: Projected probabilities of extinction over the next 100 years from current Red List categories (IUCN, b) with uncertainty calculated using non-parametric bootstrap refitting (A) and with 95% confidence intervals (B).

The approximate time taken until 50% extinction is reached for those animals currently shown as "Critically Endangered" is 380 years. For animals which are currently "Endangered" the estimated time is 800 years. For those which are currently "Vulnerable" the estimated time is 1175 years (Figure 7).[4]. Projections calculated by Mace have been included for comparison (Mace, 1994). Seven of the ten vertebrate taxa have projected times until 50% extinction which align closely with those for Animalia species currently listed as "Critically Endangered"; Gruidae (cranes) - 335 years, Boidae (boas) - 365 years, Canidae (canines) - 403 years, Anseriformes (waterfowl) - 404 years, Psittaciformes (parrots) - 421 years, Iguanidae (iguana)- 428 years and Marsupialia (marsupials) - 453 years (Figure 7).

Projected times until 50% of Mammalia, Aves, Reptilia and Amphibia become extinct vary widely (Figure 8). 50% of Reptiles currently listed as "Critically Endangered" are estimated to become extinct in 240 years and those which are currently only "Vulnerable" in 400 years. For Aves, these times are 7,500 years and 8,450 years respectively [4].

The 100 year survival rates of mammals, birds, reptiles and amphibians (Figure 9), project species losses over this time period of 92, 47, 282 and 155 respectively. These numbers equate to approximately 8%, 3%, 23% and 7% of those species currently included within Red List "Threatened" categories (IUCN, b)[4]. A mammal currently listed as "Vulnerable" has a probability of survival after 100 years of 0.955. From a listing of "Endangered" the survival probability after 100 years is 0.918, and from "Critically Endangered" the probability is 0.856. In the case of Aves these three probabilities are 0.982, 0.965 and 0.923 respectively. For Reptilia the three probabilities are 0.824, 0.768 and 0.694 respectively and for Amphibia they are 0.958, 0.930 and 0.883 (Figure 10).

100 year probabilities of extinction from existing states for all taxa, Mammalia, Aves, Reptilia and Amphibia also vary widely (Figure 11). A "Vulnerable" reptile has a higher probability of extinction over 100 years than a "Critically Endangered" mammal, bird or amphibian. A "Critically Endangered" bird has a lower probability of extinction over 100 years than an "Endangered" mammal. None of the "Critically Endangered" probabilities for these groups approaches the Criterion E definition of an extinction probability of $\geqslant 50\%$ in 10 years or 3 generations (up to 100 years). Only Reptilia meet the "Endangered" definition of $\geqslant 20\%$ in 20 years or 5 generations (up to 100 years).

[4]Numbers correct at 5 July 2018.

