Predicting population size at large scale: The case of two large felids

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A B S T R A C T

Approaches that allow capitalizing on local population estimates to derive global population estimates with associated uncertainty are urgently needed, especially for naturally rare species of conservation concern. Here we used published population density estimates to predict large-scale density patterns and derive global population estimates for two species of large felids, the leopard and the tiger. We modelled population density for the leopard (n = 392) and the tiger (n = 547) as a function of environmental and anthropogenic variables, while controlling for differences in sampling method and sampling area, time of data collection, spatial autocorrelation, subspecies and political protection. We used Bayesian inference to generate a distribution of plausible population sizes. Both species showed higher densities in high productivity areas, the leopard being more abundant in high precipitation, high level of terrain roughness and agricultural areas, and the tiger in areas with low croplands and low roughness. Primary roads density showed a negative effect on both species. Secondary roads density was associated to higher densities for the leopard but lower densities for the tiger. Livestock biomass showed a humped relationship with tigers' densities. Temporal trends in average density were negative for the tiger, experiencing an average decline of 34% (IQR: 11% − 53%). In contrast, the trend for leopards showed a marginal, yet uncertain, increase in recent years 21% (IQR: −5% − 57%). We predicted a global population estimate of 261,636 (IQR = 146,768 − 461,512) and 5201 tigers (IQR = 2596 − 10,460). Large-scale models of population density that rely on unstructured data can contribute to our understanding of species ecology, produce robust population size estimates for conservation assessment and inform large-scale conservation planning. At the same time, the uncertainty around these estimates highlights the limited knowledge available for these species which should be accounted for in conservation assessments.

1. Introduction

Conservation research conducted at the biogeographic scale is dominated by the use of species distribution data and models (Franklin, 2013). While these are fundamental for many applications, they are limiting for comparative assessments related to setting conservation targets, protected area planning and assessments, which require a knowledge of species population density (de Oliveira et al., 2009; di Marco et al., 2016; Santini et al., 2022, 2019; Williams et al., 2022). Species can indeed differ substantially in their

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average population density (Santini et al., 2018b), so while the protection and conservation status of locally abundant species is generally well captured by species distribution models, they are likely to be over-estimated in naturally rare species introducing biases in comparative assessments (Clements et al., 2018; Santini et al., 2014) and overestimating in the conservation value of protected areas (Santini et al., 2016). Protected area planning can also benefit from knowledge on how the population density of target species varies within its geographic range (de Oliveira et al., 2009; di Marco et al., 2016). These problems also apply within the context of Red List assessments, which suffers from missing data for most species' assessment (Cazalis et al., 2022). Under the IUCN Red List species can be assessed under multiple criteria, still only one is sufficient to assign a category. When multiple criteria are applied the Red List category of a species depends on the criterion that indicates the most threatened category (IUCN Standards and Petitions Committee, 2022). As such, the application of criteria C (small population and decline) and D (very small population) using large-scale abundance estimates can be very informative for assessing the status of naturally rare but widespread species whose extinction risk may be under-estimated considering their distribution only (Santini et al., 2019).

Predictive models of population density have been used to inform Red List assessments for species lacking abundance data (Santini et al., 2019), and robust average species-level predictions have now been produced for most species of mammals (Santini et al., 2022). However, species' population density depends on a variety of biotic, environmental and anthropogenic factors, so it can also vary substantially across the geographic range of a species. Consequently, such estimates are inevitably characterized by substantial uncertainty, and are not ideal for more regional scale applications aimed at assessing population size. Species distribution model predictions have often been used as proxies of population abundance under the assumption that drivers of species presence and abundance are the same, but recent studies have largely disproved this assumption (Lee-Yaw et al., 2021; Dallas and Hastings, 2018). Large-scale spatially explicit predictions of population density are possible but require substantial amount of data available only for a subset of data-rich species (e.g. *Sus scrofa*, Lewis et al., 2019; *Panthera onca*, Jędrzejewski et al., 2018).

Large carnivores have undergone substantial declines and range contractions worldwide in recent decades. These species are highly vulnerable, as they are at the top of the food chain and require large amounts of food and space for survival (Ripple et al., 2014). They are often the first species to disappear because of human activities (Gittleman et al., 2001). Habitat loss and fragmentation, illegal trade in body parts and killing due to - direct and indirect - conflicts with humans are among the leading causes of this decline. These species are an essential part of the ecosystem since they exert a top-down control, maintaining stable trophic chains at all levels. The disappearance of the world's large predators can trigger trophic cascades that affect not only their prey, but also impact the ecosystem to the point of having consequences for disease dynamics, wildfires, biogeochemical cycles, and invasive species (Estes et al., 2011; Hoeks et al., 2020).

Large felids are certainly among the best known and most attractive species worldwide among large carnivores. Still, they are also particularly problematic for conservation due to large area requirements, poaching, conflicts with human activities (i.e. livestock predation), and posing direct threats to humans (Macdonald and Loveridge, 2010). Leopards (*Panthera pardus*) and tigers (*Panthera tigris*) are among the best-studied species (e.g. Jacobson et al., 2016; Karanth, 1995). The tiger is currently classified as 'Endangered' by the IUCN Red List because it suffered severe distribution and population declines in the last century, mainly due to poaching and habitat loss (Damania et al., 2008; Dinerstein et al., 2007; Goodrich et al., 2022; Sanderson et al., 2010). The leopard is globally classified as 'Vulnerable' by the Red List. The ability of this species to live in diverse habitat types, even within human-dominated landscapes, and its broad diet, make the leopard more resilient than other large carnivores (Wang and Macdonald, 2009). Yet, widespread fragmentation, depletion of prey and conflict with humans have led to a massive population decline and range loss in the leopard (Jacobson et al., 2016). Thanks to the individually recognizable fur marks, the local population density of these species has been widely estimated through photographic capture-recapture methods (Balme et al., 2009; Chapman and Balme, 2010; Karanth, 1995; Karanth and Nichols, 1998).

