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Drivers of extinction risk in African mammals: the interplay of distribution state, human pressure, conservation response and species biology

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Although conservation intervention has reversed the decline of some species, our success is outweighed by a much larger number of species moving towards extinction. Extinction risk modelling can identify correlates of risk and species not yet recognized to be threatened. Here, we use machine learning models to identify correlates of extinction risk in African terrestrial mammals using a set of variables belonging to four classes: species distribution state, human pressures, conservation response and species biology. We derived information on distribution state and human pressure from satellite-borne imagery. Variables in all four classes were identified as important predictors of extinction risk, and interactions were observed among variables in different classes (e.g. level of protection, human threats, species distribution ranges). Species biology had a key role in mediating the effect of external variables. The model was 90% accurate in classifying extinction risk status of species, but in a few cases the observed and modelled extinction risk mismatched. Species in this condition might suffer from an incorrect classification of extinction risk (hence require reassessment). An increased availability of satellite imagery combined with improved resolution and classification accuracy of the resulting maps will play a progressively greater role in conservation monitoring.

1. Introduction

The state of biodiversity is deteriorating globally owing to increasing human pressure and insufficient conservation responses [1], despite considerable efforts and political engagement from local to global organizations and institutions [2,3]. The drivers of biodiversity decline are multiple (habitat loss, overhunting, climate change, disease, invasive species, etc.), and affect species groups differently [4]. Although conservation intervention has slowed down or reversed the decline of some species, these efforts are outweighed by a much larger number of species moving towards extinction [5]. For example, one-quarter of the world's carnivore and ungulate species have moved closer to extinction in the past 40 years [6].

Extinction risk analysis has emerged in the past 15 years as a useful analytical tool for providing scientific support to ecologists and conservation biologists [7]. It has been used to investigate the predictability of species' extinction risk from their biological characteristics (i.e. their life-history traits) and their exposure to threats, mammals often being a model group [8–11]. A number of

different techniques have been used to model the effect of intrinsic and external variables, including phylogenetic comparative methods [12], machine learning models [7] and taxonomically informed generalized linear mixed models [13].

Various extinction risk analyses on mammals have focused on teasing out the relative importance of biological (i.e. intrinsic) factors in predicting extinction risk [9,11]. Others have shown that anthropogenic threats are important predictors of extinction risk too, albeit their relative role in a predictive model is generally lower relative to biological traits [14,15]; this is perhaps related to the complexity of measuring threat impact on species compared to measuring species biological traits [16,17]. The applicability of extinction risk analysis for practical conservation outcomes can be enhanced by providing conservation recommendations that are clearly interpretable by conservation practitioners [18]. Large-scale extinction risk analyses require comprehensive datasets of different types of data. These include species biological characteristics, distribution ranges and habitat associations, environmental characteristics and threats operating within the ranges. Biological characteristics, including reproductive parameters (such as litter size) and physical traits (such as body mass), are readily available for groups such as mammals [19,20], but often the datasets are incomplete (see §2a(iv)).

Assessments of habitat can be hard to gather at a continental scale, and even when they are available there may be considerable inconsistencies in assessments between sites [21]. Instead, remote sensing instruments continuously record large amounts of data concerning land and vegetation cover, topography and climate, many of them with global coverage. The data and derived products are increasingly freely available, providing cost-effective means to collect standardized information relevant to conservation purposes [22].

The usefulness of satellite-derived products in conservation studies has already been demonstrated. For example, the Normalized Difference Vegetation Index (NDVI) has been used to test hypotheses on the recent trends in net primary productivity [23], to relate elephant density and food availability [24], and to predict habitat suitability for the reintroduction of species extinct in the wild [25]. The Moderate Resolution Imaging Spectroradiometer (MODIS) and Landsat imagery have been used in regional and global land cover studies to identify hotspots of land cover change [26,27], to monitor forest [28,29] and savannah [30] habitats, to infer their resilience [31] and to assess the impact of habitat loss on birds [32]. Remote sensing data have not yet been extensively used in extinction risk modelling, but their improved use has the potential of overcoming the historical problem of measuring the effect of threats (particularly habitat loss and alteration) on species' extinction risk [17]. Most satellite-derived data are available at regular intervals, and can be used to produce assessments of change at large scales. Satellite imagery can therefore be used to track changes in environmental conditions owing to anthropogenic impact, allowing their effect on extinction risk to be modelled.

The African mammalian fauna has been the subject of long-standing scientific attention [33] and comprises some of the most attractive species for tourists: lion (*Panthera leo*), leopard, (*P. pardus*), African elephant (*Loxodonta africana*), Cape buffalo (*Syncerus caffer*), rhinoceroses (*Ceratotherium simum* and *Diceros bicornis*) and great apes (chimpanzees, *Pan troglodytes*; bonobos, *P. paniscus*; and gorillas, *Gorilla gorilla* and *G. beringei*). Nonetheless, it has been estimated that African large mammals have lost 59% of their populations in the past 40 years even

within protected areas (PAs) [34], and African carnivores and ungulates have faced a continental-scale deterioration in conservation status in the same period [6].

Legislative protection of sites by means of PA networks is proving effective at reducing forest cover loss [35] and loss of all natural land cover in African PAs [36]. Net deforestation rates in Africa have been estimated at 0.14% per year in 2000–2010 [37], and the rate of vegetation change was generally faster outside than inside PAs, with some exceptions [38]. A recent study [39] has demonstrated that long-term presence of conservation efforts had a significant positive influence on the persistence of African great apes in 109 PAs. However, conservation resources are limited and need to be substantially increased [40]. A key step to increase the effectiveness of conservation action is the identification of clear priorities through robust analytical methods [41,42]. African mammals represent a promising model group to test a set of interacting correlates of extinction risk.