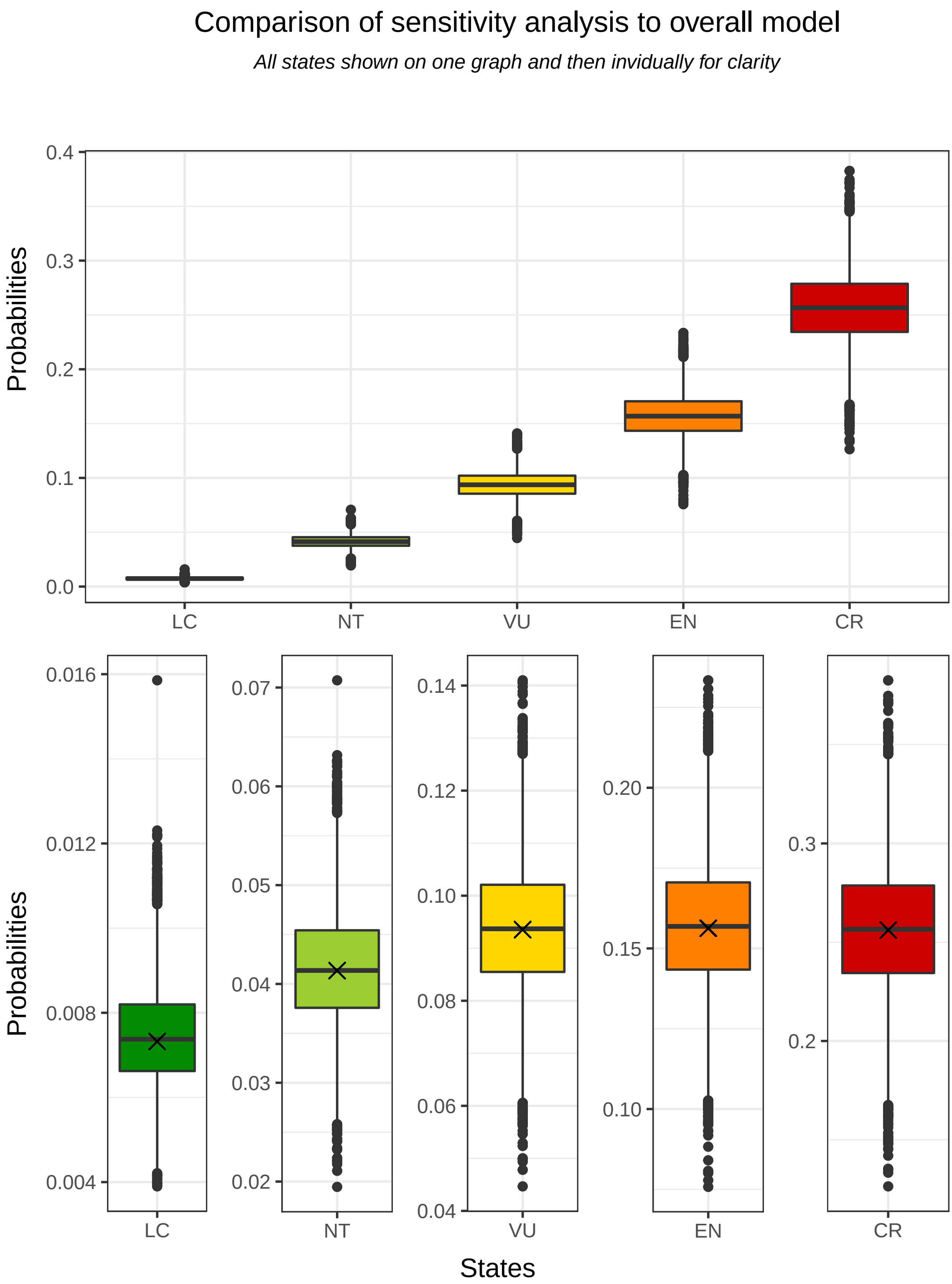


Figure 6: A comparison of the overall model to the sensitivity analysis. The sensitivity analysis resulted in ten thousand 100 year transition matrices and the extinction probabilities in these have been plotted as box and whisker plots. The data in the bottom panel is the same as in the top panel; it has been expanded for ease of reading. The black crosses represent the probabilities from the overall model 100 year transition matrix based on the Master dataset.