A robust global estimate of species abundance for these two species is lacking. The Red List assessment for the tiger reports a global estimate of 2608–3905 animals. This estimates mainly come from the sum of existing countries' estimates, based largely on capture-recapture and occupancy studies, but do not come with a global uncertainty estimate around the mean value. In addition, as the conservation of such charismatic species has a political connotation, summing up governmental estimates of the population size of these charismatic species have been labeled as "political populations", which are scientifically unsubstantiated claims to suit a political agenda (Gopalaswamy et al., 2022). Leopards are more widely distributed and in a better conservation status, so global estimates have not been yet attempted. More robust field estimates are needed, and existing estimates must be continually updated on declining species. Still, methods to upscale such local estimates to a global estimate are not yet well established in the literature.

This study aims to produce global-scale population predictions for the leopard and tiger capitalizing on the plethora of local population density estimates produced for these two species over time. We develop species-specific density models and explore the role of large-scale drivers of population density including climate, primary productivity, orography, land cover and use, human infrastructures, and accessibility and density of humans and livestock. We further account for spatial latent effects not captured by the predictors and temporal trends, as well for the heterogeneity of sampling methods used to produce the density estimates. We use Bayesian inference to generate a distribution of credible population sizes revealing the inherent uncertainty surrounding these estimates. Finally, we assess the consistency of the predictions with available estimates and assess their potential to inform the Red List assessment of the two species.

2. Methods

2.1. Data collection

We initially extracted the density estimates for the two species from an updated and unpublished version of the TetraDENSITY database (Santini et al., 2018a). The TetraDENSITY database includes georeferenced population density estimates of terrestrial vertebrate species worldwide. It was meant to be a source for macroecological research and biodiversity conservation analyses and a reference database for population density estimates for field studies. We then supplemented this initial dataset (390 estimates for both species) with additional data taken from scientific articles on Google Scholar. We used a set of keywords and combinations therein: "population density", "population size", "*Panthera tigris*", "*Panthera pardus*", and "mark-recapture". In total, we added 549 density estimates resulting in a final dataset of 392 estimates for leopard and 547 estimates for tiger (Appendix S1; Fig. 1). Overall, tiger and leopard densities were obtained using data from over 220 studies conducted in 328 sites across species ranges. From each study, we also collected the spatial coordinates of the study area, years of data collection, sampling area size, and sampling method. Because the extent of the sampling area where density is estimated can influence the resulting density estimates (Blackburn and Gaston, 1996; Gaston et al., 1999; Suryawanshi et al., 2019), we filtered the two datasets retaining only density estimates associated with a sampling area measure.

Furthermore, since the sampling method can influence the density estimates (Jędrzejewski et al., 2018), we classified the sampling method to estimate density into several categories: spatially explicit capture-recapture (SECR), unspecified photographic capture-recapture (CR), photographic capture-recapture with half mean maximum distance moved (HALF), photographic capture-recapture with full mean maximum distance moved (FULL), unspecified (NS) and others (O). Finally, to avoid pseudo-replicates and reduce the noise in the data, we averaged density estimates collected in the same year, same location (set of coordinates), and same survey method, for each species separately (Santini et al., 2022). The eventual result was a dataset of 278 observations for the leopard and 477 observations for the tiger.

2.2. Population density drivers

We complemented the population density dataset we produced with predictive variables (Table 1). Candidate variables included eight environmental (Normalized Difference Vegetation Index (NDVI), Net Primary Productivity (NPP), Terrain Roughness, Slope, Annual Precipitations, Precipitation Seasonality, Forest percentage, Cropland percentage) and five anthropogenic variables (Human Population Density, Accessibility, Primary Road Density, Secondary Road Density, Livestock Biomass). We also considered the inclusion of a protected area layer using protectedplanet.net and openstreetmap.org, but eventually discarded these data because found incomplete for some areas (e.g. Nagarahole National Park and Bardiya National Park are missing from India and Nepal respectively). NDVI and NPP were used as a proxy for potential prey presence and abundance, which is the most important predictor for the presence and density of big cats, such as tigers and leopards (Macdonald and Loveridge, 2010; Sunquist and Sunquist, 2002) in absence of human impact. Environmental factors, such as mean annual precipitation, precipitation seasonality and NPP, determine plant biomass and hence the biomass of prey species (Coe et al., 1976; East, 1984). In turn, the biomass of prey species is expected to influence felid
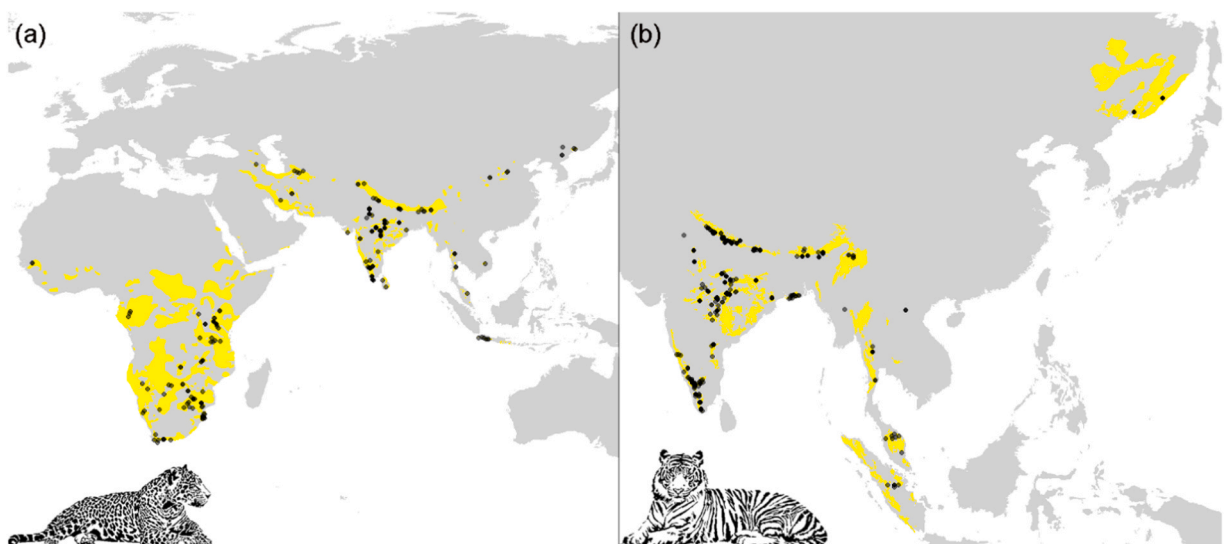

