Patterns of mammalian population decline inform conservation action

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Patterns of mammalian population decline inform conservation action

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SUMMARY

1. Evaluations of wildlife population dynamics have the potential to convey valuable information on the type of pressure affecting a population and could help predict future changes in the population's trajectory. Greater understanding of different patterns of population declines could provide a useful mechanism for assessing decline severity in the wild and identifying those populations that are more likely to exhibit severe declines.
2. We identified 93 incidences of decline within 75 populations of mammalian species using a time-series analysis method. These included: linear, quadratic convex (accelerating) declines, exponential concave (decelerating) declines, and quadratic concave declines (representing recovering populations). Excluding linear declines left a dataset of 85 declines to model the relationship between each decline-curve type and a range of biological, anthropogenic, and time-series descriptor explanatory variables.
3. None of the decline-curve types were spatially or phylogenetically clustered. The only characteristic that could be consistently associated with any curve-type was the time at which they were more likely to occur within a time-series. Quadratic convex declines were more likely to occur at the start of the time-series, while recovering curve shapes (quadratic concave declines) were more likely at the end of the time-series.
4. **Synthesis and applications:** The ability to link certain factors with specific decline dynamics across a number of mammalian populations is useful for management purposes as it provides decision-makers with potential triggers upon which to base their conservation actions. We propose that the identification of quadratic convex declines could be used as an early-warning signal of potentially severe decline dynamics. For such populations, increased population monitoring effort should be deployed to diagnose the cause of its decline and avert possible extinctions. Conversely, the presence of a quadratic concave decline suggests that the population has already undergone a period of serious decline but is now in the process of recovery. Such populations will require different types of conservation actions, focussed on enhancing their chances of recovery.

Key words: Extinction risk; indicators; monitoring; mammals, population decline; time-series analysis, management

INTRODUCTION

Wildlife monitoring programmes play a key role in understanding ecological systems, and constitute the basis for management decisions and actions (Yoccoz, Nichols & Boulinier 2001). As well as tracking a species' status in the wild, long-term population studies provide an insight into a population's usual abundance and variability prior to anthropogenic activity, and can be used to determine whether a decline is part of a natural cycle or the result of external pressure (Willis *et al.* 2007). Monitoring population declines is an especially important step in tackling biodiversity loss, as severe population reductions act as a prelude to species extinction (Ceballos & Ehrlich 2002; Collen *et al.* 2009). Yet, a recent study has raised concern over the number of monitoring programmes that have "monitored populations to extinction", with no clear guidelines on how to act when declines are first diagnosed (Lindenmayer, Pigott & Wintle 2013). Here we explore how differences in decline shape could represent useful "triggers points" within monitoring programmes, highlighting when and where rapid management intervention is called.

Recent analyses across a set of a long-term mammalian population time-series have revealed several key distinctions in wildlife population declines (Di Fonzo, Collen & Mace 2013), which provide a more nuanced understanding of extinction risk compared with simple measures of average population change or cumulative percentage loss (i.e. Criterion A of the Red List; IUCN 2001). Di Fonzo *et al.* (2013) identified three principal decline-curve types of increasing severity: quadratic concave (i.e. recovering), exponential concave (i.e. decelerating) and quadratic convex (i.e. accelerating) decline-curves (Fig. 1 a-b.; Table S1), that carry information regarding the potential urgency of conservation interventions. Moreover, there is some evidence that dominant threats can be diagnosed from distinctions in long-term abundance trend data using flexible Bayesian frameworks (Shoemaker & Akçakaya 2015).

In order to evaluate whether these decline-types represent useful triggers for conservation action, we must first determine whether their presence is associated with any particular biological, environmental or anthropogenic conditions. While it is well known that certain biological and ecological attributes predispose species to higher extinction risk (e.g. large body size, low population density, small geographic range, specific dietary requirements; Purvis *et al.* 2000), recent studies have revealed limited associations between intrinsic traits and population level trends (Cowlishaw, Pettifor & Issac 2009; Mace *et al.* 2010; Collen *et al.* 2011). Instead, they find site-specific characteristics (such as anthropogenic pressure intensity or certain environmental conditions) to be better determinants of population decline. Although these studies do not identify any link between negative population trends and species with an intrinsically higher risk of extinction, this does not preclude associations with specific decline-types. For instance, species at a greater risk of extinction could exhibit a higher frequency of severe quadratic convex declines, which might have been missed in previous population trend analyses (i.e. based on simple linear regression). A higher frequency of switching between accelerating quadratic convex declines and recovering concave trajectories (i.e. exhibited during the process of "critical slowing down" prior to catastrophic declines; Scheffer *et al.* 2009; Drake & Griffen 2010) is a further potential indicator of proximate extinction, which could be built within monitoring programmes to rapidly tackle at-risk populations before it is too late.