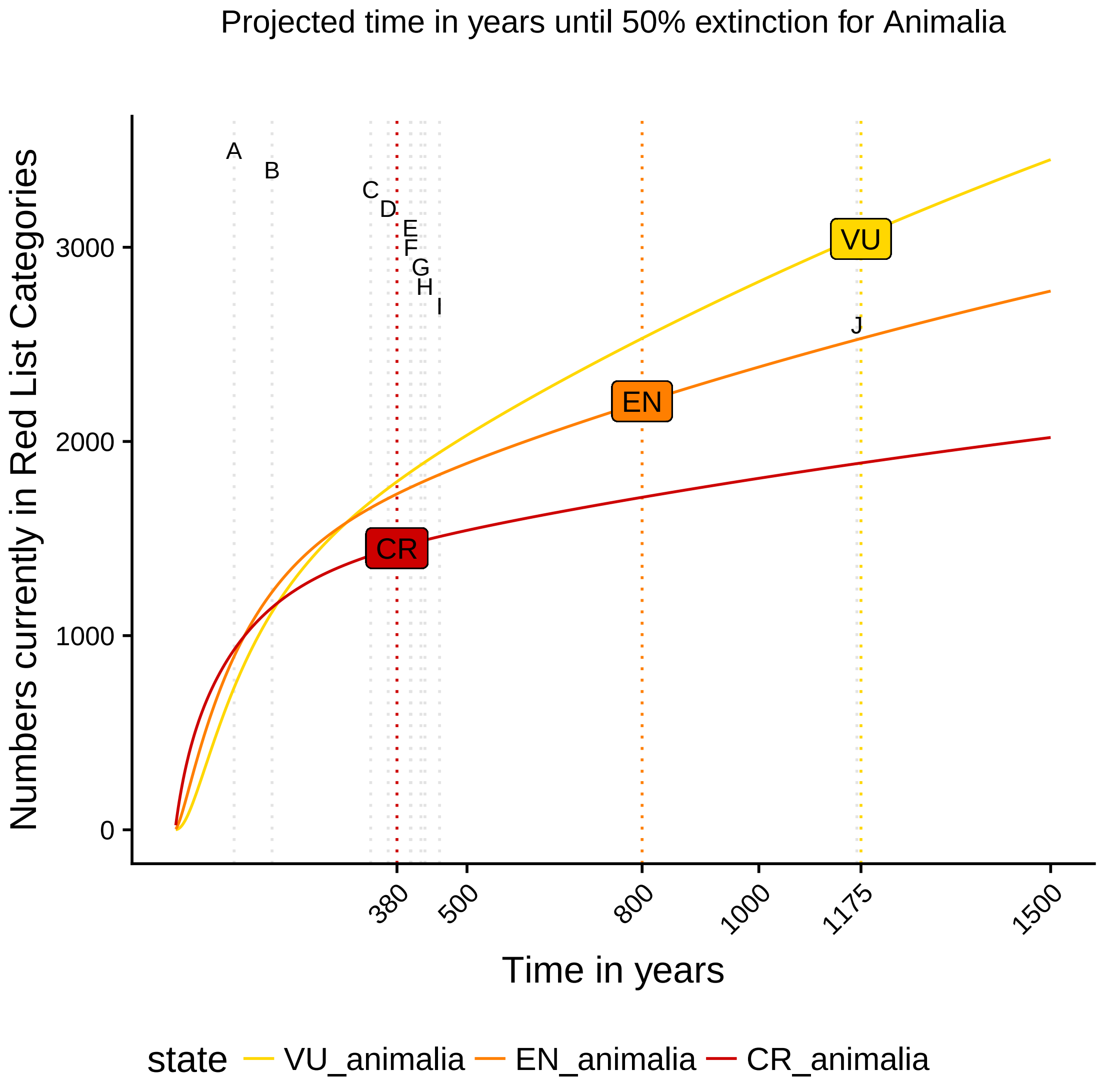


Figure 7: Projected number of years until 50% extinction is reached for Animalia. Numbers are those currently in the relevant Red List categories (correct at 5 July 2018) (IUCN, b). The letters relate to predicted times until 50% extinction calculated by Mace, for numbers in Red List "Threatened" categories at that time (Mace, 1994). Letters refer to the following taxa: A - Cervidae (deer), B - Bucerotidae (hornbills) , C - Gruidae (cranes), D - Boidae (boas), E - Canidae (canines), F - Anseriformes (waterfowl), G - Psittaciformes (parrots), H - Iguanidae (iguana), I - Marsupialia (marsupials), J - Varanidae (monitor lizards). The position of these labels in respect of the y-axis can be ignored.