Fig. 1. Spatial distribution of the density estimates in our sample for the (a) leopard and the (b) tiger. Point transparency is used to aid with the visualisation of overlapping study locations (i.e. darker points indicate a higher number of estimates for the same location). Geographic ranges for the species are visualised in yellow.

Table 1

Predictor variables used in the analysis. Expectations indicate personal hypothesis on density trends in relation to the different variables. Hypothesis are indicated as: ↑ positive relationship; ↓ negative relationship; - no relationship. The letters refer to the species to which the transformation applies: leopard (L) or tiger (T).

Variable code	Full variable name	Description and updated date	Transformation used	Source	Ref #	Expectations
NDVI	Normalized Difference Vegetation Index	Vegetation productivity measure (December 2020)	Log (T)	MODIS https://modis-land.gsfc.nasa.gov/npp.html	/	- L, ↑ T (Jiang et al., 2015)
NPP	Net Primary Productivity	Net amount of solar energy converted to plant organic matter through photosynthesis (November 2016)	Log (L)	MODIS https://modis-land.gsfc.nasa.gov/npp.html	/	↑ L, ↑ T
HPD	Human Population Density	People / km^2 (2017)	Log (L, T)	HYDE 3.2 https://easy.dans.knaw.nl/ui/datasets/id/easy-dataset:64613/tab/2	(Goldewijk et al., 2017)	↓ L, ↓ T
STRP	Primary Road Density	Primary roads' density in .asc format (2014)	Log (L, T)	GRIP https://www.globio.info/download-grip-dataset	(Meijer et al., 2018)	↓ L, ↓ T
STRS	Secondary Road Density	Secondary roads' density in .asc format (2014)	Log (L, T)	GRIP https://www.globio.info/download-grip-dataset	(Meijer et al., 2018)	↑ L, - T
LIVESTOCK	Livestock Biomass	cattle, buffaloes, goats, sheep, horses and pigs' densities (2010)	Log (L, T)	FAO http://www.fao.org/livestock-systems/global-distributions/en/	/	↑ L, - T (Yang et al., 2021)
ACC	Accessibility	Travel time from major population centers (2000)	Log (L, T)	https://forobs.jrc.ec.europa.eu/products/gam/download.php	(Nelson, 2008)	↑ L, ↑ T
TRI	Terrain Roughness	Based on the digital elevation model products of global 250 m GMTED2010	Log (L, T)	EarthEnv https://www.earthenv.org/topography	(Amatulli et al., 2018)	↑ L, - T (Mann, 2014)
SLO	Slope	Based on the digital elevation model products of global 250 m GMTED2010	Log (L, T)	EarthEnv https://www.earthenv.org/topography	(Amatulli et al., 2018)	↑ L, - T (Loveridge et al., 2022)
ANNUALP	Annual Precipitations	In the tropics precipitation values are usually related to productivity. Average of the years 1970–2000	Log (L, T)	WorldClim https://www.worldclim.org/data/worldclim21.html	(Fick and Hijmans, 2017)	↓ L, ↑ T (Rahman et al., 2018)
PSEASON	Precipitation seasonality	Coefficient of variation. Average of the years 1970–2000	Log (L, T)	WorldClim https://www.worldclim.org/data/worldclim21.html	(Fick and Hijmans, 2017)	↑ L, ↑ T
FOREST	Forest Percentage	(2015)	Logit (L, T)	NCEI (NOAA) https://www.ncei.noaa.gov/thredds/catalog/sat/landcover/HYDE_AREAVEG/catalog.html	(Meiyappan and Jain, 2012)	↑ L, ↑ T
CROP	Cropland Percentage	(2017)	Logit (L, T)	HYDE 3.2 https://easy.dans.knaw.nl/ui/datasets/id/easy-dataset:64613/tab/2	(Goldewijk et al., 2017)	↓ L, ↓ T
Y	Sampling Year	/	Log (L, T)	/	/	↓ L, ↓ T
AREA	Sampling Area	/	Log (L, T)	/	/	↓ L, ↓ T

population size and density, population structure, social behaviour and home range size (Karanth et al., 2004; Macdonald and Loveridge, 2010). We obtained livestock biomass maps by multiplying livestock density maps (FAO 2010) by the body mass of each species. An average weight of 500 kg was considered for cattle, 120 kg for pigs, and 55 kg for sheep and goats (Benítez-López et al., 2019). We also assumed 500 kg for horses and buffaloes. We created two maps only considering the potential prey for the leopard and the tiger, each being the sum of the biomass map of each potential prey. Buffalo, cattle, pigs and goats were considered important for the tiger; cattle, goats, sheep, pigs, and horses were deemed important for the leopard (Miller et al., 2016; Sangay and Vernes, 2008; Tamang and Baral, 2008; Wang and Macdonald, 2006). This discrimination is due to the food preferences of the two predators, with the tiger usually attacking larger animals and species than the leopard. Macdonald and Loveridge (2010) suggested that felids prefer natural prey. This may be because livestock is often protected and predators trying to attack livestock are more likely to die. If natural prey has been depleted though, this may lead to livestock predation.