In this study we investigate the association between the decline-curve dynamics of a sample of mammalian population data from a database of vertebrate abundance time-series and a range of characteristics (defined in Table 1). Specifically, we use generalised linear mixed modelling to investigate whether the presence of different decline-curve types is dependent on particular species-specific traits, levels of local, anthropogenic pressure, or based on particular attributes of the time-series itself. Through this study, we hope to provide insight into the conditions contributing to different decline-curves, which could be used to pre-empt the application of particular conservation management strategies. We chose to focus our study on mammals as they are a very well-monitored and extensively studied vertebrate group, with a quarter of species recorded to be threatened with extinction (Schipper *et al.* 2008).

MATERIALS AND METHODS

Data manipulation

We first selected 75 high quality mammalian population time-series for our analysis, representing 33 species, spanning 6 orders, which we drew from a vertebrate population abundance database (Living Planet Database (LPD); Collen *et al.* 2009) based on criteria from Di Fonzo *et al.* (2013). The minimum requirement was that time-series had population counts which spanned more than 5 years, had less than 8 year gap between data points, were collected from 1900 onwards, exhibited stable or declining abundance trends (using linear regression), exhibited low environmental stochasticity (based on whether the total reduction in population abundance was less than the difference between the upper and lower 95% confidence interval around the linear model fit), and were reported as being affected by one or more threats in the original source. All the data manipulation and analyses here after were carried out using the statistical programming software, R 3.1.0 (R Development Core Team 2015).

We then applied the Kalman filter (as used by Knape & de Valpine 2012) to the time-series data to account for potential sources of uncertainty arising from count errors using the ‘dlmMLE’ function ('dlm’ package; Petris 2015) Next, we identified the different decline-curves using the following steps, described in Di Fonzo *et al.* (2013), and summarised as follows : 1) we smoothed the Kalman-filtered time-series using a generalised additive modelling framework (Wood 2006); 2) detected statistically significant switches in dynamics (which we term ‘switch points’) based on changes in the trend’s second derivative sign (fully described in Di Fonzo *et al.* 2013); and 3) fit a range of algebraic functions between switch points to determine the different curve-types based on lowest Akaike Information Criterion corrected for small sample size (AICc; Sugiura 1978), based on a threshold of 4 AICc (Burnham & Anderson 2004). We excluded 8 linear declines from the dataset as these decline types could not be robustly associated with a specific pressure-type (Di Fonzo, Collen & Mace 2013). This left us with 85 decline-curve types (35 quadratic convex, 29 quadratic concave and 21 exponential concave) from 60 high quality mammalian population time-series, distributed around the globe (Fig.2; Table S2 in Supporting Information). The above analyses were carried out using the following R packages: 'AICcmodavg,' (Mazerolle 2015),'mgcv' (Wood 2006), 'timeSeries' (Rmetrics Core Team 2015), and 'msm' (Jackson 2015) . The decline-curve datasets and R scripts for this study are uploaded in Appendix S1 and S2.

We subsequently retrieved information for each population on several anthropogenic pressures, species-specific and time-series related characteristics (see Table 1 for description and sources), which we hypothesised might influence decline-curve dynamics and removed all decline-curves with incomplete information. Home range data and population density were retrieved from the PanTHERIA database of mammalian life-history traits (Jones *et al.* 2009). Generation length was retrieved from Pacifici et al. (2013). We obtained information on the number of distinct threats affecting each population from the Living Planet Index database (Collen *et al.* 2009). Maximum finite rate of population growth (r_{max}) was calculated based on Equation 1 from Slade *et al.* (1998), using data on litter size, maximum longevity and age at sexual maturity from Jones *et al.* (2009). We solved this equation using the 'uniroot.all' function in the 'rootSolve' package (Keith *et al.* 2015), and selected the highest r_{max} value in cases where there was more than one solution. To obtain values for the two spatial variables ('Human Appropriation of Net Primary Productivity as a percentage of Net Primary Productivity' and the 'Human Influence Index') we created buffer polygons with a radius of 1, 10 and 60 km around each population's point location using the 'Analysis Tool' available in ArcMap v. 9.3 (ESRI 2008) and calculated the mean value across the buffers using the 'Zonal Statistics' tool. We chose this particular range of buffer sizes as they correspond to the 25th, 50th and 75th percentile (rounded-up to the nearest tenth) of home range sizes in km^2 across the species with available home range data in the filtered dataset (n=21).

