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RESEARCH PAPER

Carnivore interactions shape leopard presence

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Abstract. The decline of large carnivores profoundly impacts ecosystems, triggering trophic cascades that disrupt ecological balance. The leopard (*Panthera pardus*) has experienced a significant decline in its geographical range, prompting concerns regarding niche displacement and interspecific interactions with other carnivores. In this study, we constructed leopard species distribution models and assessed niche displacement driven by environmental suitability for co-occurring carnivores. Although carnivores shifted the leopard niche towards biodiversity hotspots, none negatively impacted leopard presence, except for a potential influence of *Lynx lynx* and *Ursus arctos*. Interestingly, mesopredators *Felis chaus* and *Canis mesomelas* emerged as the most influential species in predicting leopard presence. Our findings suggest that ecosystems supporting mesopredators are also the most likely to host leopards. This insight underscores the complex interplay of species in shared habitats and highlights the importance of conserving the biodiversity of carnivores to safeguard their ecological roles.

Key words: niche displacement, species distribution model, predator interaction, *Panthera pardus*, Felidae, large carnivore, mesocarnivores

Introduction

The extinction of large carnivores weakens top-down effects and triggers trophic cascades leading up to secondary extinctions that disrupt the ecosystem structure and functioning (Ford & Goheen 2015, Sanders et al. 2015). Many large carnivores are now experiencing dramatic population declines, mainly due to habitat loss and conflict with humans (Ripple et al. 2014, Ceballos et al. 2015). The leopard (*Panthera pardus*) has lost over 60% of its former range (Jacobson et al. 2016), making it all the more urgent that we preserve and restore remaining populations.

Effective conservation of large felids, such as leopards, requires an in-depth understanding of their interspecific interactions with other large and medium-sized terrestrial carnivores. Empirical evidence shows a spectrum of interactions amongst carnivores encompassing suppression, scavenging, competition, predation, fear and kleptoparasitism (Caro & Stoner 2003, Comley et al. 2020, Prugh & Sivy 2020) that result in either indirect (exploitative competition usually through food) or direct (aggression over resources) (Périquet et al. 2015) negative impacts that trigger some form of behavioural response (Caro & Stoner 2003). In the case of the leopards, the impact of such interactions is mitigated through spatio-temporal avoidance of other carnivores, often by exploiting vertical habitat structures – such as moving prey carcasses into trees (Bailey 1993) – as a possible adaptive response to strong kleptoparasitism from other carnivores (Caro & Stoner 2003).

Leopards also exhibit a high level of generalism in prey preference in times of need, enabling them to

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partition resources with other carnivores as long as suitably sized prey is available (Balme et al. 2017). However, over the long term, negative interspecific interactions above the species' adaptive thresholds may result in population declines or even extinction (Hayward & Kerley 2008, Volmer et al. 2017).

In recent decades, considerable research has been undertaken to investigate the impact of other large terrestrial carnivores on leopard populations and their niche overlaps (Karanth & Sunquist 2000, Caro & Stoner 2003, Hayward & Kerley 2008, Wang & Macdonald 2009, Harihar et al. 2011, Balme et al. 2017, Karanth et al. 2017, Ramesh et al. 2017, Simcharoen et al. 2018, Chaudhary et al. 2020, Havmøller et al. 2020, Rafiq et al. 2020, Vinitpornsawan & Fuller 2020, Vernes et al. 2022, Vinks et al. 2022). Despite this extensive body of work, a consensus on how the occurrence of other carnivores drives the global leopard distribution remains elusive. Leopard interactions with other carnivores vary based on the composition of the local carnivore guild, and diverse outcomes are observed in different regions of the leopard distribution, each influenced by distinct human management practices.

For example, in the Sabi Sand Game Reserve in South Africa, lions and leopards coexist despite strong interference competition, and leopards show no negative responses in abundance or niche displacement (Balme et al. 2017). Similar patterns were observed in the Gir forest in Gujarat, India, where site-specific spatial segregation, combined with differential affinities for habitat, provides the necessary spatial resources for leopards to coexist alongside lions (Chaudhary et al. 2020). On the other hand, numerous studies indicate the negative impact of other large carnivores, leading to a decrease in the abundance of leopards or niche displacement. The negative influence of other carnivores is especially notable in regions of conservation concern for leopard populations. One example of negative carnivore influence on leopards is a decrease in leopard density and their preference for smaller prey species as a response to the rehabilitation of tigers (*Panthera tigris*) in the Chilla Range of Rajaji National Park, India (Harihar et al. 2011). Leopards avoid direct interactions with other large carnivores in temporal, spatial, and spatiotemporal segregation as alternative mechanisms to facilitate coexistence (Karanth et al. 2017, Ramesh et al. 2017). This delicate balance is susceptible to perturbations due to prey depletion (Vinks et al. 2022) and, in specific scenarios, could result in extinction (Volmer et al. 2017).