For the landcover (forest and cropland) and human population density, we extracted data for each year included in the species datasets (Meiyappan and Jain, 2012, for forest covariate; Goldewijk et al., 2017, for cropland and human population density). We also considered topographic variables, such as Terrain Roughness and Slope, since they provide refugees and cover (proxies of inaccessibility to humans), and they may be important for breeding and predation. This is particularly true for leopards, which are known to inhabit rugged and mountainous areas (Khosravi et al., 2021), while may be less relevant for the tiger.

All variables were resampled at a resolution of 0.5-degree. This resolution was deemed appropriate to represent average local conditions affecting populations considering the low average population density of the two species calculated from our dataset (~5.0 ind./100 km^2 for the tiger and 6.4 ind./100 km^2 for the leopard) to account for spatial uncertainty in the coordinates reported in the original studies, and the generally large study areas used to conduct the population density estimates for these species (81% and 87% of the density estimates for leopard and tigers, respectively, are estimated in sampling areas >100 km^2 and < 2500 km^2).

To control for temporal trends in population density, we included the year of the population density estimate as an additional predictor. To control for biases in the estimates due to differences in the sampling area, we included the sampling area as a predictor (Blackburn and Gaston, 1996). To account for differences in the legislation and conservation effort across countries, as well as historical factors, we included the country as random effects. Furthermore, we also included a random effect for the subspecies to account for possible differences in mean population density. Subspecies were assigned based on the countries according to Jacobson et al. (2016) and Liu et al. (2018). When the distribution of a subspecies straddled two countries, or there was more than a subspecies in one country, we distinguished them using latitude and longitude. This also was based on subspecies distribution illustrated in Jacobson et al. (2016) and Liu et al. (2018).

The population density estimates' distributions for the two species were highly left-skewed, so we log-transformed them to reach normality and heteroskedasticity assumptions. Similarly, we inspected the statistical distribution of all environmental variables and transformed most of them using either log or logit transformation (Table 1).

We tested the potential for multicollinearity by evaluating the correlation between the predictor variables using Pearson correlation coefficients, setting a maximum threshold at r = 0.7 (Dormann et al., 2013). As an additional test, we also calculated the variance inflation factors (VIF). Using VIF = 3 as a threshold, we removed NPP, Accessibility, Livestock Biomass, Human Population Density and Slope from leopard model and Human Population Density, Accessibility, Forest, Slope and NPP from tiger model.

The final dataset included fourteen variables for the tiger (Spatial Coordinates, Method, Sampling Year, Cropland percentage, Roughness, Country, Subspecies, Annual Precipitation, precipitation Seasonality, NDVI, Primary Road Density, Secondary Road Density, Livestock Biomass, Study Area) and fourteen predictors for the leopard (Spatial Coordinates, Method, Sampling Year, Forest percentage, Cropland percentage, Roughness, Country, Subspecies, Annual Precipitation, Precipitation Seasonality, NDVI, Primary Road Density, Secondary Road Density, Study Area).

2.3. Model fitting

To model the population density of the two species we fitted two Generalized Additive Model (GAM) with a Gaussian family error distribution using Bayesian inference (Wood and Augustin, 2002).

To ensure the comparability of effect sizes and a correct shrinking of estimates in the model, we standardized each predictor variable to a mean of 0 and a standard deviation of 1. Predictor variables were all modeled as smooth terms. To avoid overfitting, we limited the value of k to 3 in the smooth function, except for study areas in both models ($k = 4$) which is expected to show a cubic relationship.

To account for spatial autocorrelation in the estimates, we adopted a trend surface analysis approach, including tensor product interaction between the values of coordinates (northing and easting; Fletcher and Fortin, 2018). This approach also tends to improve spatial predictions by accounting for latent geographic variables that cannot be accounted for in the modelling. We did not set a k for the tensor product interaction, so that the smooth function automatically determined the complexity of the relationship. We included the method category as random effect to account for potential biases in the sampling methods. We used weakly informative priors using a normal distribution with a standard deviation of 10 for the intercept, and a standard deviation of 1 for all slope coefficients, thereby limiting the range to a plausible gradient of variation considering the scaled coefficients (Lemoine, 2019). We ran 3 MCMC chains with 3000 iterations each, using the first 1000 as warmups in the leopard model, while the tiger model required 4 chains with 4000 iterations to reach convergence. To limit the storage of MCMC chains we applied a thinning of 5. We assessed chain convergence and parameter identifiability both visually and using the R-hat diagnostic. We ran the model using the 'brms' package (Bürkner, 2017) in R (R Core Team, 2020). To assess model fit we compared posteriors predictions with observed data using the 'bayesplot' package (Gabry and Mahr, 2022). Finally, we tested for spatial autocorrelation in the model residuals using the Moran's I test using the 'DHARMa' package (Hartig, 2018).

2.4. Predictions

We downloaded the shapefiles of the current geographic ranges of the two species (updated in 2019 and 2022 for leopards and tigers, respectively) from the Red List database (Gerngross, 2019; IUCN SSC Cat Specialist Group, 2022). Then we downloaded the habitat maps following the IUCN habitat classification scheme from Jung et al. (2020). Then using the approach illustrated in Rondinini et al. (2011) to develop deductive distribution models using the habitat preferences reported by the Red List for the two species (Tables S1, S2), we reclassified habitat maps into species-level binary maps (1 presence, 0 absence). The map was first reprojected to Mollweide equal area, and then resampled using the 0.5- degree resolution grid, to obtain the proportion of habitat area for the species

in a 50 km x 50 km cell. We multiplied the proportion of habitat area per 2500 km^2 to obtain the available habitat area per cell.