A Kruskall Wallis test (Kruskal & Wallis 1952) confirmed there were no statistically significant differences between the mean values at different buffer sizes, therefore we continued the analysis at the 10 km level (see Table S3 in Supplementary Information). Spearman-rank tests (Spearman 1904) were carried out to test for co-linearity between continuous explanatory variables (Table S4 in Supporting Information), and those with a correlation coefficient of greater than 0.7 were removed from the analysis, based on the most commonly used threshold (Dormann *et al.* 2013).

Statistical analysis

We first investigated the presence of spatial autocorrelation across each decline-curve by creating a distance-based neighbours list using the 'dnearneigh' function in the package 'spdep' (Bivand 2009). We tested several cut-off distances, from 10 to 100 km, and selected the minimum distance for which all points were connected to at least another one. We then used the 'nb2listw' function from 'spdep' to supplement the neighbours list with two different spatial weights (row-standardised and binary weightings) to characterise the relationships between neighbouring points. Both spatially-weighted neighbour lists were then used in Moran's I and Geary's C tests on the response variable of interests, through the functions 'moran.test' and 'geary.test' from 'spdep'. We ran both Moran's and Geary's tests as the former is more sensitive to extreme values, and the latter is more sensitive to differences in small neighbourhoods.

Given that evolutionarily related species and populations are not statistically independent (Felsenstein 1985), we tested whether the distribution of each decline-curve type was phylogenetically correlated using the D statistic (through the 'phylo.d' function in the 'caper' package; Orme *et al.* 2014) based on Fritz *et al.* (2009)’s updated mammalian phylogenetic supertree (Appendix S1). If D was less than 0, this would indicate that species that were more closely related were more likely to decline in the same way, thus necessitating to account for phylogenetic pattern in subsequent statistical analyses.

We then modelled the presence/absence of each decline-curve type in relation to the variables listed in Table 1 using generalised linear mixed models with binomial error structures (using the ‘lme4’ package in R; Bates, Maechler & Bolker 2011). We also investigated the impact of misdiagnosing exponential concave declines as quadratic declines by re-running the analysis for all concave declines combined. We did this based on Di Fonzo *et al.* (2013)’s result that exponential concaves declines had a higher chance of misdiagnosis under simulated census error compared to other decline-types. We selected a mixed modelling framework (with “species” and “biogeographic realm” as random effects) to take into account the non-independent, nested structure of the decline-curve data, with multiple populations of the same species from the same region. To address model convergence problems, some of the explanatory variables were scaled where required. We used a multi-model inference approach (Burnham & Anderson 2004) to compare models with all combinations of explanatory variables using the ‘dredge’ function in the ‘MuMIn’ R package (Bartón 2014), and calculated model-average coefficients for the parameters included in the top models, i.e. those with a difference of less than 2 AICc . Since the binomial decline-curve type data were not expected to occur under any specific statistical distribution we did not need to test for overdispersion. We identified the variables which had a consistent effect on the presence of each decline-curve type based on whether the 95% confidence interval around their model-averaged coefficients crossed 0 (i.e. we assessed those that did not cross zero as having a consistent effect).

RESULTS

Although quadratic convex and combined concave decline-curves exhibited a higher degree of phylogenetic non-randomness compared to the other decline-curve types (Table S5; their D statistics were approximately 0), we did not account for phylogenetic structure in subsequent analyses as this was neither a strong phylogenetic signal, nor supported by a large sample size (n=35 and 58). Spatial autocorrelation was also absent across decline-curves (based on Moran's I and Geary's C tests; all p-values > 0.1; Fig. 2.). We identified 20 plausible models which described quadratic convex decline-curves with less than 2 AICc difference, containing a total of nine parameters in a variety of additive interactions (Tables 2 and S6). We found that only one time-series characteristic consistently explained the presence of quadratic convex decline-curves, with the remaining time-series descriptors, biological traits and anthropogenic measures being less important. Specifically, we found that quadratic convex declines were associated with a change in trajectory towards the start of the time-series (inferred from the negative ‘proximity to end’ estimate; Table 2). The presence of quadratic concave declines was best explained by 23 models containing additive interactions between a total of nine parameters (Tables 3 and S7). “Proximity to end” was the only parameter that was consistently associated with the presence of quadratic concave declines (with a positive model-averaged estimate), suggesting that this cure-type is more likely to occur towards the end of a population time-series. We found that the presence of exponential concave declines was best explained by 58 models, with a combination of 12 variables in additive interactions (Tables 4 and S8). None of these demonstrated a consistent effect on the presence of exponential concave declines. When we combined concave declines together in one category, their presence was best explained by 11 models, with a combination of 7 variables in additive interactions, in addition to the null model (Table S9). None of these had a consistent effect on the presence of this particular decline category.