We perform an extinction risk analysis to assess the contribution of four classes of potential predictors of extinction risk in African terrestrial mammals, we measured: (i) species distribution state (e.g. suitable habitat availability and geographical range size) as the current condition characterizing a species' distribution; (ii) human pressures (e.g. habitat alteration within a species' range) through the use of various satellite imagery products; (iii) conservation responses (e.g. PA coverage and levels of management in PAs) and (iv) biological traits (e.g. body mass and weaning age), already known to correlate with mammal extinction risk [11]. We assess the key role that satellite imagery can play in measuring environmental condition and change, allowing an improved prediction of the extinction risk of species.

We use a set of multi-resolution satellite imagery, updated conservation-relevant information and comprehensive biological characteristics to build our models. We assessed the relative importance of these drivers and identified multiple paths of interaction that determine a species' extinction risk. We calculate the accuracy of our prediction model in terms of the proportion of species whose observed extinction risk was correctly classified, and propose conservation-relevant interpretations for those species with a mismatching classification in our model.

2. Material and methods

(a) Variables and data sources

We focused our analyses on African terrestrial mammals (figure 1; electronic supplementary material, figure S1). We assigned species' threat status categories (i.e. a proxy of extinction risk) according to the Red List of the International Union for Conservation of Nature (IUCN) [43]. Following previous approaches [9,13], we classified all species as being threatened (critically endangered, endangered, vulnerable) or non-threatened (least concern, near threatened) depending on their IUCN Red List categories [44], after removing species classified as data deficient, extinct or extinct in the wild; a total of 1044 species were included in the analyses. Twenty three per cent of African mammals are currently threatened with extinction according to the IUCN Red List, a condition that is comparable with the global figure, where 25% of all mammal species are threatened [45]. Only species having at least 50% of their global distribution range in Africa were included in our analyses (all threatened species in the analyses are endemic to Africa).



Figure 1. Richness of African mammal species (number of species in each 300 m grid cell). See the electronic supplementary material, figure S1 for a colour version.

Following [1,11], we identified four main classes of variables whose influence on mammals' extinction risk can be modelled: species distribution state, human pressure, conservation response and species biology. For each species, we measured 18 predictor variables, each belonging to one of the mentioned classes (see also table 1 for a summary). We overlaid each spatial variable with each species' range, and measured a representative value of the variable for the species (as described in the subsections below). Spatial quantification of the variables was performed in GRASS GIS [46].

(i) Distribution state

Variables of distribution state represent the current level of intactness characterizing species distributions. We measured the size of species geographical ranges from IUCN distribution range polygons [43]. We also measured the current proportion of suitable habitat within each species' range, by using habitat suitability models developed by Rondinini *et al.* [47]. Habitat suitability models were based on habitat classifications according to species preferences for land cover types and elevation range, their tolerance for human disturbance and their water requirements (at a 300 m spatial resolution).

We used the mean annual NDVI value as a proxy for the current (year 2010) primary productivity within each species' range, as also done in previous publications [48]. The NDVI was calculated from composites of satellite imagery (at a 250 m spatial resolution), by applying the mean compositing method [49] on 1 year of satellite imagery recorded by the MODIS instruments aboard the Terra and Aqua satellites.

(ii) Human pressure

Variables of human pressure represent the level of anthropogenic threat affecting biodiversity. We obtained changes in the proportion of suitable habitat within species' geographical ranges between 1970 and 2010 (at a 1 km spatial resolution), from [50]. We further estimated, for each species, the net change in mean annual primary productivity (NDVI, see §2*a*(i)) and tree cover between 2000 and 2010 (at a 250 m spatial resolution). Tree cover change was calculated from the MODIS percent tree cover product [51], which quantifies the percentage of tree cover in any 250 m pixel (see also §2*c* on the relationship of this variable with species' habitat preferences).

We also calculated the proportion of each species' range overlapping with areas characterized by high values of the human influence index (HII; at a 1 km spatial resolution) [52,53]. The HII map was described as 'the sum total of ecological footprints of the human population'. It was derived from several different data sources divided into four main types: population density, land transformation, accessibility and electrical power infrastructure [52]. We defined high HII values as those being higher than 5, and then tested the effect of an increased threshold value ($HII > 10$) following [16].

(iii) Conservation response

Variables of conservation response represent the level of conservation efforts implemented for biodiversity protection. We calculated the percentage of each species' range (from 0 to 96% observed) and the percentage of suitable habitat (from 0 to 81% observed) overlapping with PAs with IUCN categories I–IV (i.e. those

Table 1. Description of the variables included in the extinction risk modelling. See Material and methods for an extended description of the variables and their sources.

class	variable	description
extinction risk	RIThreat	the response variable, binary species threat status (threatened versus non-threatened in the IUCN Red List)
distribution state	RangeSize	size of species geographical ranges
	NDVI2010	mean NDVI value within a species' range in 2010
	SuitPrev	proportion of suitable habitat within a species' range
human pressure	SuitLoss ^a	net change in the proportion of suitable habitat within a species' range, between 1970 and 2010
	NDVILoss ^a	net change in NDVI value within a species' range, between 2000 and 2010.
	TreeCovLoss ^a	net change in tree cover percentage within a species' range, between 2000 and 2010
	HII.5	proportion of a species' range overlapping with areas having an HII > 5
conservation response	HII.10	proportion of a species' range overlapping with areas having an HII > 10
	AvgCons	average amount of conservation actions measured in PAs established within a species' range
	RangeProt	proportion of a species' range overlapping with PAs
species biology	SuitProt	proportion of a species' suitable habitat overlapping with PAs
	Order	taxonomical order
	DietBreadth	number of dietary categories eaten by a species
	HabitatBreadth	number of habitat layers used by a species
	AdultBM	adult body mass
	LitterSize	number of offspring born per litter per female
	NeonateBM	neonatal body mass
WeaningAge	age when primary nutritional dependency on the mother ends	