Subsequently, we generated a dataset for predictions with all the variables used for model fitting, using the same transformations and standardized using the mean and standard deviations of the variables in the training dataset to ensure comparability of standardized values. To assess the possible environmental extrapolation in predictions data, we conducted a MESS analysis using 'dismo' package (Hijmans et al., 2017), and we removed from the prediction range areas where extrapolation was above 10% (MESS value < −10). Then, we predicted the population density of the two species across their distribution range setting the year of sampling to the latest year in the dataset (i.e., 2021 for the leopard and 2022 for the tiger) and study area to the maximum area in natural logarithm (10.127 km^2 for the leopard and 10.358 km^2 for the tiger). This ensured making predictions for the present time and assuming estimates were taken from very large areas, therefore removing the bias introduced by sampling in small areas (Blackburn and Gaston, 1996). Finally, we predicted the median posterior prediction per cell. To estimate the total population size and respective prediction intervals, we first multiplied the posterior predictions by the cell habitat area, therefore obtaining a distribution of population sizes per cell. Then, we sorted the population size distributions so that the median value would always be central to the distribution, and finally summed the population size distribution across all cells and estimated the 90% percentiles and Interquartile Range (IQR) of the population size distribution.

3. Results

The MCMC chains of the two models converged and the R-hat convergence diagnostic for all coefficients were equal or very close to 1 (Tables S3, S4). The two models explained 56.1% and 55.88% of the variance for the leopard and the tiger, respectively. The Moran's I test confirmed that spatial autocorrelation was appropriately accounted for (Table S5). The model checking through diagnostic plots indicated a good model fit (Figs. S1, S2). The majority of predictions made for the two species fell within the environmental range of the training dataset. However, there were some instances of extrapolation beyond this range, though mostly limited to within 10% of the original range of values (Figs. S3, S4).

All variables included showed an effect on the population density of the species. Leopards' population density was higher in areas characterized by abundant precipitations and high precipitation seasonality (Fig. 2a, b), in agricultural landscapes (Fig. 2h), high terrain roughness (Fig. 2e) and at intermediate levels of NDVI (Fig. 2c). Forested areas and primary roads negatively affected leopards' density (Fig. 2d, f), while secondary roads showed a positive relationship (Fig. 2g). Leopards' population density showed a weakly positive, but uncertain, temporal trend toward the end of the time period considered (21% total average in 59 years, IQR = −5 to 57%) and a negative effect of sampling area. We predicted the highest densities of leopard in savanna East Africa (> 8–10 leopards/100 km^2), Sri Lanka and Javan islands (> 6 leopards/100 km^2; Fig. 4a). In total, we estimated the current global abundance of leopards to be 261,636 (IQR = 146,768 − 461,512; 90CI = 61,097 − 1030,709) within 7075,746 km^2 of habitat area. We provide estimates for each subspecies in Fig. S5 and Table S6.

Tigers showed the highest densities in regions with high productivity (Fig. 3c). Primary road density, cropland and precipitation seasonality showed weakly negative effects (Fig. 3f, g), while secondary roads and roughness showed a stronger negative effect (Fig. 3d, h). Contrary to leopards, tigers showed a strong negative temporal trend, with a 0.79% average decline per year between 1978
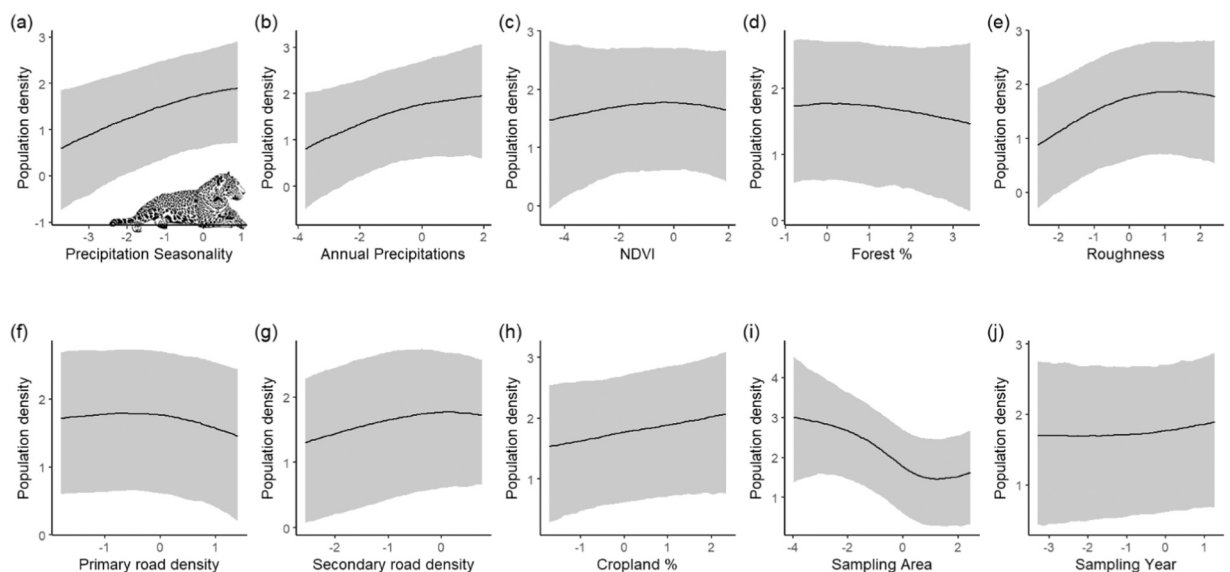

