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Climate velocity and human pressures shape global range contraction in the leopard

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Understanding the drivers of species range contraction under accelerating global change remains a central challenge in conservation science. Despite its ecological flexibility, the leopard (*Panthera pardus*) has experienced extensive range loss across all nine subspecies. Yet the relative associations of climatic and anthropogenic factors with range contraction remain poorly understood. Here, we integrated global datasets of environmental and human predictors within a unified modelling framework to quantify patterns of historical local extirpation across the species' range. Random Forest models identified climate velocity as the predictor most strongly associated with contraction patterns, followed by landscape modification, livestock density, and forest loss. Subspecies-level analyses revealed pronounced heterogeneity in predictor ranking, indicating that the relative importance of climatic and anthropogenic variables varied among leopard subspecies. Logistic models further indicated that landscape modification and climate velocity were positively associated with contraction probability, whereas forest loss showed a comparatively weaker effect size. These results indicate that both climatic displacement and anthropogenic pressures are strongly associated with global leopard range contraction patterns. Our framework provides a transferable approach for quantifying spatial vulnerability patterns in wide-ranging megafauna under accelerating environmental change.

Keywords Apex carnivore, Anthropogenic pressure, Local extirpation, Macroecology, Human modification, *Panthera pardus*, Spatial modelling

Apex predators are ecologically essential ecosystem components, which also function as flagship and umbrella species whose conservation delivers disproportionate benefits globally. Beyond their well-documented regulatory effects on herbivores and mesopredators, their wide-ranging movements, large area requirements, and strong cultural and symbolic values make apex predators central targets for biodiversity conservation[1–4]. Apex carnivores also exert indirect effects; carcass provisioning supports taxonomically diverse scavenger assemblages[5,6], and fear-mediated shifts in space use reshape herbivore–plant interactions and disturbance regimes, with consequences for nutrient cycling and ecosystem resilience[2,7]. Intentional or unintentional removal of such predators (often termed "trophic downgrading") can precipitate mesopredator release, herbivore irruptions, altered disease dynamics, and simplified food webs[1,8]. These changes increase, and sometimes trigger, ecosystem destabilization and regional biodiversity collapse[1,7,8]. Despite their multifaceted importance, most apex carnivores are threatened by local extirpation or even extinction due to a range of anthropogenic and environmental pressures, which have been rarely quantified integrally across broad biogeographic scales at the global level[2,9].

Among apex predators, the leopard (*Panthera pardus*) stands out for its exceptional ecological versatility as a habitat and diet generalist[10–12]. Its plasticity once supported a vast geographic range believed to have been the

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most expansive of all felids, spanning Africa and large parts of Asia[13]. Yet, leopards have experienced substantial population decline and extirpation, and now occupy less than a quarter of their historical range[13]. Leopards are globally classified as Vulnerable[14,15], underscoring the alarming decline of one of the planet's most broadly distributed apex predators. These declines are thought to have been primarily driven by anthropogenic pressures, including habitat fragmentation, prey depletion, poaching and escalating human-wildlife conflict[3,9,16,17]. Much of their remnant distribution area lies outside protected areas but most research is concentrated within them, creating a management blind spot[18]. Although multiple conservation interventions have been proposed to mitigate leopard declines, the relative relevance of threats driving declines may vary among subspecies and regions because threat regimes differ across the species' geographic range[2,16,17,19]. In the context of accelerating global change and continued range contraction, identifying spatial patterns of vulnerability and prioritizing effective mitigation strategies has become increasingly urgent.

Current conservation frameworks, such as the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, provide indispensable global assessments, and include subspecies-level and regional evaluations for some taxa. However, these assessments are generally conducted at the level of individual taxa or subspecies and may not fully capture intra-specific variation in vulnerability within a unified and spatially representative framework[20]. Subspecies or regional populations may vary widely in the threat regimes they encounter and in their extinction probabilities[21]. As land-use modification intensifies across biomes, apex predators encounter fine-grained mosaics of threat intensity, persecution, and governance that defy uniform treatment[9,22,23]. Meeting this increasing challenge requires the adoption of quantitative, spatially explicit modelling approaches capable of resolving fine-scale variation in extinction drivers while providing measures of uncertainty. This allows to advance beyond categorical classification toward continuous, data-driven, and context-specific risk metrics that can inform decision-making processes[24,25]. Such methodologies can integrate occurrence data, environmental, climatic, and anthropogenic covariates to identify spatial patterns of population decline and evaluate their statistical associations with human and environmental stressors across broad geographic scales.