The synergy of results from different surveys is challenging when the studied system is as complex and variable as intra-guild carnivore influences. Various factors, including anthropogenic pressures, could shift how interspecific interactions influence a species (Lewis et al. 2015). Specifically, there is a notable absence of synergic research on the influence of interspecific interactions of this guild across the distribution range of leopards. We hypothesised that, on a global scale, the influence of other carnivores would exacerbate the reduction of the leopard range. We used species distribution modelling (SDM) with climatic and landscape variables to investigate the ecological niche of the leopard and its niche displacement associated with the predicted occurrence of other carnivore species. We supplemented SDM with likelihood modelling of leopard presence conditional on the predicted presence of the other carnivores. The SDM showed that only two species, the Eurasian lynx (*Lynx lynx*) and the brown bear (*Ursus arctos*), had a negative effect on observing leopards. Surprisingly, the impact of most large carnivores, including the extensively studied species of the African and Asian carnivore guild, was relatively low on leopards, primarily manifesting as niche displacement. Our results highlight the unexpected significance of mesopredators in influencing the presence of leopards. This finding contradicts the conventional expectation that large carnivores act as regulators, restraining mesopredator populations and preventing phenomena like mesopredator release (Ritchie & Johnson 2009, Hoeks et al. 2020, Prugh & Sivy 2020).

Material and Methods

Data collection

We collated a list of carnivores from the families Canidae, Felidae, Hyaenidae and Ursidae whose weight range included or exceeded 15 kg and whose distribution included regions in Afro-Eurasia (Table 1). For each species, we downloaded their distribution ranges from the latest IUCN Red List (IUCN 2022). We considered all species' presence categories (extant, probably extant, possibly extant, possibly extinct, extinct, and presence uncertain) in evaluating whether the carnivore species overlapped with the leopard distribution range. Only species with distribution ranges with non-zero overlap with the leopard range were included in the study (Table 1).

We downloaded the species occurrence data from the Global Biodiversity Information Facility (GBIF). We limited the occurrence data to between 2004 and 2023 and filtered out data with geographical coordinate

Table 1. List of tested potential competitors includes terrestrial carnivores weighing at least 15 kg whose distribution ranges overlap with that of leopards. NA – not applicable.

Family	Species	Range overlap	Reference
Canidae	*Canis adustus*	Yes	GBIF.org (19 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.kehxa4
Canidae	*Canis aureus*	Yes	GBIF.org (19 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.ju8g9t
Canidae	*Canis lupus*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.6ea8bq
Canidae	*Canis mesomelas*	Yes	GBIF.org (19 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.j64mbv
Canidae	*Canis simensis*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.m9xx8m
Canidae	*Cuon alpinus*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.t63axw
Canidae	*Lycaon pictus*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.fcqhf5
Felidae	*Acinonyx jubatus*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.kh88eu
Felidae	*Catopuma temminckii*	Yes	GBIF.org (19 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.uvub7g
Felidae	*Caracal aurata*	Yes	Insufficient number of records
Felidae	*Caracal caracal*	Yes	GBIF.org (18 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.8kzwnb
Felidae	*Felis chaus*	Yes	GBIF.org (19 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.pa99ks
Felidae	*Leptailurus serval*	Yes	GBIF.org (19 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.qwkhcu
Felidae	*Lynx lynx*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.57uj2w
Felidae	*Lynx pardinus*	No	GBIF.org (19 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.eeectd
Felidae	*Neofelis diardi*	No	GBIF.org (18 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.5ypsww
Felidae	*Neofelis nebulosa*	Yes	GBIF.org (18 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.km8w9c
Felidae	*Panthera leo*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.a6fmhh
Felidae	*Panthera pardus*	NA	GBIF.org (15 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.j384jc
Felidae	*Panthera tigris*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.62mtyz
Felidae	*Panthera uncia*	Yes	GBIF.org (18 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.ascqsy
Hyaenidae	*Crocuta crocuta*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.v8av3n
Hyaenidae	*Hyaena hyaena*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.5u76cu
Hyaenidae	*Parahyaena brunnea*	Yes	GBIF.org (19 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.bnv3eu
Ursidae	*Ailuropoda melanoleuca*	Yes	Insufficient number of records
Ursidae	*Helarctos malayanus*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.bxydg6
Ursidae	*Melursus ursinus*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.dq9wfv
Ursidae	*Ursus arctos*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.dysj6u
Ursidae	*Ursus maritimus*	No	GBIF.org (18 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.tteyr2
Ursidae	*Ursus thibetanus*	Yes	GBIF.org (17 August 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.ym97sz

Table 2. Environmental variables used for species distribution modelling.