DISCUSSION

Our broad scale study of the distribution of different wildlife population decline-curves in relation to species-specific biological, anthropogenic, and time-series descriptor characteristic predictors demonstrates a novel association with useful management implications. We identify a key time-series characteristic associated with the presence of quadratic convex and quadratic concave declines, which can be explained in the context of different threatening processes. Quadratic convex declines were more likely to occur towards the start of the time-series: a phenomenon that could coincide with the appearance of a novel threat (Mace *et al.* 2010). Quadratic concave declines, instead, were more likely at the end of the analysed time-series. When a new pressure appears, there are four possible responses of a population: it may a) decline and then recover, b) decline to extinction, c) decline and stabilise, or d) be unaffected. Early in this process, quadratic convex declines will be more likely, especially under severe or increasing pressures (e.g. an accelerating rate of habitat conversion). Over the course of time, as the pressure stabilises or reduces, a population that has not declined to extinction must either recover or stabilise, resulting in a concave (or decelerating) curve. The quadratic convex decline-curve type is also the least prevalent across our time-series dataset (compared to concave declines), which may be a result of a 'filter effect' (Balmford 1996) causing an inherent bias against the identification of quadratic convex declines. Populations that declined in a quadratic convex manner in the past may have done so too quickly for monitoring to take place (exemplified in the Indian Gyps vultures decline; Prakash *et al.* 2012), or population monitoring may have only started following a severe decline, thereby missing earlier quadratic convex sections.

The tendency for quadratic convex declines to occur in the beginning of population time-series means that its identification could act as a signal for a novel threat, following which increased monitoring in combination with rapid conservation effort focussing on threat abatement should be put in place. The fact that quadratic convex declines have been diagnosed with high levels of accuracy under simulated deteriorations in data quality (Di Fonzo, Collen & Mace 2013) is a further reason to support its efficacy as a trigger for interventions. Instead, if concave declines were detected, it could be inferred that the population has already undergone a period of severe decline, from which its rate of decline is slowing or even recovering. The presence of this decline type suggests a different type of management strategy might be required, focussed on supporting recovery (e.g. through improving the species' habitat). The identification of different decline-curves therefore represents a novel trigger for adaptive management practices (*sensu* Walters 1986), which should be considered in addition to recently proposed measures of "percentage decline in population size, duration of population decline, loss of numbers of subpopulations, or reduction in the distribution of a species" (Lindenmayer, Pigott & Wintle 2013).

Our analyses do not pick up any relationship between body mass and severe quadratic convex declines, which we had hypothesised as more likely in larger species with an intrinsically higher risk of extinction. Similarly, we found no relation between species with lower r_{max} (i.e. of slower life-history speed, with greater risk of extinction) and a higher likelihood of quadratic populations declines. Such lack of associations may be due to the low number of quadratic convex declines in this dataset and warrants further investigation. A further characteristic of this dataset which may preclude these associations is that the species included are generally on the slower scale of the mammalian life-history speed continuum, thus reducing the statistical power of our analyses. It would be valuable to follow-up these findings by collecting information on the intraspecific variation in life-history characteristics across the various populations (as identified in Gonzláez-Suárez & Revilla 2013) in order to obtain more precise estimates for such decline-curve associations.

Statistical analysis of the distribution of decline-curve types across IUCN Red List extinction-risk categories did not reveal any clear patterns. Contrary to expectation, more severe, quadratic convex declines were no more likely to occur in populations of more threatened species than species with lower extinction risk, despite IUCN Criteria A being based on 'high population decline rate'. The inconsistency between decline-curve severity and species extinction risk may be explained by the fact that percentage loss in population size and population decline-curve type measure two different processes. The first metric considers the species' risk of extinction based on the total reduction in population abundance, whereas the latter provides information on how the rate of population decline changes over time. This result highlights how determining populations' decline-curve type could be a valuable refinement to IUCN Criterion A, indicating a higher risk of extinction for species with population(s) declining at an accelerating rate (Di Fonzo, Collen & Mace 2013).