Within this broader context, although several leopard subspecies have distinct Red List assessments, the global "Vulnerable" listing does not fully capture the substantial variability in extinction risk observed across the leopard's nine subspecies. Subspecies diverge markedly among bioregions because ecological contexts, environmental and anthropogenic pressures vary in intensity and magnitude[12,26,27]. At one extreme, the Arabian leopard (*P. p. nimr*) and Amur leopard (*P. p. orientalis*) face near-imminent extinction with each surviving in small populations (fewer than ~ 200 individuals) in highly fragmented, human-dominated landscapes[28,29]. The Indochinese leopard (*P. p. delacouri*) has undergone one of the most rapid and severe population collapses and is now considered critically endangered across its range[30,31]. In contrast, the African leopard (*P. p. pardus*) and the Indian leopard (*P. p. fusca*) maintain comparatively larger—and in some regions still stable and viable—populations, supported by broader distributions, prey availability, and pockets of effective protection[13,16,17,32]. This heterogeneity in subspecies trends likely emerges from the interaction of evolutionary history, habitat adaptability, governance quality, and the spatial intensity of anthropogenic pressures. Hence, identifying the environmental and anthropogenic predictors associated with differential contraction patterns among subspecies is indispensable for understanding why vulnerability varies across the leopard's range and for designing targeted, context-specific conservation strategies[9,15,21,22,33].

The leopard's wide distribution, ranging from humid tropical forests and dry savannas to alpine zones and arid deserts, has often been assumed to buffer extinction risk[13]. Yet in the Anthropocene, this plasticity can conceal cryptic declines as species persistence increasingly occurs in small, isolated populations in fragmented mosaics of human-modified landscapes[9]. Anthropogenic changes of natural habitats alter prey communities, amplify conflict-driven mortality, and constrain dispersal pathways—fostering demographic isolation and genetic erosion[33–36]. These pressures occur alongside climatic instability, including rising temperature extremes, altered precipitation regimes, more frequent droughts and floods. All these factors can exacerbate physiological stress and degrade habitat suitability across a wide range of ecosystems and biogeographic contexts[10,37–41]. Climate velocity measures the rate at which a species must shift geographically to maintain access to suitable climatic conditions as climate changes, and is increasingly used as an indicator of climatic displacement across landscapes[37,42]. Such climatic changes could also reshape human-leopard interactions and exacerbate conflict arising from shared land use, damage to domestic animals, and rare attacks on humans[43]. Together, habitat transformation and climate change form a dual axis of vulnerability that increasingly constrains the ecological resilience and persistence of leopard populations. Given its ecological versatility, the leopard offers a suitable model species to examine how anthropogenic and climatic stressors may be jointly associated with extinction risk across biogeographic gradients, particularly under accelerating climatic displacement and anthropogenic impacts[9,41].

Recent advances in remote sensing, global human footprint mapping, and climate modelling offer unprecedented opportunities to quantify large-scale correlates of extinction risk at high spatial resolution[44]. Integrating these datasets within statistical or machine-learning frameworks allows modelling of species persistence as a probabilistic function of both anthropogenic and environmental covariates[25,45–47]. When applied to extinction risk assessments, such tools allow quantification of statistical associations between specific pressures (e.g., deforestation rates or infrastructure development) and ecological conditions associated with species persistence. These processes include, but are not limited to, habitat degradation, prey depletion, dispersal limitation, and human-driven landscape transformation across taxa and regions. The key outputs of such modelling efforts are spatially-explicit risk surfaces that can inform management and conservation. Nonetheless, integrative subspecies-level modelling remains exceedingly rare for leopards[19,48], leaving key gaps in our understanding of how risk gradients emerge within this wide-ranging species and where management and conservation actions would yield the greatest benefits. Additionally, identifying the environmental and

anthropogenic factors associated with vulnerability patterns may help inform conservation planning across different socio-ecological contexts.