^aThe acronym 'Loss' was used to indicate the rationale of the variable, even if the net change in variable values over time was measured (i.e. including losses and gains).

areas more strictly targeting biodiversity conservation). This was done by overlaying IUCN range polygons [43] and habitat models [47] with PA polygons from the world database of PAs [54]. We represented missing-shape PAs (14% of the PAs in Africa totalling 1% of the African PA surface) with circular polygons, centred on the reported PAs' coordinates and having a radius calculated from the reported PAs' size. We are aware that representing missing-shape PAs with a circular buffer may have a (likely minor) influence on our calculation of species' PAs coverage [55], but we expect that this would equally affect all species in our sample.

The level of actual conservation interventions was assessed from management-related data for a total of 825 African PAs (electronic supplementary material, figure S2). Data on management levels were collected by Birdlife for important bird areas (IBAs), many of which are also overlapping with PAs [56] (see §2c on the rationale for using this dataset). For each site, we considered the information on implementation of conservation action available in the World Bird Database (WBDB) [56], scored from 0 (very little or no conservation action are in place), 1 (some limited conservation initiatives are in place), 2 (substantive conservation measures are being implemented but these are not comprehensive and are limited by resources and capacity) to 3 (the conservation measures needed for the site are being comprehensively and effectively implemented). These data were then merged with those from Tranquilli *et al.* [39], who scored levels of conservation intervention for a set of central African PAs characterized by great apes' past presence and current presence/absence. We reconverted the latter dataset according to the WBDB classification system before merging. For each species, we finally calculated the average level of conservation action allocated to PAs for the period 1990–2012.

(iv) Species biology

Biological variables, also referred to as life-history traits, represent baseline biological characteristics of species. We accounted for species taxonomy by including order as a categorical variable [15]. We then used PanTHERIA [19] as a data source for biological traits. PanTHERIA represents the most comprehensive dataset on mammalian life-history traits, derived from over 100 000 single records collected, yet it is characterized by missing data for all the collected variables. Among all of the available variables, we selected those for which missing data were completed with the use of a multiple imputation procedure (as described in [11]), in order to reduce the effect of data omission in our dataset while still retaining all species in our sample. The resulting variables were diet breadth, habitat breadth, adult body mass, litter size, neonate body mass, weaning age. These variables are a representation of species' physical characteristics (e.g. body mass) and life-history speed, along the axes of 'reproductive timing' (e.g. weaning age) and 'reproductive output' (e.g. litter size), as described in [57].

(b) Extinction risk model

We used random forests (RFs) and classification trees (CTs) to build our model of extinction risk prediction. RF, a machine learning technique, has been introduced as a supportive tool for macro-ecological analysis [7]. It has been successfully used in comparative extinction risk analyses for terrestrial [9] and marine [58] mammals as well as for amphibians [59].

We used RF modelling to test the ability of our variables to classify threatened and non-threatened African mammals, based on their IUCN Red List categories [9,59]. RF models

combine a series of CTs ($n = 500$, in our case) based on the predictor variables. Each CT classifies the species through a recursive binary partitioning that aggregates them into regions (or 'nodes') that are increasingly homogeneous with respect to their extinction risk. At each step in fitting a CT, an optimization is carried out to select a node, a predictor variable and a predictor or cut-off that result in the most homogeneous subgroups of species, as measured by the Gini index [7]. In this way, we could quantify a series of model-related measures of accuracy, together with relative variables importance and 'classification proximity' among species, as described below.

We measured RF model classification accuracy by calculating the proportion of correctly classified species (throughout a cross-validation routine implemented in the RF model). We also verified the model performance in terms of sensitivity (ability to classify threatened species correctly) and specificity (ability to classify non-threatened species correctly). We further calculated K statistics and true skill statistics (TSS), both weighting overall sensitivity and specificity performances [60]. We then measured the relative importance of each variable for the RF model construction. The importance of each variable in the RF model was measured through its contribution to: (i) model accuracy for threatened species, (ii) model accuracy for non-threatened species, (iii) model accuracy for all species, and (iv) mean decrease in the Gini index, across the RF trees [61].

Based on the final model classification, we calculated the classification proximity of species in the RF model, i.e. a measure of classification similarity between species, calculated from the number of times in which two species ended up in the same terminal node of the RF trees, during model recursive partitioning. We used this metric to represent species in a multidimensional scaling (MDS) analysis (i.e. a principal coordinate analysis). We also investigated the presence of mismatching threat status classifications in our RF model, i.e. threatened species classified as non-threatened and vice versa in most of the RF trees.

We then created a single conditional inference CT of classification to evaluate visually a representation of the interaction between predictor variables in determining pathways of extinction risk [62]. Statistical analyses, RFs and CTs, were performed in R [63] using the packages 'randomForests' [64] and 'party' [62].

(c) Addressing limitations in the use of variables

Our use of geographical range size as a predictor of extinction risk may lead to circularity with the IUCN Red List criteria, in particular criterion B on restricted distribution range [44]. This issue has previously been resolved by excluding species listed under criterion B (in the IUCN Red List) from the analyses, often a substantial proportion of species [9,65,66]. Other approaches employed to resolve this issue include the use of indices of relative geographical range decline as proxies of extinction risk [14], or IUCN Red List information on species population trend [59], rather than Red List categories. Instead of excluding a large number of species from our analyses (thus reducing both the representativeness of the sample and the sample size), we performed two tests, one including range size as a predictor variable and one excluding it. We verified that a weak relationship exists between range size and the other external variables in our model ($R^2 < 0.05$ for all relationships), so that by excluding range size from the RF model it is likely that we removed its effect almost entirely. We then followed the classical approach and repeated the analyses after excluding species listed only under criterion B, to show the consistency among our models (classification accuracy and variable importance).