Fig. 2. a-j) Partial effects of the predictor variables in the model for the leopard. Population density is log-transformed and expressed as individuals per 100 km^2. Predictor variables are scaled to mean 0 and SD 1, therefore the majority of the data are distributed between − 1 and 1. The shading encompasses the 95% confidence interval.
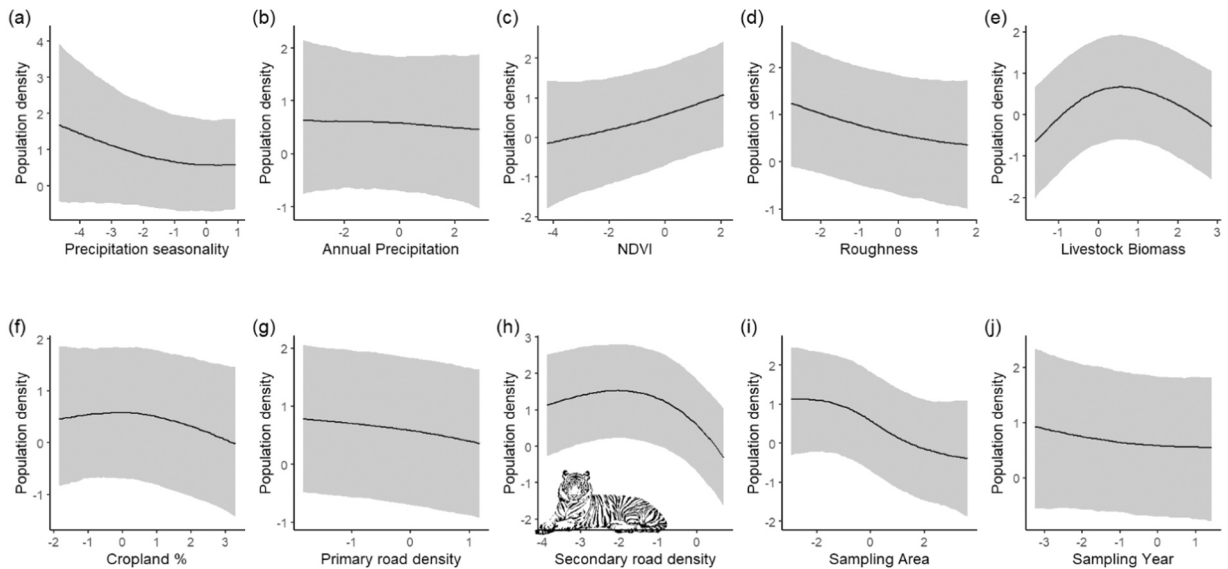
Fig. 3. a-j) Partial effects of the predictor variables in the model for the tiger. Population density is log-transformed and expressed as individuals per 100 km². Predictor variables are scaled to mean 0 and SD 1, therefore the majority of the data are distributed between − 1 and 1. The shading encompasses the 95% confidence interval.

and 2022 and a total average decline of 34% (IQR = 11–53%) in about 45 years. The same as for the leopard, the sampling area had a strongly negative effect. We predicted a higher density of tigers in South and North India (> 3 tigers/100 km²) and on the Himalayan mountains (> 3.5 tigers/100 km²; Fig. 4b). We predicted a global tiger population of 5201 (IQR = 2596 − 10,460; 90CI = 931 − 28,916) individuals in 958,960 km² of habitat area. We provide population estimates for each subspecies in Fig. S6 and Table S6.

The random effects showed a little effect of the methodological approaches employed to estimate population density in both species, with non-spatially explicit methods that tend to overestimate densities (Figs. S7a, S8a). 'Countries' and 'subspecies' random effects showed little differences between Africa and Asia for the leopard, but African and island subspecies showed higher densities compared to the others (Figs. S7b, c). On the contrary, in the tiger we did not find a clear difference between subspecies but found a clear effect of countries (Figs. S8b, c).

4. Discussion

Technological advance in the last few years has allowed field researchers to improve field estimate of local wildlife density using camera traps and mark-recapture approaches (Green et al., 2020). Large felids are among the most studied taxa, given their conservation importance and the possibility of individual recognition. Here we capitalised on the large volume of population density estimates produced over the years across the species range to estimate patterns of population density in two species of large felids. Predictions point to a population of about 250,000 leopards and about 5200 tigers left worldwide. Below we elaborate on the ecological and conservation insights provided by our results and discuss possible applications of similar approaches in the context of species conservation assessments.

4.1. Drivers and trends in population density

The effects of the model predictors in the leopard and tiger analyses met several of our expectations (Table 1). NDVI served as a proxy for prey abundance (Pettorelli et al., 2009), a crucial factor in determining carnivores' presence, abundance and distribution (Karanth and Stith, 1999). Tigers showed a strong positive response to this variable, while leopards showed a weaker positive response. As expected, terrain roughness was positively related to leopard's density and negatively to tiger density.

Contrary to our expectation, we found a mild negative effect in leopards at high forest values, indicating that higher densities are found in mixed or more open areas, such as savannah grasslands or semi-arid habitats. This pattern may reflect the availability of preys in different habitats. Leopards are quite flexible in the diet and prey from ungulates to monkeys. However, preferred prey species are small-to-medium size ungulates (Hayward et al., 2006), which are mostly abundant in open grasslands, savannas, shrubland and heterogeneous landscapes.

Leopards are also adapted to several habitat types, including human-dominated landscapes (Kuhn, 2014; Odden et al., 2014) where they occasionally feed on livestock (such as goats and sheep) or even domestic dogs in urban areas (Athreya et al., 2016). We indeed found a positive effect to cropland percentage and secondary road density predictors, but negative to primary roads.