To address this gap, we integrated spatially-explicit environmental and anthropogenic predictor layers into a unified modelling framework to quantify patterns of historical range contraction for nine leopard subspecies and tested two primary hypotheses. First, we hypothesized that anthropogenic pressures (e.g., landscape modification, forest loss, and human infrastructure) are the dominant predictors of historical extirpation across the leopard's global range. Second, we hypothesized that climatic dynamics, particularly climate velocity, act as additional large-scale spatial correlates of contraction, contributing to spatial heterogeneity in extinction risk across subspecies. Specifically, we evaluated the relative contributions of anthropogenic disturbance and climatic displacement variables associated with observed patterns of local extirpation across the leopard's historical range. We then applied the resulting global model to the contemporary distribution to identify areas where currently occupied habitat exhibits relatively elevated vulnerability based on the spatial associations identified in the historical extirpation analyses. Together, these complementary components allowed us to evaluate: [i] the predictors associated with historical local extirpation across the leopard's range, and [ii] the spatial distribution of relative vulnerability patterns within the extant distribution. By integrating these elements, our work contributes complementary information to classic categorical conservation assessments, such as the IUCN Red List of Threatened Species, providing a spatially-explicit, data-driven framework capable of informing subspecies-specific recovery planning.

Results

Global drivers of historical range contraction

The global Random Forest (RF) permutation-importance analysis revealed clear and hierarchical patterns in predictor importance associated with historical range contraction across the leopard's distribution (Fig. 1). Climate velocity emerged as the most influential predictor, followed by landscape modification, livestock biomass density, and proportional forest loss (Fig. 1). Variables including human impact, climate extremes, built-up area, human biomes, and road density also showed substantial contributions to model accuracy, whereas human population density and the Human Footprint Index exhibited comparatively lower importance values (Fig. 1).