Among general variables of habitat suitability and intactness, we also tested the effect of tree cover change in determining species' extinction risk. We are aware that the role of this variable would probably be more influential for forest-dependent species rather than for savannah and grassland-related species.

Nonetheless, we believe that the tree cover loss in a certain area has much broader impacts. In fact, it has been demonstrated that habitat clearance has contagious effects in forest and grassland [67]. For this reason, we are confident that our measure of tree cover change is likely to be influential on the extinction risk of species with diverse habitat preferences.

Measuring the levels of conservation intervention by using management information collected for IBAs that overlap with PAs is probably not ideal for our study species. However, this is one of a very few datasets of management information readily available at a continental scale and directly related to conservation efforts, as well as a good geographical complement to the information provided in [39] for central Africa. We used this variable as a proxy of 'conservation attention' in PAs, which is potentially also of broader relevance for mammals.

(d) Satellite information: testing the effect of spatial resolution

Several low (30–1000 m), medium (4–30 m) and high (0.6–4 m) spatial resolution optical sensors aboard different satellites provide imagery on a daily (MODIS, AVHRR), or regular basis (ASTER, Landsat 7-8, MERIS, SPOT 4-5). We clarify that 'low' and 'medium' resolution are intended here in remote sensing terms, rather than biological modelling terms. The imagery products from some of these sensors are freely available and are the preferred choice for many biodiversity and conservation studies.

We tested the effect of using low-resolution satellite imagery in our analyses. We compared the 250 m resolution MODIS percent tree cover layer with a 30 m resolution Landsat-derived forest classification. The latter product was obtained from a classification of Landsat 5 TM and 7 ETM+ imagery, selected using a web-service platform of the Joint Research Centre of the European Commission (<http://acpobservatory.jrc.ec.europa.eu/content/land-cover-change>). The best available imagery in the period of 2008–2012 was selected for a sample of 47 African PAs (electronic supplementary material, figure S3) and a 20 km buffer surrounding each of them (1–5 Landsat scenes per PA map were used). Pre-processing of the selected imagery (radiometric calibration, cloud masking, topographic correction, de-hazing, radiometric normalization, mosaicing and gap filling) was based on the methodology described in [68,69].

The original Landsat-derived maps contained the following classes: cloud/shadow, water, forest, shrubs, grass, bare soil, burnt and other vegetation. We grouped these classes in a second step into forest versus non-forest classes, and checked for their consistency visually with the original Landsat imagery (electronic supplementary material, table S1). Each classified PA map was then validated to high-resolution imagery by visually comparing a random selection of 50 points per map (including forested and non-forested pixels) using Google Earth software (Google Earth). For each classified PA, we calculated the overall classification accuracy as well as combined TSS [60], accounting for both sensitivity (correctly classified forested pixels) and specificity (correctly classified non-forested pixels).

After the validation, we compared for each PA the mean proportion of forest areas derived from Landsat with the value of tree cover percentage derived from MODIS. Our aim was to verify whether a linear relationship exists between these two products.

3. Results

(a) Classifying species' extinction risk

The RF model on the full-species set had high classification accuracy (93% correctly classified species in the cross-validation procedure). The model performed well both in

Table 2. Performance statistics of the RF classification model. Both the performance of the full model and the performance of the model without the range size variable are reported.

parameter	all variables	RangeSize removed
no. species	1044	1044
proportion correctly classified	0.927	0.900
sensitivity	0.803	0.682
specificity	0.964	0.965
true skill statistic	0.767	0.647
K statistic	0.788	0.696

terms of sensitivity (80% of correctly classified threatened species) and specificity (96% of correctly classified non-threatened species) (table 2). Overall, both TSS (0.77) and K statistic (0.79) reported good performances (unity being the maximum possible in both cases). When removing the variable 'range size', the overall model accuracy decreased slightly (from 0.93 to 0.90), yet model sensitivity and TSS decreased more substantially (from 0.80 to 0.68 and from 0.77 to 0.65, respectively).

We calculated the importance of each variable according to four measures, and reported a mean rank value for each (figure 2a). Range size was the most important variable in our model. Nonetheless, variables representing each of the four predictor classes (table 1) were all present among the most important ones. This was observed also when removing range size as a predictor of extinction risk (figure 2b). Two of the satellite-derived variables were influential descriptors of species extinction risk, with both tree cover change and NDVI 2010 coming into the first half of ranked variables in our RF models (figure 3). In particular, tree cover change was important both in the models with range size (sixth most important variable) and in the model without range size (third most important variable).

When repeating the RF analyses on the full set of variables but excluding all threatened species listed only under criterion B in the IUCN Red List, the degrees of freedom in our model were reduced to 904 (electronic supplementary material, table S2). This had little impact on overall RF model accuracy (still over 90% of species were correctly classified), but impacted more substantially the model sensitivity (now 0.64). Additionally, this had very little impact on our variables' ranking: range size remained the most important variable and eight out of the nine most important variables remained the same with respect to the full-species model (electronic supplementary material, figure S4).

(b) Classification proximity

A classical MDS analysis, based on the relative proximity of each species in each terminal node of the RF, suggested threatened species are clustered in one 'arm' of the coordinate space, whereas non-threatened species are widely distributed across the remaining plot area (figure 3). The two clusters are not discrete, and there is partial overlap between threatened and non-threatened species. This enabled us to identify 29 non-threatened and 47 threatened species (electronic supplementary material, tables S3 and S4, respectively) with

a mismatching classification in our RF model (i.e. those incorrectly classified in the majority of the RF trees).