Some potential limitations of the information used here may have affected our findings. Firstly, there was a temporal mismatch between individual population time-series and the predictors of anthropogenic pressure (i.e. HII and HANNP) that will have reduced their explanatory power. The population time-series used in this analysis were recorded between 1950 and 2010, ranging across all decades, whereas the human pressure datasets provided single "snapshots" of the populations' local conditions that may not represent the pressures affecting the population during the time it was monitored. Secondly, population abundance estimates were compiled from numerous sources, using a variety of monitoring methods and sampling effort, including potential observation errors that may have obscured our ability to correctly categorise decline-curves (as described in Solow 1998; Knape & de Valpine 2012). Our analyses were also limited to the time-frame over which the data were collected, preventing us from assessing the declines with respect to a historical population baseline (recommended by Porszt *et al.* 2012; d'Eon-Eggertson, Dulvy & Peterman 2014) or over a period of three generation lengths (recommended by the IUCN Standards and Petitions Subcommittee 2010). This may have reduced our ability to diagnose declining populations to begin with, however would not have subsequently affected the analysis. Additionally, our study did not take into account the effect of possible conservation actions on population dynamics, which could have potentially biased our decline-curve results. The paucity of information on the presence and timing of conservation actions across the dataset prevented us from using it within a comparative analysis; however its possible influence on population dynamics merits future investigation through more detailed case-studies. Finally, we included a high number of explanatory variables in our models (with respect to sample size), which may have resulted in potential model overfitting. To reduce the chances of this occurring, we recommend augmenting the dataset through an updated search for suitable population time-series, expanding the study to include data from more animal taxa. A larger dataset would enable division of the time-series into training and testing sets, maximising performance on the training set and testing its efficacy on the unseen portion of data.

In addition to acting as a novel type of conservation trigger, dividing observed mammal population decline-curve types into categories of increasing decline severity has the potential to provide important insights for wildlife management. Although not a prioritisation mechanism on its own, differences in decline-type could be incorporated within Criterion A of the IUCN Red List as a more continuous indicator of the urgency with which species' population declines need addressing (while also considering the potential costs and probability of success associated with their recovery). For example, species with a greater number of severe declines could be allocated a higher risk of extinction within the same Red List category, despite not having met the criteria for moving up a category at the species-level. Assessing differences in population decline-curve dynamics could also be useful for prioritising Red List (re)assessments, where an elevated presence of quadratic convex population declines could instigate a closer evaluation of a species' extinction risk. We acknowledge that such changes in the IUCN extinction risk assessment protocol might be difficult to implement unanimously due to differences in the availability of population time-series data for highly threatened species and budget limitations to monitoring additional populations. Extinction-risk categorisations which include information on population decline-curve type may therefore be of greater use to local/regional assessments, where the data is generally of higher resolution.

Our study illustrates how the identification of different decline-curve types can provide a signal for a change in management action: quadratic convex declines could be used to trigger rapid conservation action to prevent potential extinctions, while the identification of quadratic concave dynamics could promote increased conservation effort towards the recovery of dwindling populations. In order to confirm the efficacy of these decline-curve types as signals for management change, we recommend performing this analysis over a much wider sample of population time-series, both already collected and in the process of being monitored. Further testing on the power to detect differences in decline dynamics in wild populations will also be required (sensu Nichols & Williams 2006).

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DATA ACCESSIBILITY

- The mammalian supertree will be available in Appendix S1; originating from Fritz et al. (2009). DOI: 10.1111/j.1461 0248.2009.01307.x
- Raw decline-curve datasets will be uploaded in Appendix S1
- R scripts for the comparative analyses are uploaded as Appendix S2

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TABLES

Table 1. Hypothesised predictors of decline-curve type. Bolded variables were included in statistical modelling following correlation testing.

Variable category	Predictor variable	Description of index (where applicable)	Data source (where applicable)	Hypothesis
Anthropogenic	**Human appropriation of Net Primary Productivity (NPP) as a percentage of NPP (HAPNPP; %)**	Composite index based on a per capita consumption rate of food and fibre products calculated at country-level (using information from the Food and Agricultural Organisation of the United Nations from 1995). Grid layer at¼ degree resolution.	Imhoff *et al.* (2004)	There will be a higher likelihood of severe quadratic convex declines in locations with higher HAPNPP.
	Human Influence Index (HII)	Human pressure metric incorporating indices for population density, land transformation, access and electrical power infrastructure. Full details in Sanderson et al. (2002). Grid layer, at 30 arc second resolution.	Last of the Wild Data Version 2 (Wildlife Conservation Society & Center for International Earth Science Information Network 2005)	There will be a higher likelihood of severe quadratic convex declines in locations with higher HII.