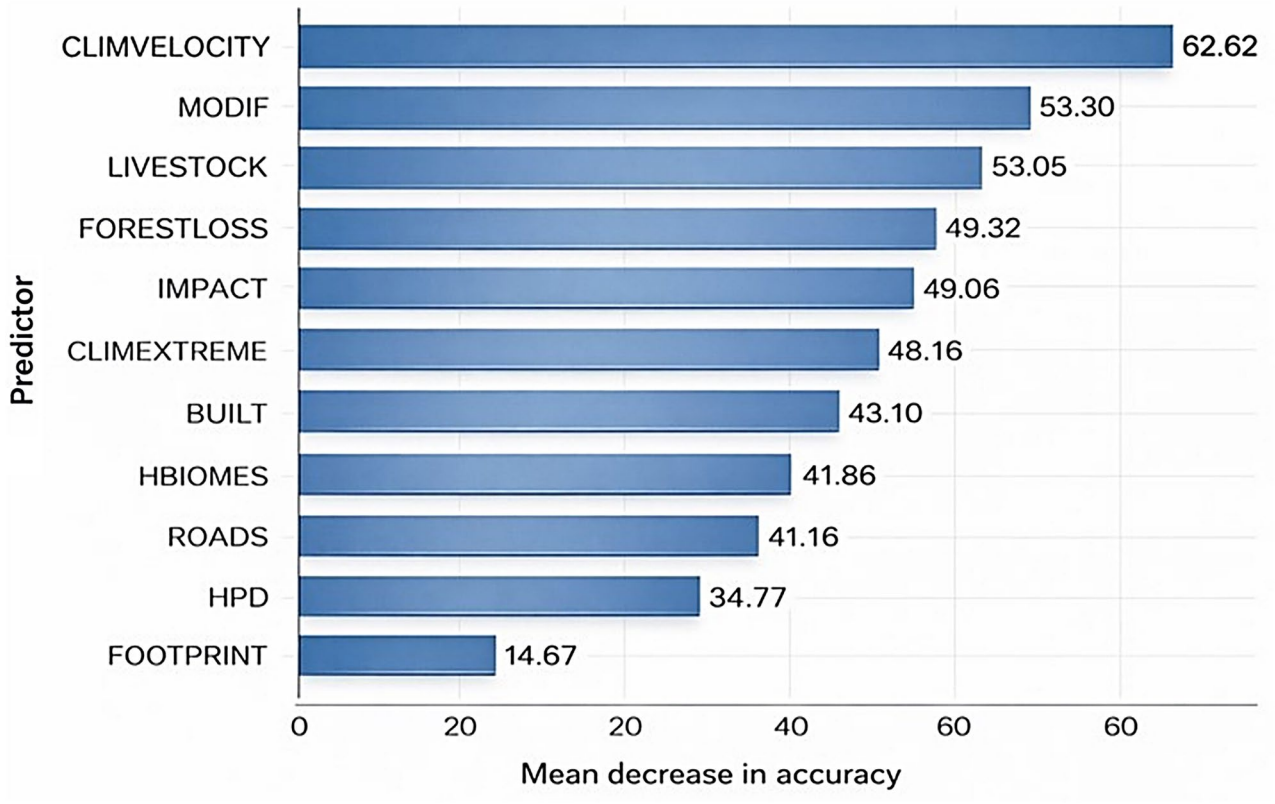


Fig. 1. Random Forest (RF) permutation importance of the predictors of range contraction in leopards (*Panthera pardus*) across their global range. Values represent the mean permutation-importance scores averaged across subspecies-specific Random Forest models. Higher values indicate a greater contribution to model accuracy within the Random Forest framework. Predictor abbreviations are defined as follows: CLIMVELOCITY (climate velocity), MODIF (human modification), LIVESTOCK (livestock biomass density), FORESTLOSS (forest loss), IMPACT (human impact areas), CLIMEXTREM (climate extremes), BUILT (built-up area), HBIOMES (human biomes), ROADS (road density), HPD (human population density), and FOOTPRINT (Human Footprint Index).

Subspecies-level variation in predictor importance

Predictor-ranking patterns varied within the nine leopard subspecies (Fig. 2). For *P. p. pardus*, livestock density, landscape modification, and climate velocity were among the highest-ranked predictors. For *P. p. fusca*, climate velocity, climate extremes, and forest loss ranked highest. In *P. p. nimr*, climate velocity ranked highest, followed by livestock density and climate extremes. For *P. p. orientalis*, livestock density and human impact were among the highest-ranked predictors, with climate velocity also ranking among the leading predictors. In the Javan leopard (*P. p. melas*) and the Sri Lankan leopard (*P. p. kotiya*), no single predictor consistently dominated the ranking patterns across variables. Forest loss and climate velocity ranked highest in the Persian leopard (*P. p. tulliana*), whereas climate velocity and climate extremes ranked highest in the North Chinese leopard (*P. p. japonensis*). Finally, forest loss ranked highest in *P. p. delacouri* among the evaluated predictors (Fig. 2).

Multivariate clustering of subspecies based on predictor importance

Hierarchical clustering of permutation-importance profiles identified broad similarities in multivariate predictor-importance structure among leopard subspecies (Fig. 3). *P. p. pardus*, *P. p. fusca*, and *P. p. tulliana* showed relatively similar predictor-importance profiles, whereas *P. p. kotiya*, *P. p. melas*, *P. p. orientalis*, and *P. p. nimr* exhibited comparatively distinct multivariate configurations. *P. p. delacouri* and *P. p. japonensis* occupied intermediate positions between these broader groupings. These clustering patterns reflect similarity in the relative distribution of predictor-importance values within subspecies-specific Random Forest models rather than shared ecological responses or directly comparable absolute importance magnitudes across subspecies (Fig. 3).