(c) Interaction among extinction risk predictors

A conditional inference CT for the classification of extinction risk in African mammals (figure 4) showed the complex interaction between multiple predictor variables in different classes. For example, species having a relatively small distribution range (less than 11 192 km²) that is substantially covered by PAs (greater than 24% overlap) but is also largely overlapping with areas of high human impact (greater than 47% overlap) face a high probability of being threatened ($\approx 95\%$; see pathway 1–15–17–18 in figure 4). In contrast, rodent species with relatively small overlap with PAs (less than 24%) but with a relatively large distribution range (greater than 23 163 km²) have a very low probability of being recognized as threatened with extinction ($\approx 2\%$; see pathway 1–2–10–12–14 in figure 4).

(d) The effects of spatial resolution

For a sample of 47 PAs, we classified forest presence according to Landsat scenes and validated the classification with Google Earth. The validation process demonstrated good accuracy in the classification of forested versus non-forested areas in all of the maps. Proportion of correctly classified pixels, sensitivity (ability to detect forest areas) and specificity (ability to detect non-forest area) were all above 85% (table 3). We measured the correlation between 'medium-resolution' satellite imagery (forest cover from Landsat) and 'low-resolution' imagery (tree cover percentage from MODIS) in our sample PAs. The two satellite products showed a good correlation in our test PAs (linear model with zero intercept; $\beta = 1.43$, s.e. = 0.13, $R^2 = 0.72$). On average, the Landsat classification predicted a higher proportion of forest cover compared with the tree cover percentage detected by MODIS (figure 5).

4. Discussion

(a) Role of extinction risk predictors

We performed a comprehensive analysis of factors affecting extinction risk of African mammals and followed Butchart *et al.* [1] in considering multiple classes of factors influencing extinction risk of species. The effects of all these factors are, ultimately, mediated by species biology, which explains why some species are less prone to endangerment than others, under similar external conditions. The most important predictors of extinction risk in our RF model were range size, proportion of range in PAs, weaning age, neonatal body mass, proportion of protected suitable area and change in tree cover (figure 2a). Some of these variables, such as range size or weaning age, have already been identified as important predictors of mammals' extinction risk [15]. Yet, the importance of other variables, such as the change in tree cover as assessed from remote sensing, are identified here for the first time. Collecting tree cover data at a continental scale using methods other than remote sensing would be impossible. Although monitoring land cover changes automatically at continental scales remains challenging [70], our results here highlight one of the potential future application of global change data from satellites (see also [29]) in conservation-related analyses.

The level of protection (both referring to the presence of PAs within species ranges and within suitable habitat in the

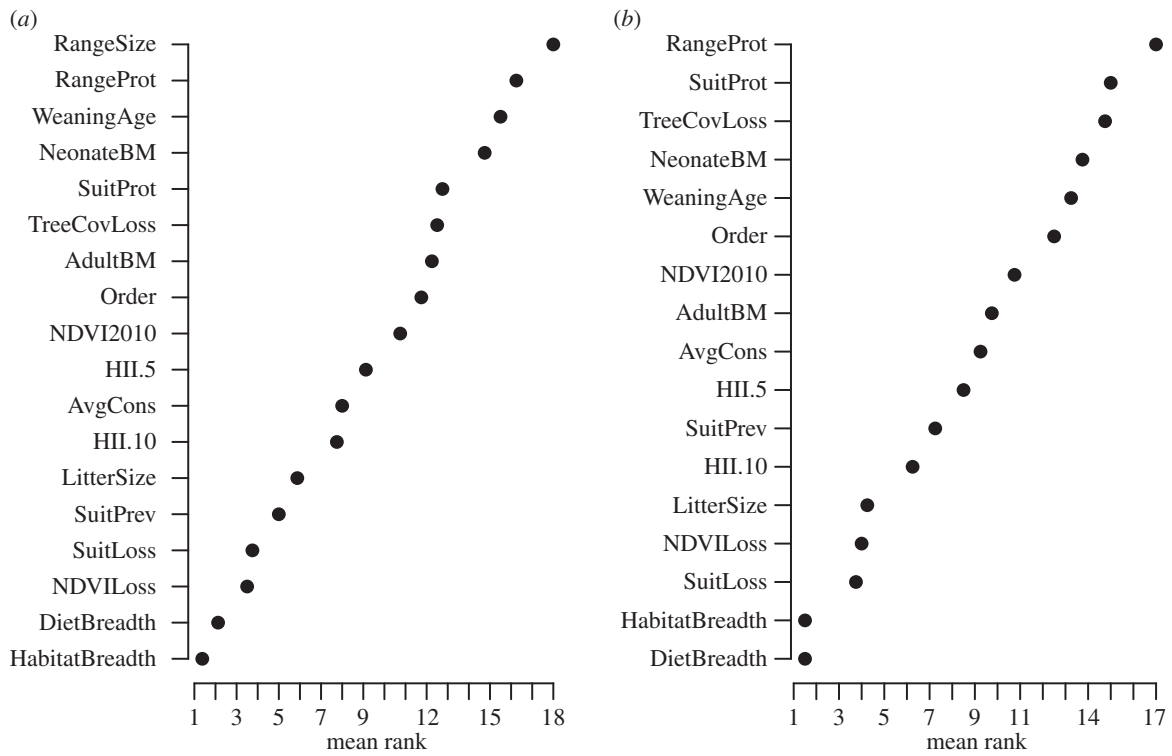


Figure 2. Relative importance of each predictor variable included in the RF model. The importance of each variable was estimated according to four measures (see S2). Variables were ranked according to their importance for each measure and a final mean rank was calculated and reported. All variables were tested in (a), while range size was removed before the test in (b). See table 1 for a description of the variables.