Variable	Description (units)
Climatic:	
bio01	Annual mean temperature (°C)
bio02	Mean diurnal temperature range (°C)
bio03	Isothermality (bio02/bio07) (× 100)
bio04	Temperature seasonality (SD × 100)
bio05	Max temperature of warmest month (°C)
bio06	Min temperature of coldest month (°C)
bio07	Temperature annual range (bio05-bio06, °C)
bio08	Mean temperature of wettest quarter (°C)
bio09	Mean temperature of driest quarter (°C)
bio10	Mean temperature of warmest quarter (°C)
bio11	Mean temperature of coldest quarter (°C)
bio12	Annual rain (mm)
bio13	Rain in wettest month (mm)
bio14	Rain in driest month (mm)
bio15	Rain seasonality (coefficient of variation)
bio16	Rain in wettest quarter (mm)
bio17	Rain in driest quarter (mm)
bio18	Rain in warmest quarter (mm)
bio19	Rain in coldest quarter (mm)
Landscape:	
Elevation	Elevation above sea level (m)
Cropland	Land proportion used to cultivate food (%)
Anthropogenic	Anthropogenic transformation of biomes (%)
Human.modification	Cumulative human modification of terrestrial ecosystem (%)
Biotic (only for leopard SDM):	
species SDM	SDM prediction for each species (probability)
Carnivora	Sum of SDM predictions of other carnivores (unitless)

errors flagged by the GBIF database. To minimise bias caused by geo-referenced occurrence data in collections, we only used those occurrence points that mapped within the distribution range of the species (including the range where the taxon is now considered extinct by the IUCN, as described above). To be included in the study, a species had to have at least 30 occurrence records after filtering.

We used climatic and landscape variables for species distribution modelling of all considered species (Table 2). We also fitted a second SDM for the leopard that included the calculated biotic variables (see below). We downloaded the climatic data from spatial rasters at 30′ resolution for the bioclimatic variables from WorldClim 2.1 (Fick & Hijmans 2017). We included four landscape variables in the models, i.e. elevation, downloaded from WorldClim, and anthropogenic influence (Ellis et al. 2010, 2014), cropland cover (Ramankutty et al. 2008, 2010) and human modification of the biomes (Kennedy et al. 2019, 2020), downloaded from the Socioeconomic Data and Applications Center (SEDAC) database.

All geographical data were transformed to the WGS 84 projection (EPSG:4326). Climatic data rasters were masked to exclude large freshwater bodies. Using bilinear interpolation, landscape rasters from the SEDAC database were resampled to match climatic data raster geometry.

Species distribution modelling

We used the climatic and landscape variables for SDM for each species based on the GBIF occurrence data.

Data collected in a non-standardised manner, such as those from independent collections and citizen-science initiatives, tend to be regionally clustered. Environmental conditions within these clusters may then be overrepresented in the data. To remove the influence of the clustered occurrence data, we first thinned the downloaded occurrence points within the species range to sample one value per raster cell in the environmental layers. To further reduce the spatial sampling bias caused by clustered occurrence points, we thinned the remaining data points by a minimal distance of 30 km.

Species distribution models require presence-absence data. However, verified absence data are difficult to obtain (Barbet-Massin et al. 2012), so pseudo-absence data generated within the studied region are used instead of the true absence records. Pseudo-absences sample the available environmental space in regions with no occurrence points. We sampled pseudo-absences for each species as random points across Afro-Eurasia. When the thinned occurrence dataset included at least 500 data points, we sampled 3× more pseudo-absences and 4× more pseudo-absences otherwise.

Environmental variables are often correlated, and such relationships between variables influence the results of statistical analyses. Using principal component analysis (PCA; cf. Sau et al. 2023), we removed collinearity among environmental variables by transforming them into orthogonal predictors. We fitted the PCA model using the pseudo-absences data and then used the model to predict the PC loadings for species' occurrence data. We estimated the number of informative PCs to retain based on Velicer's minimum average partial test with Spearman's correlation. The minimum average partial test retains PCs when the variance in the correlation matrix represents systematic variance.

We fitted the SDMs using logistic regression, maximum entropy (Maxent), random forests and boosted tree models. Logistic regression assumes a monotonic relationship between species presence and environmental predictors. The remaining three methods are machine learning algorithms that model variable responses of species occurrence to the predictors, including cases when the response is non-monotonic. The Maxent model aims to achieve a distribution closest to geographical uniformity, maximising entropy (Phillips et al. 2017). Random forests and boosted trees use a collection of regression trees. Random forests create deep decision trees and combine them to reduce variance. Boosted trees iteratively enhance weak decision trees to improve model predictions (Elith et al. 2008).

The machine learning algorithms require tuning of a set of model hyperparameters. We performed hyperparameter tuning for each model using a grid of five combinations of the model hyperparameters, and we evaluated their performance through spatial cross-validation. The training set, comprising 80% of the spatial data points, was used to fit the model, and its performance was assessed on the remaining 20% of the data points. We used the area under the receiver operator characteristic curve as the evaluation criterion (cf. Santika et al. 2019). We then assembled the models with an area under the curve > 0.75 and used the ensemble for the SDM prediction of each species across Afro-Eurasia.