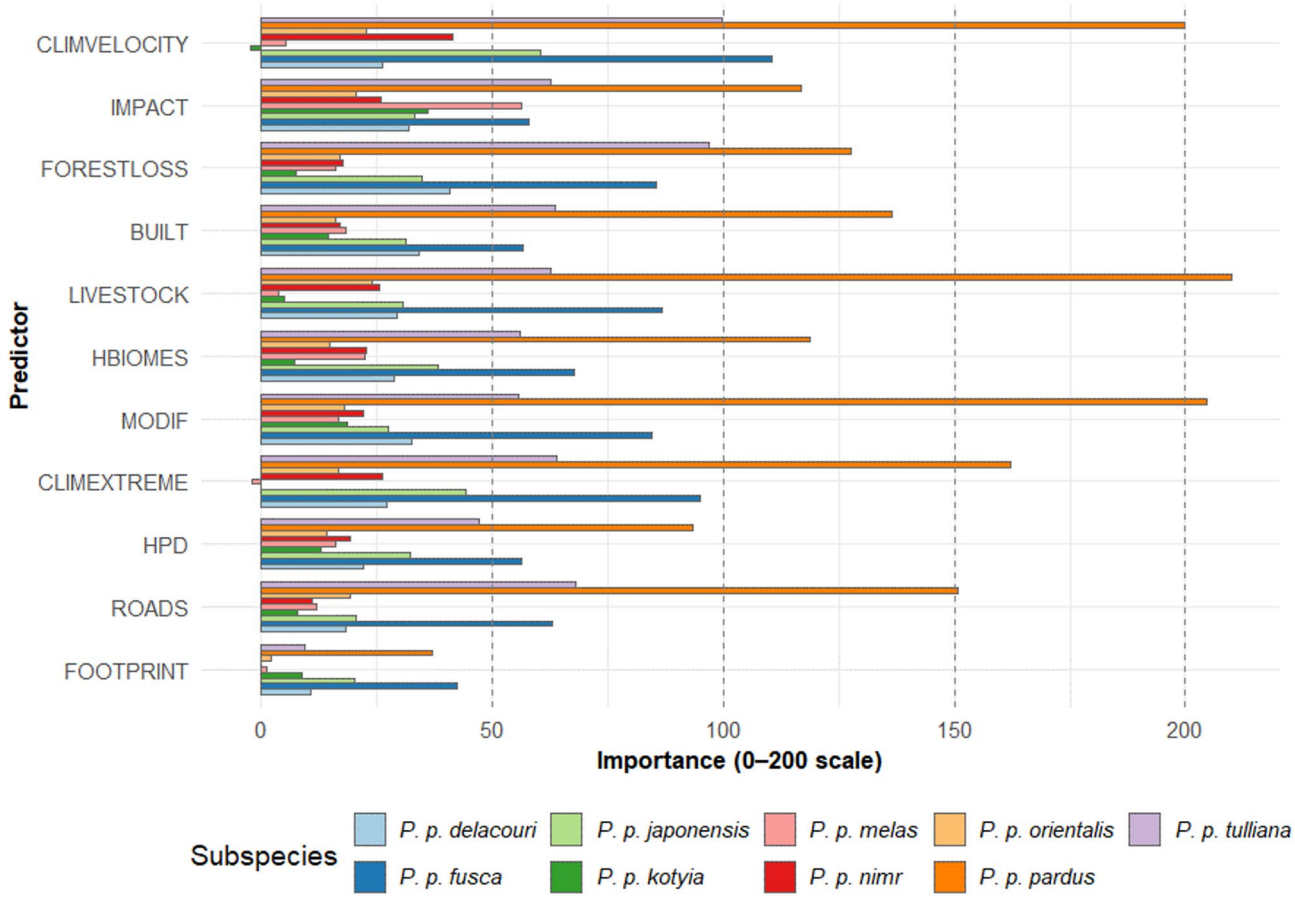


Fig. 2. Subspecies-level Random Forest permutation-importance scores for predictors of leopard range contraction. Each set of colored bars represents a single subspecies, and predictor importance should be interpreted only by comparing variables within the same subspecies (i.e., within each color group), not across subspecies. Bars represent the mean decrease in accuracy (0–200 scale), reflecting the relative contribution of each predictor within each subspecies-specific Random Forest model. Negative values indicate negligible importance and may occur when permutation slightly improves model accuracy. Permutation-importance values are therefore interpreted as relative rankings within models and are not directly comparable in absolute magnitude among subspecies. Predictor abbreviations correspond to those defined in Fig. 1.