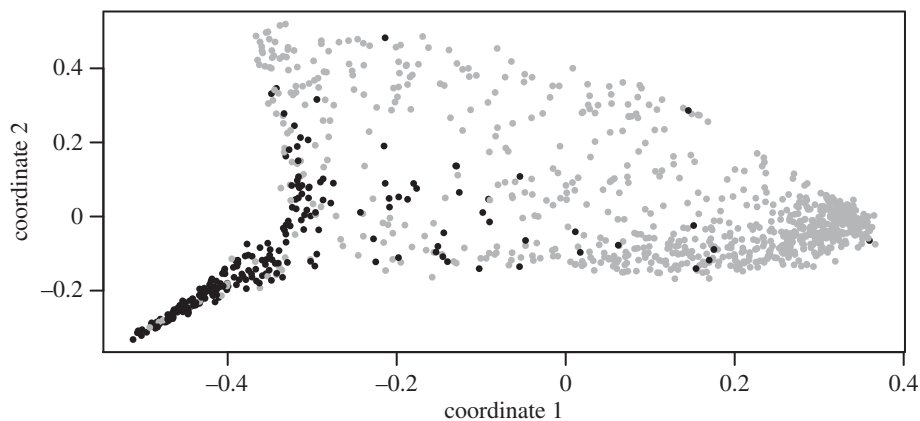


Figure 3. Classical MDS of African mammals based on their 'classification proximity' in the full RF model (all variables included). See S2b,c for analytical details. Black circles denote threatened and grey circles denote non-threatened species.

ranges) was an important predictor in our model. The establishment of PAs has often been related to the protection of charismatic species [71], which are generally large-bodied, characterized by relatively slow life histories and affected by a variety of threats (particularly habitat loss and hunting). Our results suggest a link between establishment of PAs and retention of a non-threatened status for mammals, yet we could not fully explain whether this is due to the role of the PAs in reducing habitat loss or other conservation benefits linked to the PA, such as reduced poaching and lower human disturbance.

The level of conservation effort in PAs did not have a strong effect in our model. This may depend on the fact that the information on conservation efforts was not properly defined to be effectively linked to the conservation status of our study species. Although we expected that the conservation efforts data referred to important bird areas overlapping with PAs

could potentially be a broad proxy of conservation attention, these data might not necessarily have a direct relevance for mammals. Additionally, it is likely that, at the scale of our analyses, the presence of the PAs inside the whole distribution range of a species is more important than the relative levels of conservation efforts. Recent large- and local-scale studies have demonstrated the crucial role of the different conservation efforts on species protection inside PAs [4,39]. Improving the availability of conservation interventions data, both inside and outside PAs, is strategic, since this has a potential to improve our understanding of the complex relationship between threats–traits–conservation efforts.

(i) The role of geographical range size

The use of range size as a predictor of species threat status, derived from IUCN Red List, may lead to model circularity.

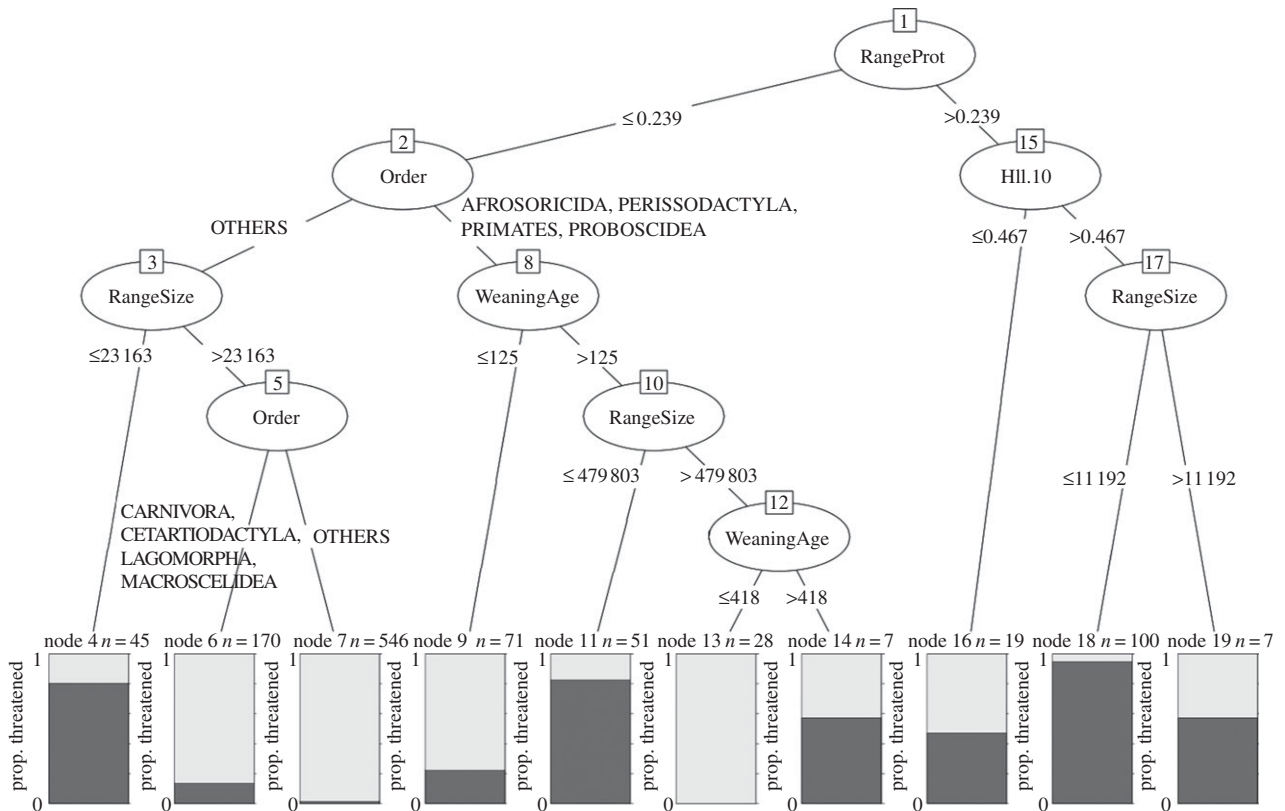


Figure 4. Conditional inference CT for African mammals. Each terminal node reports (in dark grey) the proportion of included threatened species.