In addition to the SDM with climatic and landscape variables as predictors for leopard SDM, we constructed a further model that also included biotic variables. The biotic variables included SDM predictions from models of those species whose range overlapped with that of the leopard (Table 1) and a variable representing cumulative carnivore pressure at a site. The leopard SDM model that included biotic variables was fitted analogically as described above, with model hyperparameters tuned on a grid of ten combinations. To interpret the model ensemble, we calculated variable importance for each model and ordered PC loadings according to the mean importance of the respective PC to the SDMs.

Carnivore influence on leopard niche

We calculated three different statistics to evaluate the influence of biotic predictors on the leopard SDM. First, we calculated niche overlap and niche similarity. Where x_i is the predicted probability of the leopard SDM with climatic and landscape variables at a raster cell i, and y_i is the analogically predicted probability of the leopard SDM that also included the biotic variables, niche overlap was given as Schoener's $D = 1 - \frac{1}{2}\sum_{i=1}^{n}\left|\frac{x_i}{\sum x} - \frac{y_i}{\sum y}\right|$, and niche similarity was calculated as $I = 1 - \frac{1}{2}\sum_{i=1}^{n}\left(\sqrt{\frac{x_i}{\sum x}} - \sqrt{\frac{y_i}{\sum y}}\right)^2$, where $\sum x = \sum_{i=1}^{n} x_i$ and $\sum y = \sum_{i=1}^{n} y_i$ for all n raster cells. We also calculated the spatially explicit niche displacement as $y_i - x_i$ for all raster cells.

We assessed carnivore influence on leopard niche displacement using both Spearman's ρ and Pearson's r correlation coefficients, correlating leopard spatially

explicit niche displacement with the SDM prediction of each other carnivore. When the absolute value of $\rho > r$ the relationship between the variables was monotonous but not linear.

We compared the ecological niches of the carnivores using hierarchical clustering. We constructed the dendrogram with the unweighted pair group method with arithmetic mean, and we used pairwise niche similarity I values in the form of $1 - I$ as a dissimilarity measure.

Likelihood modelling

We calculated the conditional probability of observing a leopard based on the presence of other carnivores as a function of the probability of their meeting a scaled by the probability of reciprocal extinction rate E as

$$P(l|\mathbf{E},\mathbf{a}) = \sum_{i=1}^{c} \log L_i \qquad \text{equation 1}$$

$$L_i = \begin{cases} e^{-10}, & \text{if } (a_i(1-E_i) - a_i E_{l_i}) \le 0, \\ a_i(1-E_i) - a_i E_{l_i}, & \text{otherwise,} \end{cases}$$

where $\mathbf{E}$ is a matrix of c carnivores that includes the probability of extinction E_i of species i in the presence of leopards l and the probability of leopard extinction E_{l_i} in the presence of species i. For each raster cell, the vector $\mathbf{a}$ of length c is a product of the predicted probability of the leopard SDM including all variables and the probability predicted from the SDM of species i.

To parameterise the model, we calculated the reciprocal probability of extinction of leopards and other carnivores from the overlap of their distribution ranges downloaded from the IUCN Red List (IUCN 2022). The probability of leopard extinction E_{l_i} in the presence of species i is the fraction of their shared range, where leopard range is tagged as extinct and possibly extinct and species i's range is tagged as extant. The probability of extinction of species i, E_i is the fraction of their shared range with the leopard, where the species i is extinct or possibly extinct, and the leopard is extant.