	Threat number	Number of reported threats associated with the time-series (ranged from 1 to 3).		There will be a higher likelihood of severe quadratic convex declines in locations with more threats.
Species-specific biological	**IUCN Red List Category**	Category indicating species extinction risk: Extinct, Critically Endangered, Endangered, Vulnerable, Near Threatened, or Least Concern.	IUCN (2001)	There will be a higher likelihood of severe quadratic convex declines in populations with higher extinction risk.
	Log adult body mass	Grams	panTHERIA database (Jones *et al.* 2009).	Heavier species represent longer lived species (Stearns 1983), which have been found at greater risk from extinction compared to faster lived animals (Purvis *et al.* 2000). Based on this association we would expect a relatively higher frequency of quadratic convex declines within their population time-series.
	Animal population density	Individuals/km^2	panTHERIA database (Jones *et al.* 2009).	We expect a higher likelihood of severe quadratic convex declines in populations that live at higher density, as these will be more prone to rapid collapse under an Allee effect (Allee 1931).
	Generation length	The weighted mean age of mothers within a population (IUCN Standards and Petitions	Pacifici et al. (2013)	We expect longer-lived species to exhibit a higher frequency of convex declines due to being intrinsically at higher risk of extinction.

		Subcommittee 2010), measured in days.	
	Maximum finite rate of population growth (r_{max})	Calculated using Eq. 1 in Slade *et al.* (1998), with data on maximum longevity, number of offspring per year, and age at sexual maturity from Jones *et al.* (2009). We assumed a 50% female: male ratio in our calculations.	As above, we expect longer-lived species with lower r_{max} values to exhibit a higher frequency of convex declines due to being intrinsically at higher risk of extinction.
Time-series descriptor	**Series fullness**	Ratio of number of raw data points with respect to the overall time-series length.	Exponential concave declines require relatively more data for accurate diagnosis (Di Fonzo, Collen & Mace 2013) therefore these may be more likely to be detected in fuller time-series.
	Time-series length	Number of years monitoring took place (calculated from the first to final year of the monitoring period).	Based on the above information, exponential concave declines may also be more likely in longer time-series.
	Slope	Based on a linear regression over each switch-point delimited sections with respect to time.	Quadratic convex declines may be more likely within time-series with more negative slopes, where the external pressures are higher.
	Switch point number	Number of significant switches in dynamics	Quadratic convex and concave declines may be more likely in highly

	over the entire time-series. Switch points were diagnosed following Di Fonzo et al. 2013.	fluctuating time-series than exponential concave declines (are characterised by a longer “tail”).
Mean lambda	Mean change in population abundance over the entire time-series.	Quadratic convex declines may exhibit the most negative change in population abidance over time.
Cumulative lambda	Cumulative change in population abundance over the time-series (calculated by adding up the individual, yearly lambdas).	Quadratic convex declines may exhibit the most negative cumulative change in population abidance over time.
Proximity to end	The final year of the declining section divided by the total length of the time-series (e.g. if the decline occurred from year 8 to year 17 and the entire time-series was 20 years long, “proximity to end” would be 17/20).	Quadratic convex and quadratic concave declines may be more likely to occur towards the start of a time-series (representing increased fluctuations in response to a novel threat) whereas exponential concave declines may be more likely towards the end of a time-series on account of its longer “tail”.

Table 2. Results from generalized linear mixed models fitted to quadratic convex declines (n=35). The table presents the model-average coefficients of the parameters from the most plausible models (<2 ΔAICc). Bolded parameters indicate those with a statistically significant effect. Parameter numbers correspond to parameters listed in Table S6.

Number	**Parameter**	**Model averaged estimate**	**Model averaged lower 95% CI**	**Model averaged upper 95% CI**
	Intercept	-3.806	-10.797	3.186
1	Mean lambda	6.541	-0.423	13.505
2	**Proximity to end**	**-2.856**	**-5.096**	**-0.615**
3	r_{max}	-0.509	-1.236	0.219
4	Animal population density	0.464	-0.245	1.173
5	Series fullness	1.233	-0.693	3.158
6	Human Influence Index	-0.393	-1.104	0.318
7	Slope	0.268	-0.383	0.919
8	Threat number	-0.385	-1.119	0.348
9	Human Appropriation of NPP	-0.295	-1.396	0.806

Table 3. Results from generalized linear mixed models fitted to quadratic concave declines (n=29). The table presents the model-average coefficients of the parameters from the most plausible models (<2 ΔAICc). Bolded parameters indicate those with a statistically significant effect. Parameter numbers correspond to parameters listed in Table S7.