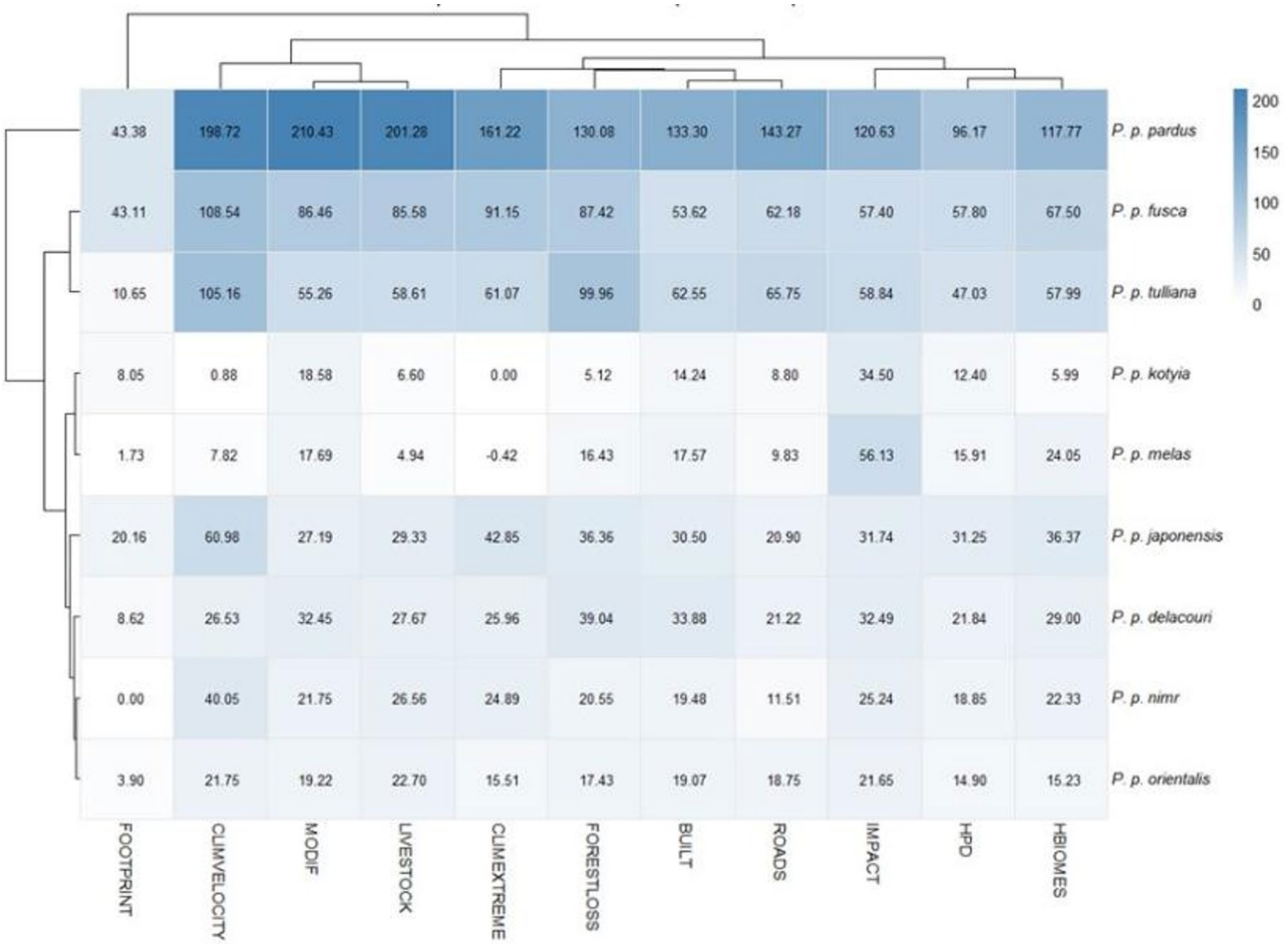


Fig. 3. Heatmap of Random Forest permutation-importance scores across predictors and subspecies. Darker blue tones indicate higher predictor importance. Hierarchical clustering dendrograms illustrate similarity in multivariate importance profiles among subspecies, highlighting grouping structure based on shared ecological response patterns. Predictor abbreviations correspond to those defined in Fig. 1.