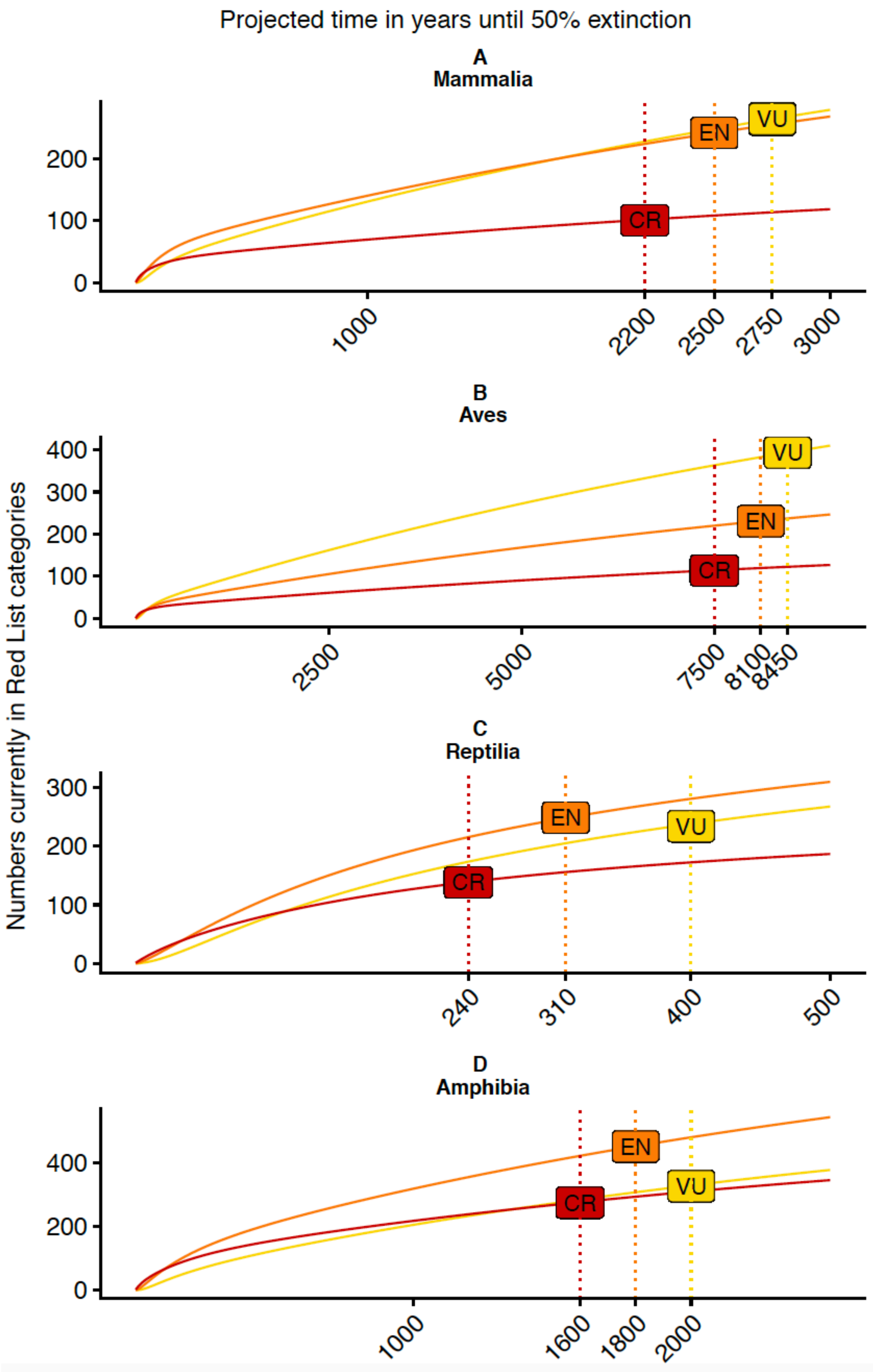


Figure 8: Projected number of years until 50% extinction is reached for (A) Mammalia, (B) Aves, (C) Reptilia and (D) Amphibia. The y-axis reflects absolute numbers of species based on the current distribution of species into the Red List categories shown (at 5 July 2018) (IUCN, b).

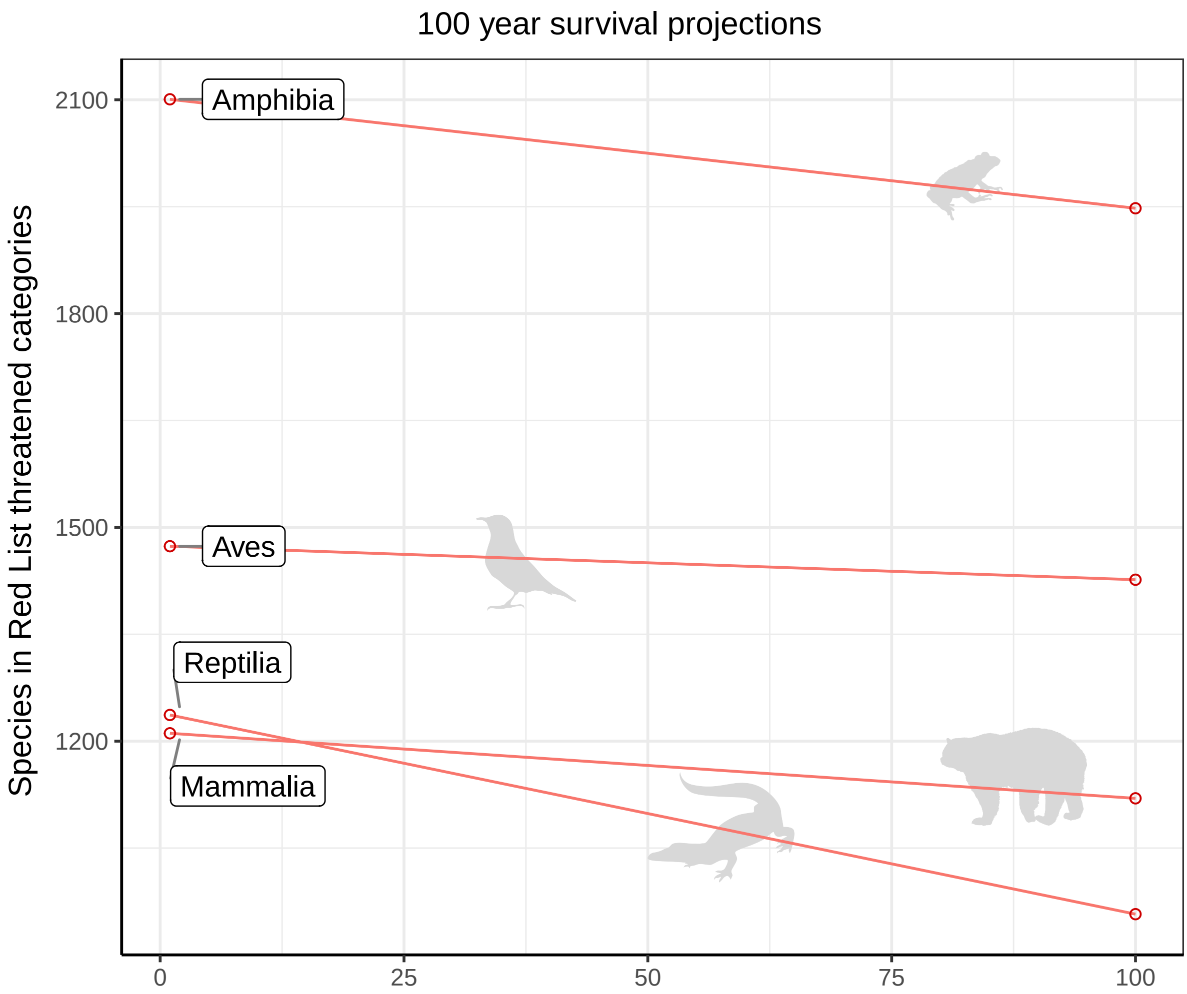


Figure 9: Numbers of mammals, birds, reptiles and amphibians currently in Red List (IUCN, b) "Threatened categories" (correct at 5 July 2018) and their projected survival over the next 100 years. This follows the same format as Figure 1 but here the y-axis shows numbers of species rather than probabilities. Projected species extinctions over this time period are 92, 47, 282 and 155 respectively.