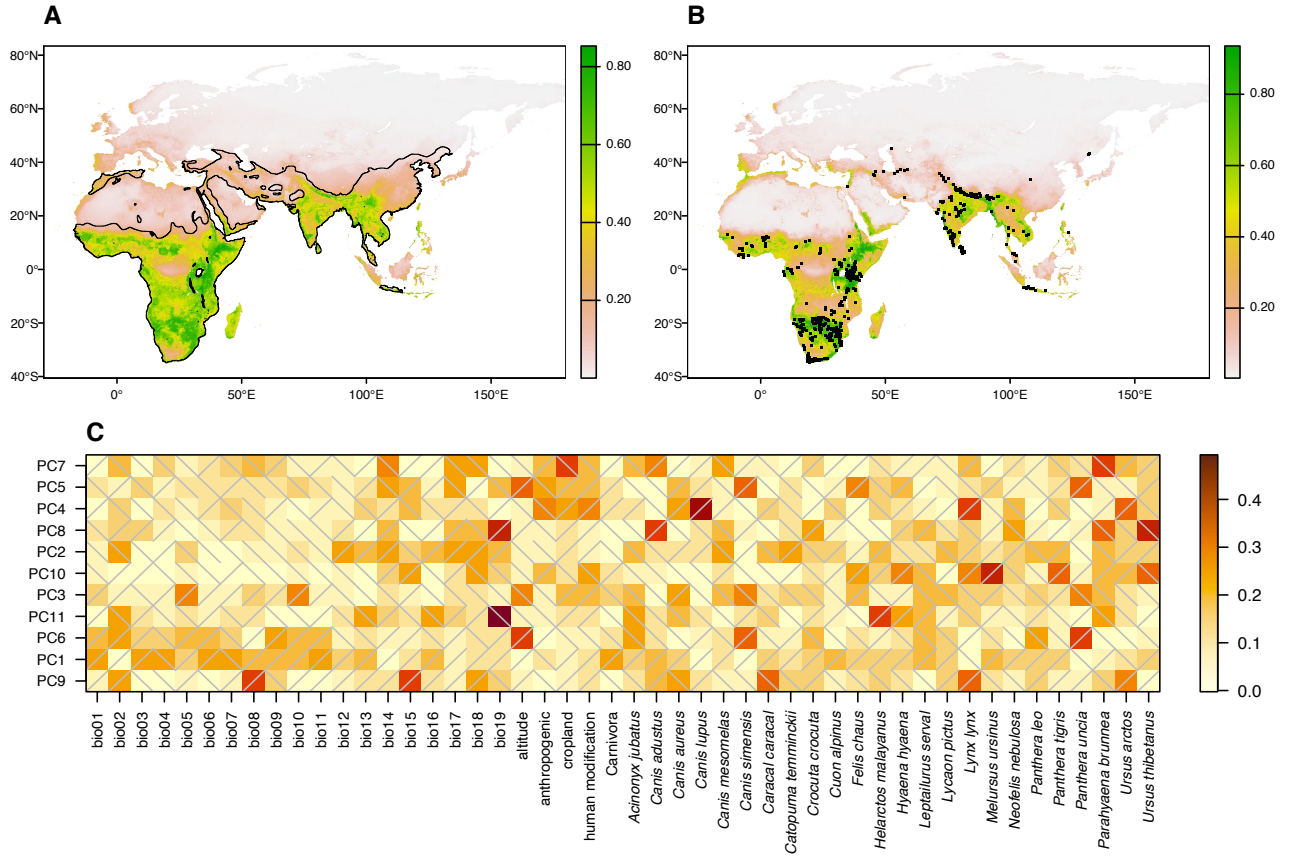

Fig. 1. Leopard niche displacement. (A) Predictions from the leopard species distribution model (SDM), including climatic and landscape variables. The outline indicates the historical leopard range (Stein et al. 2020). (B) Predictions based on a leopard SDM that also includes biotic variables show a global reduction in suitable habitat. Dots represent thinned points of leopard occurrence based on data from the past 20 years. (C) Interpretation of principal components used for leopard SDM. Colour corresponds to the absolute values of principal component loadings of climatic, landscape and biotic variables; grey lines correspond to the sign of the value with increasing slope indicating values ≥ 0 and decreasing slope values < 0. Number of PCs used for the SDM was selected with the Velicer's minimum average partial test. PCs are ordered with respect to their mean importance in the SDMs, the PCs at the bottom being the most important predictors.