On the contrary, as expected, tigers' density exhibited a negative relationship with cropland and primary and secondary roads. Considering tigers have disappeared from many anthropogenic landscapes (Dinerstein et al., 2007), the mild negative effect of
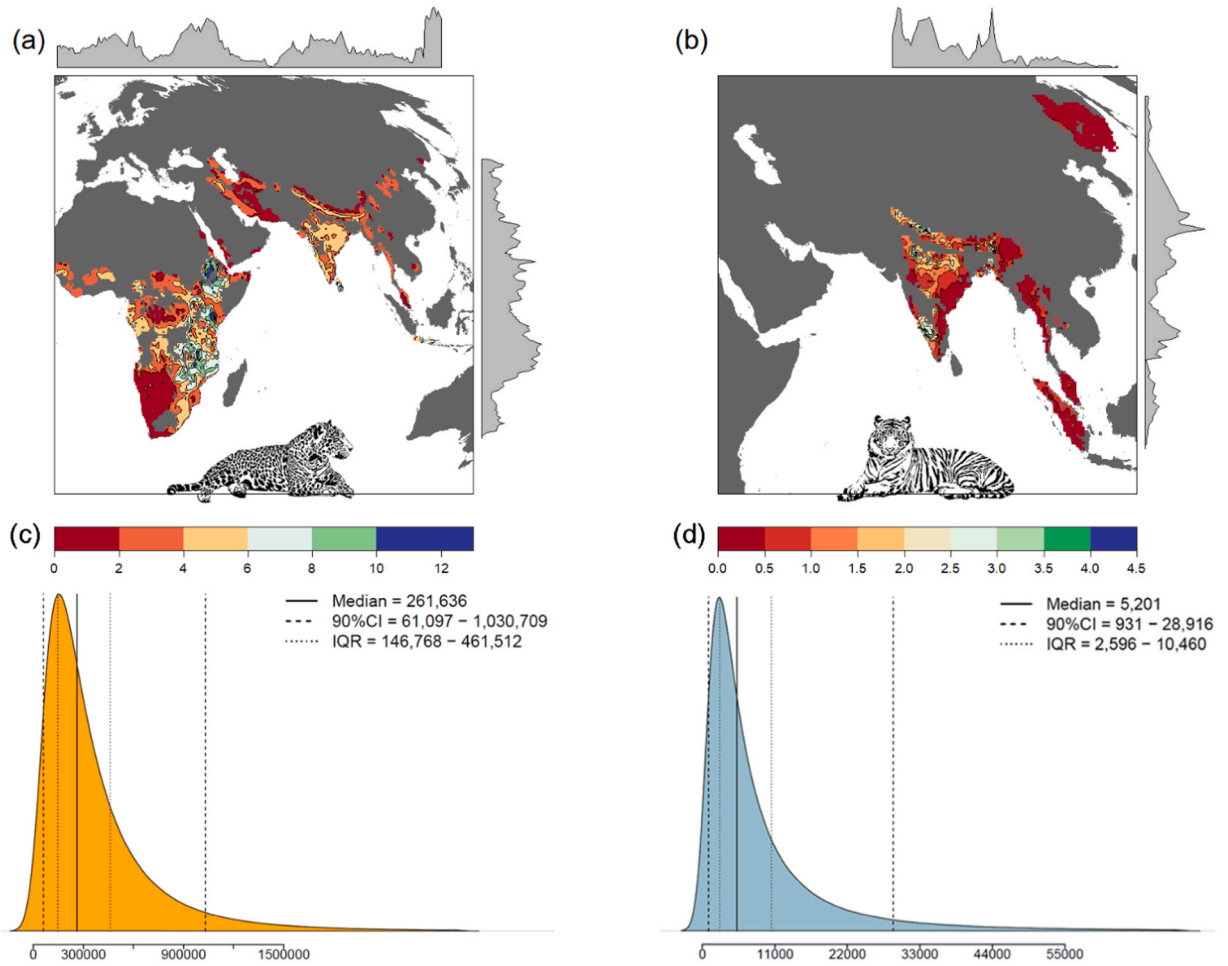
Fig. 4. Final results for the two predictions. Above the estimated densities (ind./ 100 km^2) of the species are shown within their geographical range. Below abundance distributions for the two species are displayed with median, 90%CI and IQR. a, c) Density and abundance predictions for the leopard; b, d) Density and abundance predictions for the tiger.

cropland on tigers' abundance is at first surprising. This is probably due to the low spatial resolution employed in this study, where high percentage of cropland must be interpreted as proportion of the grid cell covered with agricultural landscape. Clearly, unless habitat fragments (e.g. protected areas) are very extensive, the density of population estimated is expected to be influenced by the surrounding landscape (Semper-Pascual et al., 2023).

We also found a humped relationship between tiger density and livestock biomass (Rather et al., 2021), suggesting intermediate densities of livestock may be beneficial providing more resources. In fact, predation on livestock is quite common (Rajaratnam et al., 2016; Bargali and Ahmed, 2018), although it does not seem to be an important resource for tiger populations which mostly select wild preys (Macdonald and Loveridge, 2010). High level of livestock biomass (hence high level of disturbance) instead was associated to low tiger density, probably due to high human disturbance and mortality risk.

While leopards have lost most of their historical range, population density appear to have slightly increased in the last period. Although this trend remains highly uncertain (IQR = −5 to 57%), it might result from the protection of the species worldwide. In contrast, tiger population density showed a steep decline over time (~34% in 45 years). Note that this only represent the decline in average density in areas where the population persists, the overall decline considering range loss is estimated to be substantially higher (>50% in 25–30 years; Goodrich et al., 2022).

Finally, as expected density scaled negatively with sampling area and reached an asymptote in both models, and random effects captured systematic differences in the estimates derived from different estimation methods.

4.2. Predictions of population density patterns and total abundance

Predicting population size over wide areas presents several challenges. Field estimates of population density are limited in space and influenced by the methodological approach and sampling area considered (e.g. Blackburn and Gaston, 1996; Suryawanshi et al.,

2019; Thapa et al., 2014). Further, if a temporal trend in densities exists, their comparability is limited. Hence, simply summing up available estimates is not a good option. Our models capitalized on the plethora of estimates produced for these two felids over the years and managed to account for the known confounding effects of sampling area, temporal trends, and systematic differences in estimates produced by different statistical approaches.

Our models' spatially explicit predictions highlight areas of high and low densities of leopards and tigers and can inform the allocation of conservation efforts on these species. For example, similar-sized protected areas are expected to protect a different number of individuals in different parts of their range. Our estimates can inform conservation assessments indicating how large protected areas should be to protect a minimum number of individuals in different regions of the species range (Clements et al., 2018; Santini et al., 2016; Williams et al., 2022; Wolff et al., 2023).