The MSM model fits the data well although it does underestimate the number of "Least Concern" listings after about ten years (Figure 12 Supplementary Information). Prior to 2003 the majority of "Least Concern" listings were not included on the Red List, although there were some inclusions for 1996. Of the 70,577 "Least Concern" listings retained in the Master dataset, 50,217 were added from 2003 onwards. They are now included for transparency and to ensure the "Threatened" species can be considered "in context" (IUCN, b).

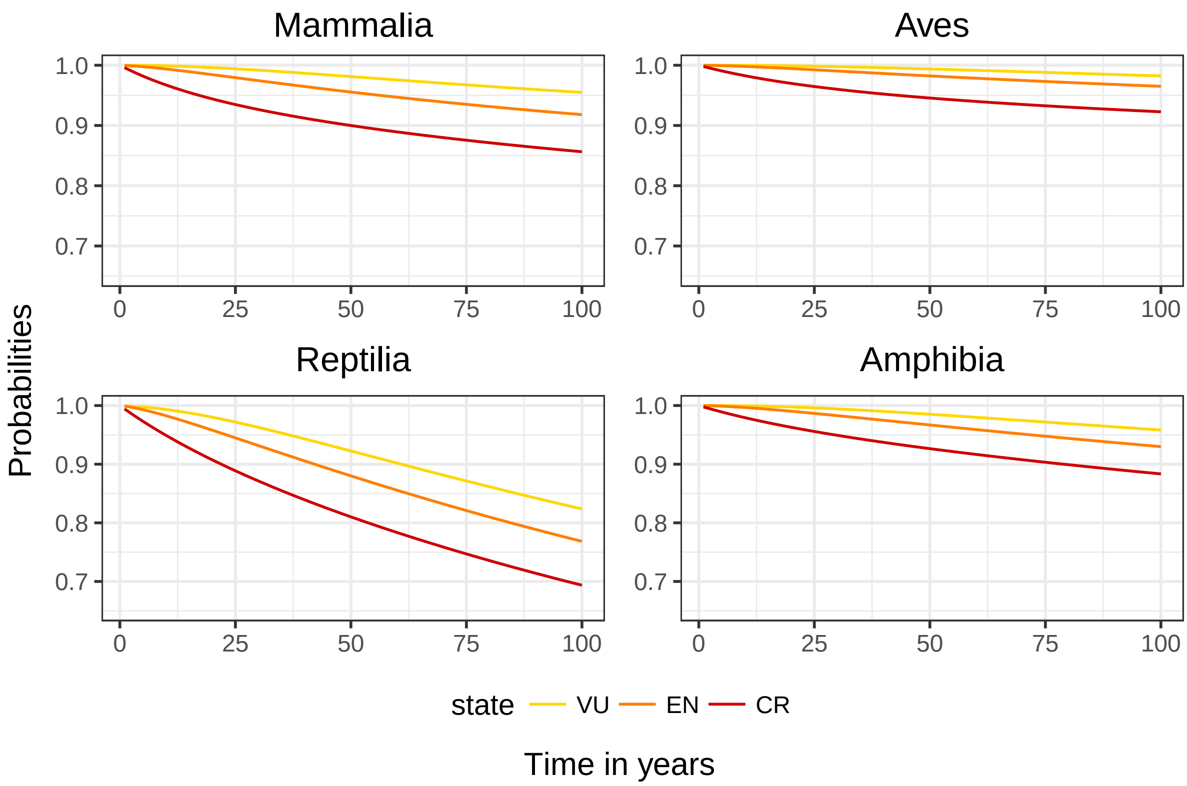


Figure 10: 100 year survival probabilities of Mammalia, Aves, Reptilia and Amphibia from current Red list category (IUCN, b).