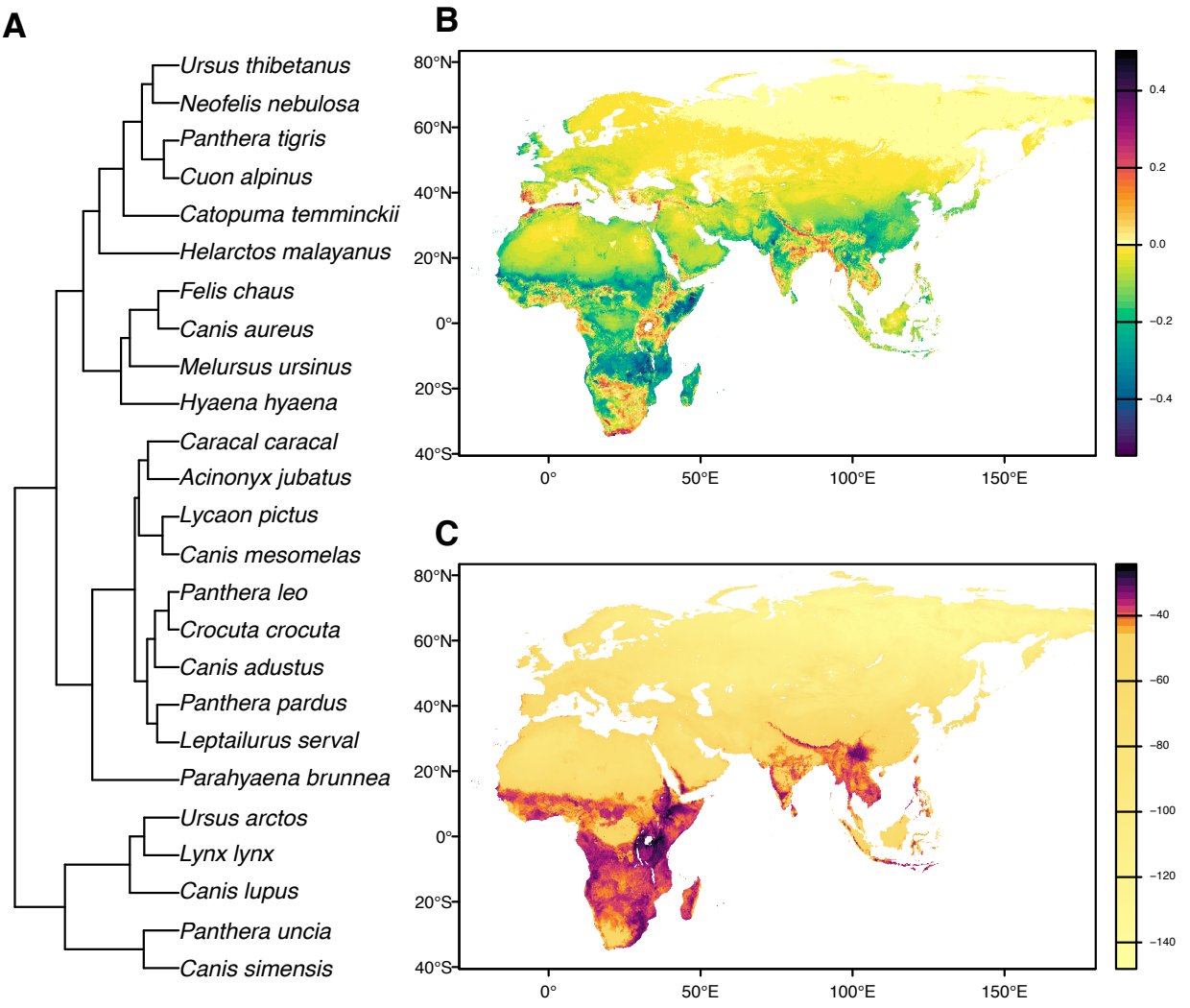

Fig. 2. Spatial and ecological interactions of leopards with the carnivore guild. (A) Unweighted pair group method with arithmetic mean dendrogram of niche dissimilarity 1 − *I* of large and medium-sized terrestrial carnivores. (B) Niche displacement of leopard species distribution model (SDM) when biotic variables were included alongside climatic and landscape variables in the leopard SDM. The colour scheme indicates changes in the predicted probability of presence when comparing a leopard SDM with climatic and landscape predictors only and a leopard SDM that also includes biotic predictors. (C) Conditional probability of observing a leopard based on the presence of other carnivores (Equation 1).

We tested the sensitivity of the likelihood model to parameter values using Morris's elementary effects method. To reduce the parameter hyperspace, we tested reciprocal extinction rates E on a set of 10,000 random points in Afro-Eurasia, for which we fixed the parameters in **a** in equation 1. We tested 48 factors with 15 repetitions of 30 levels across 15 grid jumps. To identify important factors influencing the model, we averaged the means of absolute values of the elementary effects (μ^*) and their standard deviations (σ) across all randomly sampled raster cells.

All analyses were performed in R 4.2.1 (R Core Team 2022) using the packages sf 1.0-14 (Pebesma & Bivand 2023), terra 1.7-41 (Hijmans 2023), tidysdm 0.9.0 (Leonardi et al. 2023a), pastclim 1.2.4.9004 (Leonardi et al. 2023b), EFA.dimensions 0.1.7.7 (O'Connor 2023), and sensitivity 1.28.1 (Iooss et al. 2023).

Results

In this study, we constructed SDMs of large and medium-sized carnivores from the families Canidae, Felidae, Hyaenidae and Ursidae based on their GBIF occurrence records from the last 20 years (Table 1). Using PCA to remove the collinearity of the environmental variables, seven PCs of climatic and landscape variables were sufficiently informative to describe the ecospace for all species, except black-backed jackal (*Canis mesomelas*) and snow leopards (*Panthera uncia*), which utilised six and eight PCs to fit the SDMs, respectively. The leopard SDM based