Number	Parameter	Model averaged estimate	Model averaged lower 95% CI	Model averaged upper 95% CI
	Intercept	-2.473	-5.147	0.201
1	**Proximity to end**	**2.601**	**0.067**	**5.135**
2	r_{max}	0.414	-0.133	0.961
3	Series fullness	-1.764	-3.855	0.327
4	Threat number	0.468	-0.245	1.181
5	Human Appropriation of NPP	-1.402	-6.818	4.015
6	Switch point number	0.281	-0.271	0.834
7	Slope	0.473	-1.265	2.212
8	Animal population density	-0.309	-1.173	0.555
9	Time-series length	-0.425	-1.187	0.337

Table 4. Results from generalized linear mixed models fitted to exponential concave declines (n=21). The table presents the model-average coefficients of the parameters from the most plausible models (<2 ΔAICc). Bolded parameters indicate those with a statistically significant effect. Parameter numbers correspond to parameters listed in Table S8.

Number	**Parameter**	**Model averaged estimate (SE)**	**Model averaged lower 95% CI**	**Model averaged upper 95% CI**
	Intercept	2.858	-3.348	9.063
1	Slope	-0.516	-1.514	0.483
2	Switch point number	-0.512	-1.169	0.145
3	Mean lambda	-5.708	-11.975	0.560
4	Human Appropriation of NPP	0.438	-0.347	1.222
5	Threat number	-0.684	-1.778	0.410
6	Series fullness	1.246	-0.942	3.435
7	Animal population density	-0.394	-1.296	0.508
8	r_{max}	0.315	-0.257	0.887
9	Cumulative lambda	-0.096	-0.397	0.205
10	Proximity to end	1.247	-1.457	3.951
11	Human Influence Index	-0.315	-1.011	0.381
12	Time-series length	0.913	-3.933	5.760

Table 5. Results from generalized linear mixed models fitted to combined concave declines (n=58). The table presents the model-average coefficients of the parameters from the most plausible models (<2 ΔAICc). Bolded parameters indicate those with a statistically significant effect. Parameter numbers correspond to parameters listed in Table S9.

Number	**Parameter**	**Model averaged estimate (SE)**	**Model averaged lower 95% CI**	**Model averaged upper 95% CI**
	Intercept	2.130	-3.014	7.273
1	Animal population density	-0.528	-1.175	0.119
2	Mean lambda	-4.292	-10.734	2.150
3	r_{max}	0.471	-0.573	1.515
4	Cumulative lambda	-0.015	-0.052	0.021
5	Switch point number	-0.144	-0.517	0.230
6	Time-series length	-0.166	-0.634	0.302
7	Human Appropriation of NPP	0.285	-0.911	1.481
8	Proximity to end	0.568	-1.428	2.564