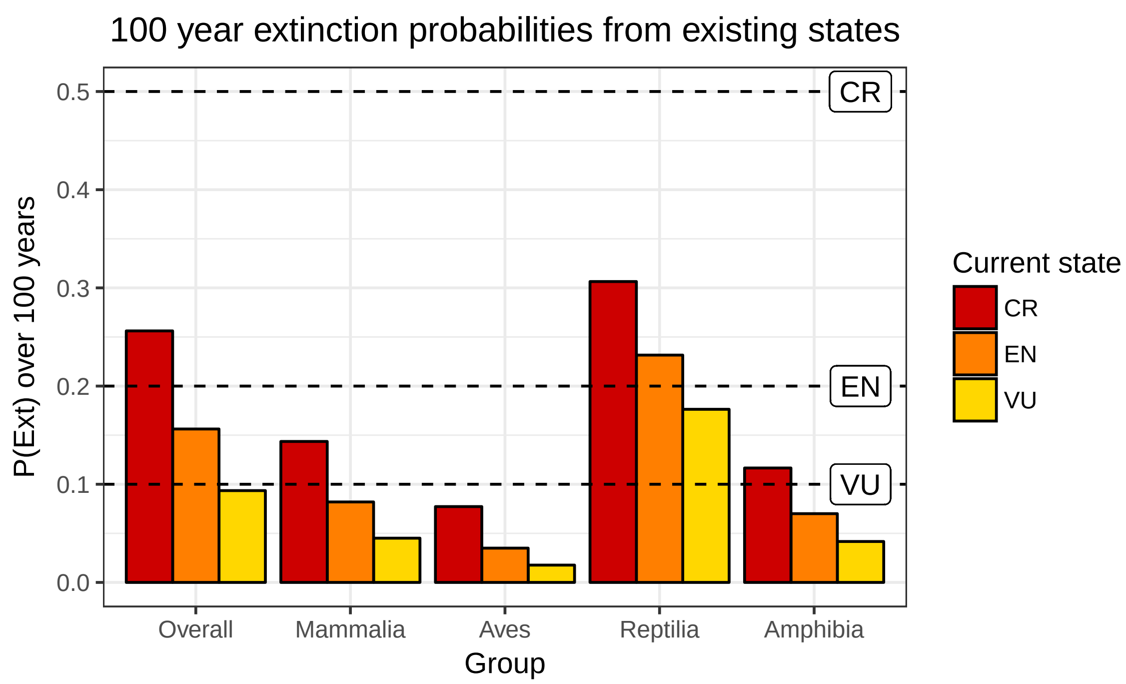


Figure 11: 100 year extinction probabilities from existing states for all taxa in the overall model, Mammalia, Aves, Reptilia and Amphibia. Dashed lines represent Criterion E definitions for allocating current states. The Criterion E definition for a "Critically Endangered" species is a probability of extinction of $\geqslant$ 50% in 10 years or 3 generations (up to 100 years). For an "Endangered" species the definition is a probability of extinction of $\geqslant$ 20% in 20 years or 5 generations (up to 100 years). For "Vulnerable" it is $\geqslant$ 10% in 100 years.

Discussion

A broad range of analyses follow IUCN mappings for probabilities of extinction (Table 1) but there has been little emphasis on checking the methodology behind these mappings. Here I have calculated probabilities of extinction risk, with an envelope of uncertainty surrounding the figures to give them context, using large amounts of historic IUCN data (Table 2). Probabilities have also been calculated for Animalia, Mammalia, Aves, Reptilia and Amphibia (Table 3).

Whilst the overall model based on all taxa has proved robust (Figure 6), the variability within the data (Figure 11) and the taxonomic bias (Table 3) is striking. Red List categories are applied across all taxa, but it is apparent the categories are not equal across taxa. For example, a "Critically Endangered" bird with a 100 year probability of extinction of 0.077 (Table 3), is not comparable with other taxa, where being categorised as "Critically Endangered" means an extinction probability of 0.306 over 100 years, as is the case for Reptilia. These results clearly demonstrate that the Red List categories (IUCN, a) are not equivalent across taxa. This has ramifications going forwards, not least in terms of the direction of conservation funding. A reptile which is only classed as "Vulnerable" may be less likely to be prioritised for conservation funding than a "Critically Endangered" mammal. Looking at the underlying extinction probabilities however shows that for the former the probability of extinction is 0.176 and for the latter it is 0.144 (Table 3).

Aves are the largest taxa in the Master dataset (Figure 3), with 10,280 species and 66,551 listings included. Over 75% of these listings (50,555 listings) are "Least Concern" and only 9 are "Extinct" listings. The bias towards "Least Concern" listings could be because Aves are routinely assessed more frequently than other taxa, even where a species is not currently "Threatened". It may mean they are less at risk but if conservation work has prevented "Threatened" Aves becoming extinct, this success will be reflected in the MSM model. If this is the case will conservation continue to prevent extinction as more species move into "Threatened" categories over time? Further work could be undertaken to review the reasons for the large number of "Least Concern" listings here and see what impact these reasons have on the probabilities of extinction.

Probabilities of extinction for Reptilia are concerning (Table 3) when compared to those for Mammalia, Amphibia and Aves. There are only 987 species of reptile in the Main dataset, however, and the confidence intervals around these probabilities are wide. This illustrates the need for much more data to be added to refine the MSM model. Taking account of area of occupation and population sizes to enable the data to be split by variables other than just by taxa would help understand some of the underlying variability. Declining populations and population losses always precede extinctions (Ceballos et al., 2017). Species-area relationships are complex and current methods for estimating extinctions can overestimate the losses (He and Hubbell, 2011) and habitat fragmentation and small population ranges increase extinction rates (Crooks et al., 2017).