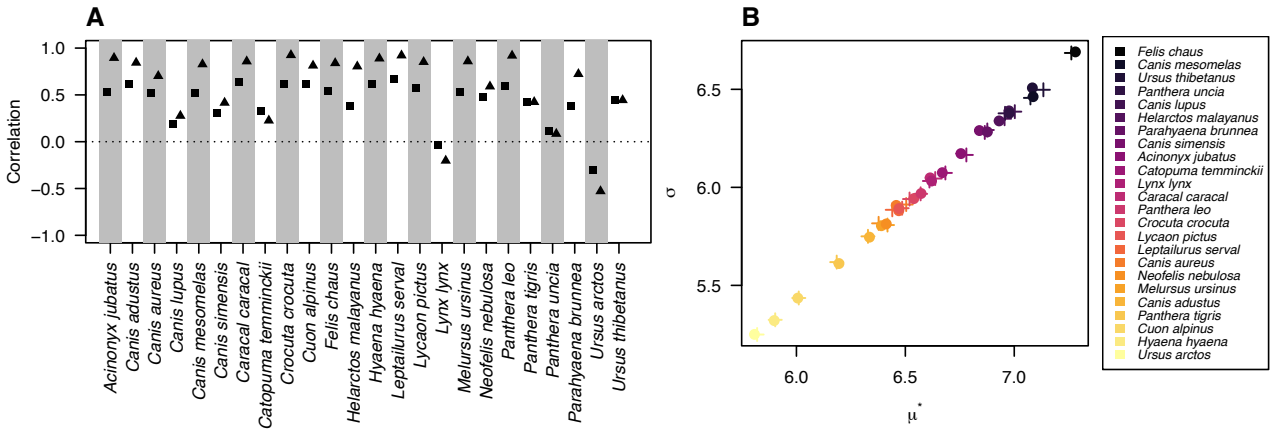

Fig. 3. Carnivore contributions to the likelihood of observing leopards. (A) Pearson´s (squares) and Spearman´s (triangles) correlation between the likelihood of observing leopards given the influence of the presence of other species (Fig. 2) and the leopard SDM predictions. Confidence intervals do not exceed the point symbols due to the large amount of data (df = 1347184). (B) Mean Morris´s elementary effects and their standard deviations based on sensitivity analysis of reciprocal extinction rates on the likelihood model of observing leopards given the influence of other carnivores. The colour scheme indicates paired species extinction rates in the presence of leopards (crosses) and leopard extinction rates in the presence of each species (circles).

on the climatic and landscape variables confirmed that the most suitable ecological niche for the species was located across the region of historical leopard occurrence (Fig. 1A; Stein et al. 2020). To investigate the influence of other large carnivores on leopard niche, we included predictions from the SDM of each target species SDM as covariates in the leopard SDM model (Table 1, Fig. 1B). The most important PCs used as environmental predictors were PC9 and PC1 (relative contribution to the model ensemble prediction: 19.2% and 19.0%, respectively; Fig. 1C). The variables with the highest loadings on PC9 are bio08, bio15, *Caracal caracal*, *L. lynx*, and *U. arctos*, meaning that high values at PC9 describe environment with a rainy season in warm months that is unsuitable for the caracal, but suitable for the Eurasian lynx and the brown bear. The environment characterised by the PC1 ranges from a polar climate at low PC1 values to a tropical climate at high PC1 values. Landscape variables, especially those related to human environmental impact, had low importance (light beige colours in rows corresponding to PC9 and PC1; Fig. 1C).

Species from the African carnivore guild clustered with the leopard based on the pairwise 1 – I dissimilarity measure of their respective SDM predictions (Fig. 2A). The clustering analysis result indicates that the leopard ecological niche is most similar to the niches of serval (*Leptailurus serval*), side-stripped jackal (*Canis adustus*), spotted hyena (*Crocuta crocuta*), and lion (*Panthera leo*).

When we added the SDM predictions of the carnivores to the leopard SDM, the combined effect of climatic, landscape and biotic variables on the leopard SDM shifted its ecological niche (niche overlap: Schoener's $D = 0.80$, niche similarity: $I = 0.96$; Fig. 2B). The spatially explicit niche displacement showed that including the biotic variables in leopard SDM reduced probability of leopard occurrence in the Sudanian savanna, the eastern Somali Peninsula, the Zambesi drainage basin and, to a lesser extent, also in the Iranian plateau up to an area northwest of the Indian subcontinent and in China (Fig. 1A, B, Fig. 2B).

The likelihood of observing a leopard given the presence and interaction of other large carnivores (Equation 1) was highest in the East-African Rift, the northern Indo-Gangetic Plain, and the Sichuan Basin (Fig. 2C). While the likelihood of observing leopards had a positive, non-linear relationship with the probability of co-occurrence with most large carnivores overlapping the leopard's range (Pearson's $r > 0 \wedge$ Spearman's $\rho > r$, $P < 0.001$, df = 1347184; Fig. 3A), there was a negative correlation of likelihood of observing leopards with two species distributed across temperate Eurasia, i.e. the European lynx and the brown bears, but not with wolves (*Canis lupus*) nor snow leopards (Fig. 3A). Sensitivity analysis revealed that the most important reciprocal extinction rates influencing the model outcome were those between leopards and mesopredators, such as the jungle cat (*Felis chaus*), the black-backed jackal, the Asian black bear (*Ursus thibetanus*) and the snow leopard (Morris's elementary effects test: $\mu^* > 7.0$, $\sigma > 6.4$; Fig. 3B).

Discussion

While our models indicate that none of the carnivore species utilised in this study had a decisive negative

impact on the presence of leopards, they also identify mesopredator species, such as the jungle cat and the black-backed jackal, as pivotal for modelling the likelihood of observing leopards. However, it is crucial to emphasise that the extinction rates tested in the present study do not reflect causal relationships and cannot be interpreted as mesopredators driving the extinction or supporting the persistence of leopards. The theory underlying the relationship between leopards (large carnivores) and mesopredators encompasses well-documented ecosystem functions, such as top-down effects that regulate mesopredator populations and abundances. As apex predators, leopards also play a crucial role in preventing mesopredator release (Ritchie & Johnson 2009, Ramesh et al. 2017, Hoeks et al. 2020).