FIGURE

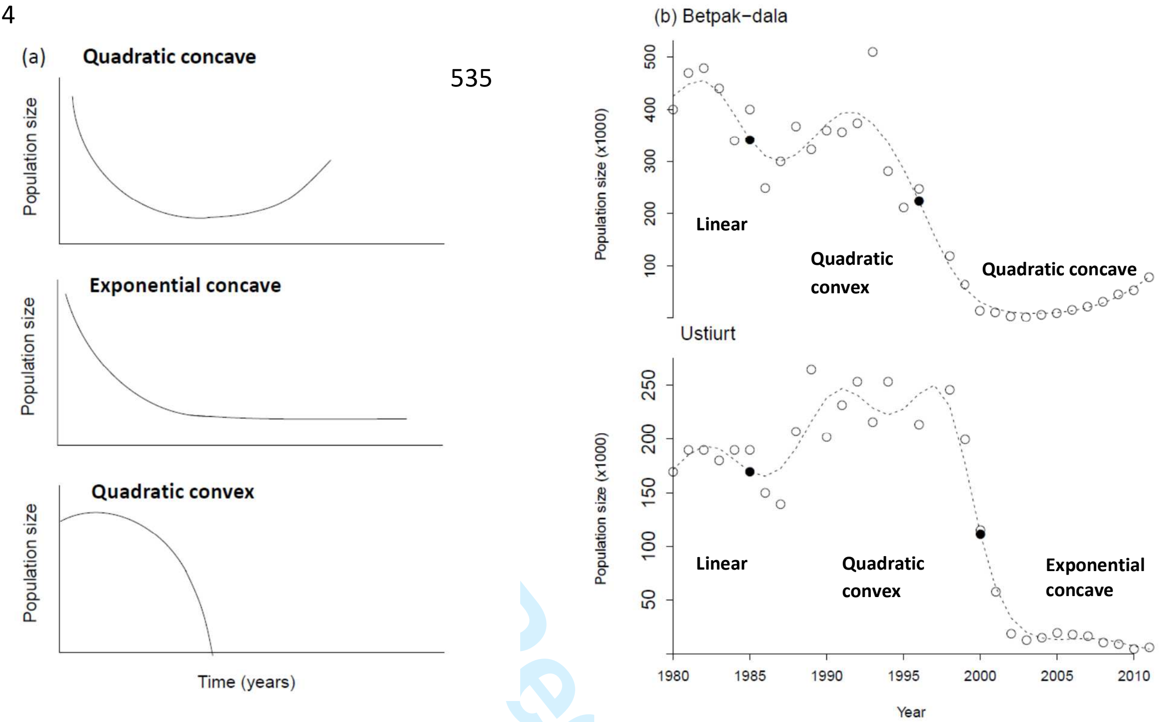

Figure 1. (a) From top to bottom: Quadratic concave, exponential concave, and quadratic convex decline patterns found in wildlife populations, associated with simulated decreasing proportional pressure, constant proportional pressure, and increasing fixed pressure (from Di Fonzo, Collen & Mace 2013); (b) Exemplary time-series of Saiga populations from Betpak-data and Ustiurt regions in Kazakhstan (Institute of Zoology of the Ministry of Education and Science of the Republic of Kazakhstan 2011). Raw data are indicated by open points, switch points are indicated as closed points, and dotted lines reflect the smoothed time-series generated from the GAM. The Betpak-dala population dynamics are best-fit by: (A) linear, (B) quadratic convex, and (C) quadratic concave curves (from 1980 onwards, separated by switch points), whereas the Ustiurt population dynamics are best fit by (A) linear, (B) quadratic convex, and (C) exponential concave curves. The statistical output for the best-fit curves is presented in the Table S1 in Supporting Information.

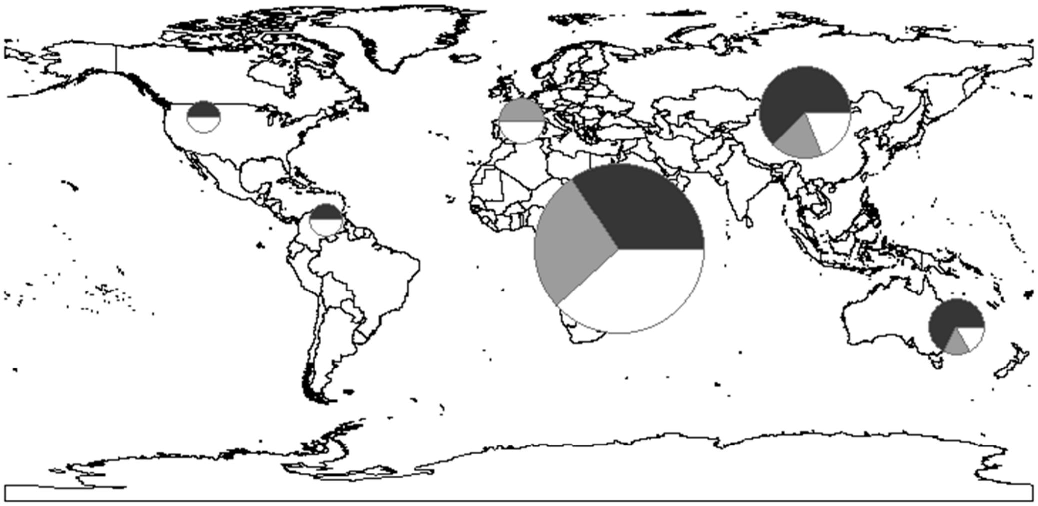

Figure. 2. Terrestrial mammalian decline-curve types grouped according to continent. Dark grey portions of pie-charts represent quadratic convex declines (most severe), grey portions represent exponential concave declines (mid-severity) and white represent quadratic concave declines (least severe). The size of the pie-chart is relative to the number of declines per continent (n= 55 in Africa, n=16 in Asia, n= 2 in North America, n= 4 in Europe, n=2 for Latin America and the Caribbean and 6 in Australasia).