Comparing projections of times to 50% extinction of species currently in "Threatened" states with earlier work, (Mace, 1994) and (Smith et al., 1993) among others, has produced interesting results (Figure 7). Mace was of the view that the estimated times to 50% extinction were too short due to the way generation times were incorporated within the calculations and so increased generation times to a median of 6 years. This increased the estimates from an average of around 430 years to 610 years (Mace, 1994). This still fits well with the projections for Animalia found here (Figure 7), and the figures for Reptilia (Figure 10C), although 430 years also fits well here. It is still a much lower estimate that those for Mammalia and Aves found here (Figures 10A and B). Direct comparisons are not possible due to the lack of data for the specific species reviewed by Mace (Table 4, Supplementary Information). In addition, generation time has not been taken into account here and is an area where future work would prove fruitful. Larger mammals,for example, often have far longer lifespans than 6 years.

Plants are under-represented in the dataset (Figure 3). Most of the plants included in the 1997 "IUCN List of Threatened Plants" (IUCN, b) have yet to be re-evaluated against Red List current guidelines (IUCN, a). As more plant data is added to the Red List, further work could also separate probilities of extinction to include plant taxa, and move away from the very strong vertebrate bias. Over three quarters of the species retained in the Master dataset are chordates which is indicative of this bias for vertebrates in the Red List, The most comprehensively assessed groups in the Red list are amphibians, birds, mammals, freshwater crabs, warm-water reef building corals, conifers and cycads (IUCN, b).

The bias in the Red list towards vertebrates is unsurprising. Colleony et al. found that in conservation terms "Animal charisma trumps endangered status" (Collony et al., 2017) and"charismatic" species (which in the main comprise large vertebrates) influence fund-raising efforts and conservation behaviours in tourists (Skibins et al., 2013). The appeal of an individual species can actually predict their conservation status (Brambilla et al., 2013) and Ceballos et al, provide the example of the Catarina popfish which became extinct in 2014. It was a lesser known vertebrate species with small range and did not elicit any real concern. (Ceballos et al., 2017).

The probabilities of extinction calculated here (Figure 2) for all taxa in the overall model broadly agree with those suggested by Isaac et al., at least in the "Near Threatened", "Vulnerable" and "Endangered" categories (Isaac et al., 2007). The "Critically Endangered" probability here is lower(Figure 2), but the transitions in my Master dataset will include those for taxa where practical conservation work is being undertaken. Further work could ascertain how those actively conserved taxa affect the probabilities of extinction. Taxa which are in a “Critically Endangered” state are far more likely to be subject to some form of conservation action, and this could well lower this extinction probability.

Probabilities of extinction do differ across taxa (Figure 3), but these figures should be treated with a degree of caution, particularly in the case of Reptilia where there are fewer than 1,000 species in the datset (Figure 3).

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I would like to thank my supervisor, Dr James Rosindell, for his continued patient support, ever-helpful discussions and sage insights/comments throughout the course of this project.

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544 # Supplementary Information

Vertebrate species	Estimated % extinct in 100 years	Estimated years to 50% extinction
Boidae	17	365
Varanidae	6	1168
Iguanidae	15	428
Anseriformes	16	404
Gruidae	19	335
Psittaciformes	15	421
Bucerotidae	34	166
Marsupialia	14	453
Canidae	16	403
Cervidae	50	101

Table 4: Estimates of extinction rates and probabilities extracted from Mace et al. (Mace, 1994)

Red List Categories	Red List Codings	Number
Least concern	LC, LR/lc, nt[5]	1
Near threatened	NT, LR/nt, LR/cd	2
Vulnerable	VU, V	3
Endangered	EN, E	4
Critically endangered	CR, Ex?, Ex/E	5
Extinct in the wild	EW	6
Extinct	EX, Ex	7
Data deficient	DD	0

Table 5: Red List statuses were mapped to numbers for algorithmic purposes. Mappings from all remaining categories are shown.

[5]Here “ nt ” is “ not threatened ”.

Current Category	Correct Category	New code	Existing code
Data deficient	Data deficient	0	0
Data deficient	Least concern	1	
Least concern	Least concern	2	1
Near threatened	Least concern	3	
Data deficient	Near threatened	4	
Least concern	Near threatened	5	
Near threatened	Near threatened	6	2
Vulnerable	Near threatened	7	
Data deficient	Vulnerable	8	
Near threatened	Vulnerable	9	
Vulnerable	Vulnerable	10	3
Endangered	Vulnerable	11	
Data deficient	Endangered	12	
Vulnerable	Endangered	13	
Endangered	Endangered	14	4
Critically endangered	Endangered	15	
Data deficient	Critically endangered	16	
Endangered	Critically endangered	17	
Critically endangered	Critically endangered	18	5
Extinct in the wild	Critically endangered	19	
Extinct	Critically endangered	20	
Data deficient	Extinct in the wild	21	
Critically endangered	Extinct in the wild	22	
Extinct in the wild	Extinct in the wild	23	6
Data deficient	Extinct	24	
Critically endangered	Extinct	25	
Extinct	Extinct	26	7

Table 6: Mapping of categories from Table 5 into 27 new categories to take account of species which have been mis-categorised. Only transfers between states which might reasonably be considered to have been mis-categorised are included in these new categories.