Unlike mesopredators, we found no importance or direct influence of large carnivores on leopard local extinction due to contact between the two species. Reciprocal extinction rates with large carnivores, such as lions, tigers, or brown bears, showed low importance in modelling leopard presence. This finding is despite the results classifying the lion and the spotted hyena as large carnivores with a niche most similar to that of leopards (Fig. 2A). These findings align with the results of Volmer et al. (2017), who indicated that a competitor influencing the decrease in the population of the large felid species could be a smaller carnivore with faster generation growth. To summarise, the importance of the reciprocal extinction rates between leopards and mesopredators primarily highlights the coincidental nature of their historical range changes, emphasising the need for a more nuanced understanding of the ecological dynamics at play.

Studies suggest a similar trend of extinction risk across the carnivore diversity regardless of the species size, and models predict an even higher risk in the future (Cardillo et al. 2004, Rostro-García et al. 2023). None of the species included in our study exerts a decisive impact on leopard extinction rates. Instead, we propose that the concept of Jacobson et al. (2016) and Ripple et al. (2014) that leopards face extinction and suppression due to human-induced disruptions to the ecosystem becomes increasingly relevant. We argue that habitat changes associated with human activities have a lesser impact than direct exploitation of leopards. We included variables characterising human-induced changes to the landscape as predictors for the SDM. Our results indicate that human impact on the environment in the form of cropland cover, biome modification, and anthropogenic influence is of low importance in predicting leopard distribution. While some of the included landscape variables (Table 2) are likely correlated with wildlife exploitation, directly testing the consequences of wildlife exploitation, such as wildlife management, persecution by poachers, and illegal trophy hunting on leopards, requires a large-scale, ideally, global, introspection of legal and illegal hunting activities. Local data on hunting intensity exist (Bogoni et al. 2020, Dobbins et al. 2020, Neumann et al. 2022), but no global data are available at this time (but see indirect data inferred from IUCN assessments in Harfoot et al. 2021). The need for global hunting intensity data becomes particularly apparent with respect to unresolved conflicts between humans and large felids (Inskip & Zimmermann 2009).

We evaluated the displacement of the ecological niche of the leopard with respect to the human-induced landscape modifications and predicted occurrence of the other carnivores. This result follows from the research of Leedham et al. (2023), who show that the climatic niche of leopards remains conservative with small niche displacements between subspecies. Our results expand on the premise of niche displacement between leopard subspecies by evaluating the influence of local carnivore guild on the realised niche of leopards. We demonstrate the dependency of the leopard niche on climatic variables such as mean temperature in the wettest quarter and rain seasonality, which model the leopard niche similarly to its historical range (Fig. 1). We also, and more importantly, show that other carnivores limit the leopard ecological niche across most of the leopard historical range (Fig. 2). Carnivore influence on leopards varies across Afro-Eurasia (Harihar et al. 2011, Balme et al. 2017, Vinks et al. 2022), with the spatial heterogeneity indicating the importance of preserving biodiversity hotspots. As demonstrated in our results (Fig. 2A, B), the shift in the leopard's ecological niche towards biodiversity hotspots lays the foundation for understanding how leopards navigate the intricate balance of interspecific interactions.

While Caro & Stoner (2003) suggest that leopards are one of the most vulnerable species to direct competition over food, Balme et al. (2017, 2020) point out the greater adaptability of leopards to available prey in the face of resource scarcity on the one hand, and specialisation in the case of higher abundance and diversity of prey on the other. Our results indicate that the presence of competitors can also promote leopard persistence in the ecosystem

(Fig. 2C). This contrast underscores the importance of trophic cascade dynamics and the role of large carnivores, like leopards, in shaping prey behaviour and habitat use (Atkins et al. 2019).

Overall, our findings support claims about leopards being able to adapt to different interspecific interactions (Kittle et al. 2017) in terms of shifting their niche along spatial, temporal or trophic axes. The large ecological valence of leopards promotes their potential to share ecospace with other carnivores (Balme et al. 2017, Chaudhary et al. 2020, Rafiq et al. 2020, Vinitpornsawan & Fuller 2020), resulting in mutual coexistence with other large and medium-sized predators in a delicately balanced system that is threatened by anthropogenic pressure and its concomitant impacts.

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Author Contributions

Conceptualisation: N. Martínková, M. Škrobánek; Investigation: M. Škrobánek; Methodology: N. Martínková; Formal Analysis: N. Martínková; Writing – Original Draft: N. Martínková, M. Škrobánek; Writing – Review & Editing: N. Martínková, M. Škrobánek.

Data Availability Statement

The datasets used in the study are listed in Table 1. The R code is available at GitHub at https://github.com/nmartinkova/Leopard-ecoCompetition.

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