Table 3. Results of the visual ground-truthing validation of the forest cover in 43 African PAs (and surrounding buffer) as classified by interpretation of the Landsat TM scenes. For each map, 50 random points (including forest and non-forest) were extracted and visually compared with Google Earth imagery. Separate statistics are reported for each area. It was not possible to validate four additional maps, owing to the excessive presence of clouds.

parameter	value
no. areas	43
proportion correctly classified	0.91 (s.d. 0.08)
specificity	0.89 (s.d. 0.12)
sensitivity	0.86 (s.d. 0.22)
true skills statistic	0.72 (s.d. 0.23)

In fact, range size is used in the IUCN Red List assessment to apply the criterion B on restricted distribution [44]. Yet, restricted distribution is not itself sufficient to trigger criterion B, and other conditions (such as severe fragmentation or ongoing population decline) must also be met at once to qualify a species as threatened in the Red List. Nonetheless, various methods have been proposed to avoid having potential circularity in the use of range size as a model predictor (see §2c).

We tested our RF model on the whole set of predictor variables, and then removed range size to repeat the test. Additionally, we repeated the analyses after excluding those threatened species listed only under criterion B. Our comparisons critically showed that in all of our tests the overall accuracy and, most importantly, the sensitivity of the RF models were higher with respect to previously published extinction risk analyses on mammals (e.g. [9]). Nonetheless, removing species listed only under criterion B or removing

range size from the variables reduced the ability to classify threatened species correctly. In all tests, our measure of relative importance of variables confirmed that: (i) all of the four different classes of variables were influential in predicting extinction risk, (ii) the three RF models shared seven out of the nine most influential predictors of extinction risk (with only small changes in their ranked importance), (iii) range size was the most important predictor even after removing species listed only under criterion B, as also found in [65].

We acknowledge that the use of IUCN range polygons to represent species distribution is probably subjected to potential errors and gaps in the data (e.g. [72]), yet this is the most updated data source available for mammals (as well as many other groups) globally. We thus stress the importance of maintaining and ensuring a constant update and refinement of this key information.

(ii) Using satellite imagery in extinction risk analysis

In our models, we tested the effect of multiple satellite-derived maps of habitat state and habitat change (i.e. human pressure). Previous extinction risk analyses have generally considered a limited number of external correlates (especially threats) with respect to intrinsic (biological) correlates. This is perhaps related to the uncertainty affecting threat measurement, and limited data availability [16,17]. Our results suggest that an increased use of satellite imagery can contribute to enhancing our understanding of how multiple factors drive species' extinction risk at a large scale.

Remote sensing is a powerful and increasingly available technology in conservation. Its tools and applications provide opportunities to monitor changes in the conservation status of threatened species in areas impacted by habitat conversion [32] and can inform the classification of species' extinction

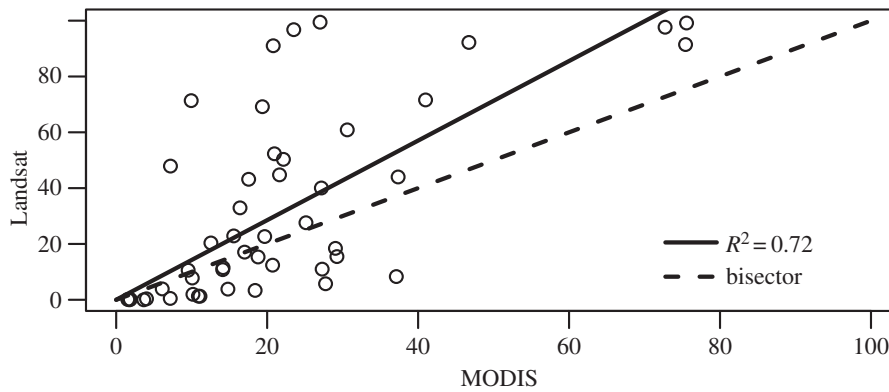


Figure 5. Comparison of the 2010 percentage of forest cover in a sample of African PAs (and surrounding buffer). The solid line represents the linear fit (with zero intercept) between the Landsat maps and the MODIS maps, whereas the dashed line is the bisector ($y = x$). The sampled areas were the same as in table 3.

risk, thus reducing the problem of outdated assessments in the IUCN Red List [73] (see §4b).

Satellite imagery is available from a variety of sources; however, the spatial and temporal resolutions, as well as its cost, determine its applications. In our extinction risk analysis, we used a series of satellite-derived products from freely available sources, with spatial resolutions ranging from 250 m (for MODIS) to 1000 m (for the HII composite map). We also showed that the classification of medium-resolution (30 m) Landsat imagery produced reliable maps of forest cover for a sample of African PAs. The Landsat-derived forest cover was also well correlated with a MODIS-derived tree cover product (250 m), one of the most important predictors in our model. A higher spatial accuracy is now being reached in the classification of forest cover change at a global scale [29], thus improving our ability to track local drivers of habitat alteration, such as non-industrial logging.