Within R (R Core Team, 2017), the following packages were used to download, clean and prepare, analyse and produce graphical representations of the data:

1. dplyr (Wickham et al., 2017)
2. ggplot2 (Wickham, 2009)
3. ggpubr (Kassambara, 2018)
4. ggrepel (Slowikowski, 2018)
5. gridExtra (Auguie, 2017)
6. gridGraphics (Murrell and Wen, 2018)
7. jsonlite (Ooms, 2014)
8. msm (Jackson, 2011)
9. png (Urbanek, 2013)
10. reshape2 (Wickham, 2007)
11. rredlist (Chamberlain, 2017)
12. tidyr (Wickham and Henry, 2018)

An indication of how the data fit the model has been produced by the "msm" package (Jackson, 2011) by estimating the observed numbers of species in each state and comparing these numbers with the expected number of species forecasted by the model over a 20 year period (Figure 12). Expected prevalences are calculated from the fitted transition probability matrix P. It can be seen that the model fits the data in the Master dataset reasonably well, although it does underestimate those species in the "Least Concern" state after about 10 years.

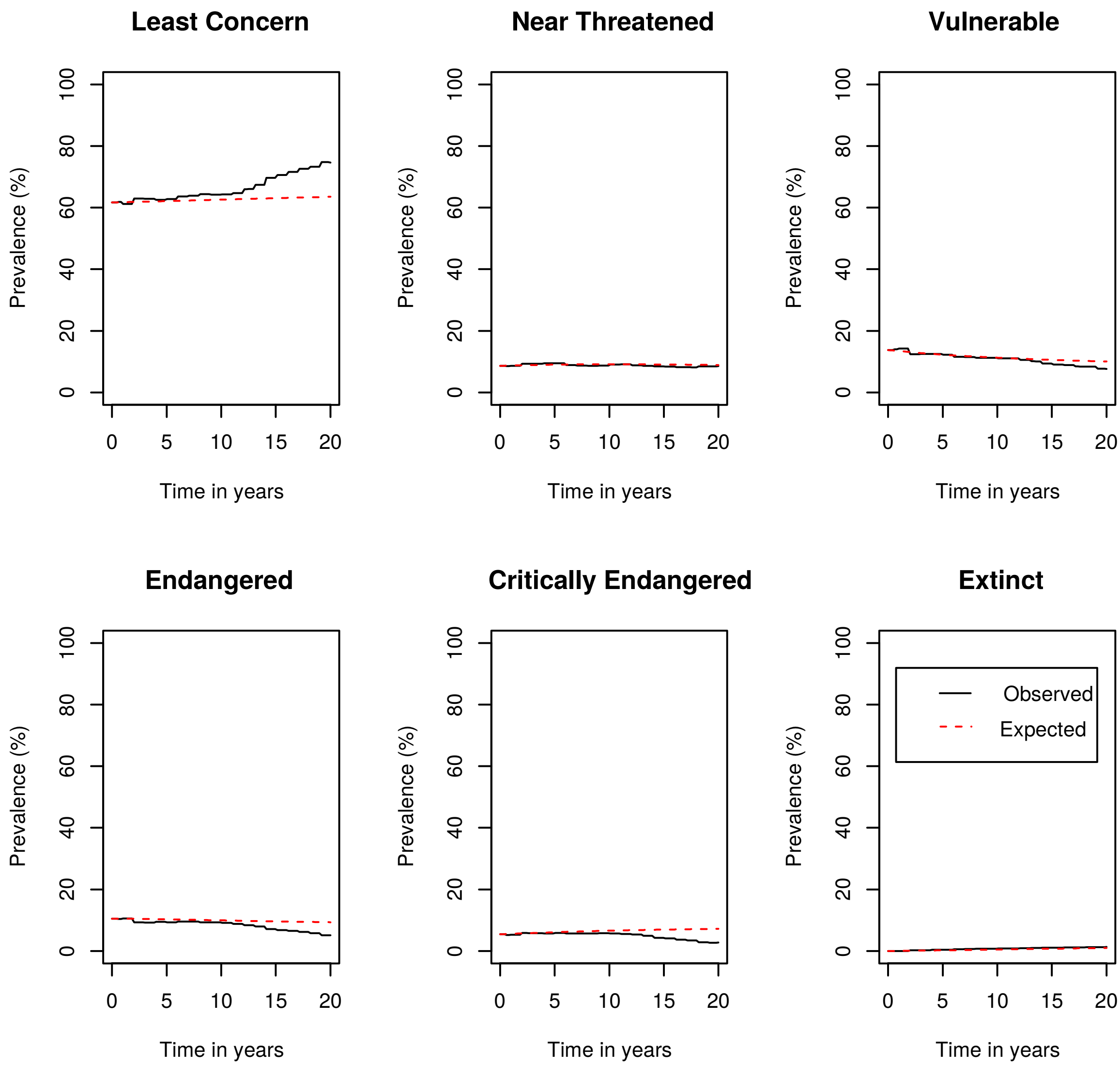

Figure 12: Observed versus expected prevalence, by state