Total population estimates can be informative for global and regional assessments in the absence of more robust information. For the leopard, our estimate is the first global estimate ever made. While leopards' geographic range continues to shrink globally (Stein et al., 2020; Jacobson et al., 2016), based on which is classified as VU under criterion A2, its absolute population size is not yet a concern. However, nine subspecies of leopards are recognized by the Red List, five of which were last assessed in 2008 under criterion C2 (population size and decline). Combining our spatial prediction with the range maps of the subspecies may provide further information about their status. For example, *Panthera pardus melas* and *P. p. japonensis* populations are estimated to be lower than the VU thresholds of D criterion and *P. p. orientalis* and *P. p. nimr* populations below the CR and EN thresholds of D criterion, respectively. Our estimate for *P. p. kotiya* population lead to a VU category under D criterion (Fig. S5; Table S6). These estimates should be corrected for mature individuals only depending on known local age structures, and combined with recent change in subspecies distribution, so that can inform criterion C2 possibly suggesting higher extinction risk categories.

The IUCN Red List recently assessed tigers' status and trend, quantifying tigers' population between 3726 and 5578 individuals in 2021, with a mean estimate of 4485 (Goodrich et al., 2022). Our prediction of the total population size of the tiger is very close to the estimates reported in the last Red List assessment of the species. For example, our estimate for *Panthera tigris tigris* population align with Red List estimate for India, Nepal, Bangladesh and Bhutan estimates (3288 vs. 3419) and so do *P. t. sumatrae* (358 vs. 393) and *P. t. jacksoni* estimates (117 vs. ~100). The Red List assumes a 70% of mature individuals, which leads to an estimate 3140, following the same assumption our estimates would point to a median of 3640 individuals. Accordingly, the tiger is classified as Endangered under criterion A2 which concerns population reduction over time. Our estimate points also in a similar direction, since we estimate a decline of 25% in 3 generation times (generation length 7–10 years) only considering population density in extant areas. This, combined with the steep decline in its distribution (>40% loss only between 1998 and 2006; IUCN Standards and Petitions Committee, 2022) would point to at least a Vulnerable category under criterion C1, or Endangered if we were using lower boundary estimates of the total population size. Overall, our estimate that relies on a large sample of estimates collected over 40 years exposes the inherent uncertainty in such large-scale predictions given our limited knowledge. Our results call for a more explicit consideration of uncertainty in conservation assessments.

4.3. Caveats

While it would not be possible to estimate population density at this spatial scale without relying on local density studies, using population density estimates collected for other purposes implies some caveats. First, researchers conducting studies with camera traps from which the data were taken often tend to choose undisturbed areas where the presence of the species is established (Jędrzejewski et al., 2018) and densities are usually higher. This may lead to bias toward higher densities in the analysis, and results should be interpreted with caution. Moreover, most density sampling occurred inside protected areas, not reflecting the actual situation of animals outside them, where presence and densities are often lower (Balme et al., 2010). The lack of effect of protected area coverage on tiger population density may indeed reflect the paucity of estimates collected outside protected areas, therefore suggesting a lower population estimate globally.

Second, our method assumes that the species occupy all the available habitat areas within its geographic range. However, species may be temporarily absent in some areas, especially in the case of meta-population dynamics, or permanently absent because of constant human disturbance or persecution, and our models would not capture this. As such, our global predictions must be interpreted as optimistic estimates given possible biases in population density estimates locations, and a total occupancy assumption.

Also, we use cropland covariate, but we do not distinguish between different types of crops that may impact differently on species. We also use NDVI (and NPP) as a proxy of resource availability, even if this may not represent actual wild prey abundance. However, prey densities data are only available for a limited number of areas and time (e.g. only some Protected Areas in India, such as Similipal Tiger Reserve or Pench Tiger Reserve; Jhala et al., 2020), therefore limiting predictions to these studied locations.

Additionally, the accuracy of the population size estimates relies not only on the goodness of the statistical model prediction, but also on the expert-based identified boundaries of the geographic range drawn by Red List experts, the specified habitat preferences, and the accuracy of the land cover maps used. For this reason, the prediction intervals, which only account for statistical uncertainty, have to be taken as the lowest bound of the real prediction uncertainty. Considering these limitations that overall are expected to lead to an over-estimate, conservatively, we recommend that global conservation assessments relying on these estimates adopt a precautionary approach by focusing on a low interval of the distribution (e.g. the 25th interquartile), while acknowledging the uncertainty.

Finally, by using time as a covariate we assumed that species have the same rate of change throughout the range. This necessary simplification might have led to some inconsistencies in the geographic predictions (e.g. overestimation in area with higher rate of decline and underestimation in areas with lower rate of decline).

5. Conclusions

Despite some limitations, our approach allows to produce robust population size estimate given the available knowledge and can help reconstructing historical spatio-temporal trends. The method presented here may be used for several purposes. First, identifying large-scale population density drivers can help anticipating future losses due to environmental change, and planning conservation considering how density varies across space (de Oliveira et al., 2009; Jędrzejewski et al., 2018). In the context of planning, it can also inform the minimum size of protected areas to be effective (Clements et al., 2018; Pressey, 2004; Santini et al., 2014; Williams et al., 2022), which should vary with environmental and anthropogenic gradients. In addition, such estimates can be helpful for Red List assessments in case more robust estimates are unavailable (Santini et al., 2019).

While holding potential, developing these models is not always feasible as it requires a substantial amount of data. A limiting factor is the lack of distribution and abundance estimate data for most species. This is particularly true for those species that receive less research and conservation effort by the research community. Aside from charismatic species such as the leopard and the tiger, suitable candidates are ungulate species for which many estimates are available (Santini et al., 2018a). Large-scale studies employing camera traps not targeting specific species can provide valuable unbiased samples for many species. Machine-learning algorithm that automatically recognize species with reasonable accuracy can prove fundamental to process large quantities of data (e.g. Tabak et al., 2019). Such data, coupled with statistical models to relate locally estimated density with informative covariates can prove fundamental for future biodiversity monitoring.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data supporting this research are provided as part of the supplementary materials.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02677.

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