Our analysis illustrates the value of stronger links between the remote sensing and the conservation scientific communities. Our extinction risk models benefitted from the use of satellite-derived assessments of land cover condition and forest change. Regular updates of both, and other land cover variables, could contribute to more accurate extinction risk modelling in the future; however, remote sensing specialists are needed to produce the tools to undertake these large-scale assessments and validations.

(b) Classification proximity and mismatching classifications

In an MDS analysis, based on the frequency that pairs of species are in the same terminal nodes of our RF model, threatened species were generally clustered together and overlapped only partially with non-threatened species, which were instead spread across the remaining coordinate space. This is probably due to the fact that threshold levels of extinction risk (i.e. characterizing threatened species in the IUCN Red List) arise only when a limited set of conditions are met (e.g. high threats and slow life history). This is also likely related to the spatial (i.e. biogeographic) and evolutionary signal in extinction risk [48].

Twenty nine non-threatened species (electronic supplementary material, table S3) were misclassified as threatened in our RF model (i.e. they are represented in the 'high-risk' branch of figure 3). This could be an effect of the model being unable to consider some of the factors potentially mitigating threats impact on species. However, an alternative

explanation is that the current IUCN assessment for these species may be erroneous and needs review, and some of the currently non-threatened species are facing conditions that may result in a substantial increase in their extinction risk in the near future. In this latter case, our results are pinpointing species in potential need of increased conservation attention. Incorrectly classified non-threatened species in our model mostly included small mammals (such as the near threatened Zambian mole rat, *Cryptomys anelli*) and primates (such as the aye-aye, *Daubentonia madagascariensis*, which was until recently classified as endangered), but also included the white rhinoceros, *Ceratotherium simum*, a charismatic species that suffers from high levels of poaching (something with no direct surrogate in our current analysis) despite receiving substantial conservation attention [74]. These species should be carefully considered for future reassessments of their conservation status in the IUCN Red List. We believe that a wider (both taxonomically and spatially) application of our method can provide an important tool for Red List (re-)assessments [73].

On the other hand, 47 threatened species (electronic supplementary material, table S4) were misclassified as non-threatened in our RF model (i.e. they are not represented in the 'high-risk' branch of figure 3). A likely explanation for this mismatch is that we were not able to consider all of the threatening factors affecting mammal species extinction risk in Africa. In fact, our use of satellite imagery allowed us to consider a set of habitat loss-related drivers (such as the loss of tree cover), while we could only approximate (e.g. through the use of HII) harvest-related threats, such as persecution, poaching and bushmeat consumption. Direct kill (in its various forms) is a key driver of extinction risk for mammal species globally [75] and is particularly severe for African mammals [76]. Many of the threatened species with a mismatching classification in our model are known to be persecuted by locals as a preventive measure (or as a retaliation) for livestock predation (e.g. the lion, *Panthera leo*), while others are poached for their horns (e.g. the black rhino, *Diceros bicornis*) [74], or are killed for their meat at unsustainable levels (e.g. Dorcas gazelle, *Gazella dorcas*) [43]. Other threatened species in this group are affected by a combination of direct kill and other drivers not included in our model, e.g. the western gorilla (*Gorilla gorilla*) population is facing a rapid decline owing to commercial hunting and spread of the Ebola virus [77]. Despite providing a clear improvement in resolution (for extinction risk analysis), habitat variables in our model are likely to be significant at the landscape scale. On

the other hand, threatened small-bodied species incorrectly classified in our model (i.e. some bats and rodents) may also respond to finer scale habitat modification. As already mentioned, it is also possible that the status of some of the incorrectly classified threatened species in our model needs to be reassessed in the IUCN Red List, again highlighting a potential use of the proposed approach [73].

(c) Interaction among extinction risk correlates

Our analysis demonstrates that there are multiple routes to extinction (figure 4). In all the described paths, interacting factors determine large changes in the probability of a species to be threatened. For example, all other conditions being similar (taxonomy, range size, level of protection), species characterized by a weaning age longer than 418 days are substantially more likely to be threatened than those with a lower weaning age value (figure 4, terminal nodes 8 and 9). Similarly, species characterized by a significant level of protection but facing high levels of human impact (e.g. outside PAs) may have a high or moderate probability of being threatened with extinction, depending on their range size being smaller or larger than ~11 000 km² (figure 4, terminal nodes 18 and 19). Interestingly, this same range size threshold has been already been identified as a good predictor of threatened birds [78].

Candidate variables in our RF model correctly predicted the extinction risk of over 80% of both threatened and non-threatened species (i.e. high sensitivity and high specificity). Our results demonstrate the combined effect of multiple classes of drivers in shaping the current extinction risk of African mammals. In previous extinction risk analyses [15,58], biological factors played a central role in explaining model variance, whereas external factors were generally less relevant. We showed that using a number of satellite-derived measures of human pressures and distribution state changes the situation. Our measures of relative variable importance highlighted that both biological and external factors are included among the top-ranked variables in all our models (figure 2).

5. Conclusion

The current extinction risk in African mammal species can largely be explained by the combined effect of multiple correlates. The type and dimension of responses of species to human disturbances and conservation actions are determined by their biology. Our work illustrates how the use of multiple satellite imagery sources can improve our ability to track external drivers of extinction risk. Our results suggest that conservation interventions (e.g. establishment of PAs) are beneficial in reducing species' extinction risk, provided that a combination of biological and external conditions is verified. This evaluation is of practical significance, as advocated by Cardillo & Meijaard [18], because conservation planners can use our results as a guideline to improve the allocation of conservation resources.

Our method can have broader applications, both for other regions and for other taxa, and its application of extinction risk analysis to inform Red List reassessments has great potential. We envisage that an increased availability of freely accessible satellite data as well as an improved resolution and classification accuracy of the resulting maps will play a substantial role in future conservation monitoring and will increasingly be part of an enhanced toolbox for conservation scientists.

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