Subspecies-specific probabilities of historical local extirpation

The logistic regression model revealed significant variation in modelled local extirpation probability across the nine leopard subspecies (Table 1). Two subspecies showed significantly higher local extirpation probabilities: *P. p. nimr* (odds ratio [OR] = 4.95, $p < 0.001$) and *P. p. orientalis* (OR = 2.55, $p < 0.001$). Five subspecies exhibited significantly lower local extirpation probabilities, with ORs below 1: *P. p. kotiya* (OR = 0.01, $p < 0.001$), *P. p. melas* (OR = 0.10, $p < 0.001$), *P. p. fusca* (OR = 0.05, $p < 0.001$), *P. p. pardus* (OR = 0.16, $p < 0.001$), and *P. p. tulliana* (OR = 0.26, $p < 0.001$). By contrast, *P. p. delacouri* (OR = 0.94, $p = 0.602$) exhibited a non-significant effect relative to the reference category (*P. p. japonensis*), indicating no detectable difference in local extirpation probability. Predictor effects showed several positive statistical associations with local extirpation probability, including landscape modification ($\beta = 0.664$, OR = 1.94, $p < 0.001$), human impact areas ($\beta = 0.191$, OR = 1.21, $p < 0.001$), forest loss ($\beta = 0.184$, OR = 1.20, $p < 0.001$) and climate velocity ($\beta = 0.346$, OR = 1.41, $p < 0.001$). Built-up extent showed a weak positive association ($\beta = 0.081$, OR = 1.08, $p = 0.043$) but did not meet the predefined significance threshold ($p < 0.005$). In contrast, road density, human footprint, and human biomes showed non-significant associations. Several predictors were significantly negatively associated with local extirpation probability, including human population density ($\beta = -0.086$, OR = 0.92, $p < 0.001$), livestock density ($\beta = -0.086$, OR = 0.92, $p < 0.001$) and climate extremes ($\beta = -0.246$, OR = 0.78, $p < 0.001$).

Spatial patterns of current relative vulnerability

Spatially-explicit predictions from the logistic regression model revealed strong geographic heterogeneity in relative vulnerability across the leopard's present distribution (Fig. 4) and among its nine subspecies (Fig. 5). The highest contiguous model-estimated probabilities of local extirpation (red tones) occurred primarily in sub-Saharan Africa, Southwest Asia, and portions of South Asia. In contrast, southern Africa and parts of Southeast Asia were dominated by low-probability zones (blue tones), corresponding to lower model-estimated local extirpation probabilities. Intermediate classes (green to orange) were dispersed across East Africa, the Indian subcontinent, and Indochina, indicating mixed levels of predictor influence within these regions. Our values

Variable	Estimate (β)	SE	Odds ratio (OR)	99.5% CI (lower–upper)	*p*-value	Direction
(Intercept)	2.758	0.08	15.77	13.41–18.55	< 0.001	↑ Positive
Subspecies (*P. p. delacouri*)	−0.061	0.12	0.94	0.75–1.18	0.602	↔ Non-significant
Subspecies (*P. p. fusca*)	−3.037	0.09	0.05	0.04–0.06	< 0.001	↓ Negative
Subspecies (*P. p. japonensis*)	–	–	1	–	–	Reference category
Subspecies (*P. p. kotiya*)	−4.396	0.27	0.01	0.01–0.02	< 0.001	↓ Negative
Subspecies (*P. p. melas*)	−2.343	0.19	0.1	0.07–0.14	< 0.001	↓ Negative
Subspecies (*P. p. nimr*)	1.599	0.19	4.95	3.40–7.19	< 0.001	↑ Positive
Subspecies (*P. p. orientalis*)	0.936	0.24	2.55	1.58–4.12	< 0.001	↑ Positive
Subspecies (*P. p. pardus*)	−1.823	0.08	0.16	0.14–0.19	< 0.001	↓ Negative
Subspecies (*P. p. tulliana*)	−1.353	0.1	0.26	0.21–0.31	< 0.001	↓ Negative
HPD	−0.086	0.03	0.92	0.87–0.96	< 0.001	↓ Negative
BUILT	0.081	0.04	1.08	1.00–1.17	0.043	↔ Non-significant
ROADS	0.059	0.04	1.06	0.99–1.14	0.096	↔ Non-significant
FOOTPRINT	−0.021	0.02	0.98	0.95–1.01	0.163	↔ Non-significant
IMPACT	0.191	0.02	1.21	1.17–1.25	< 0.001	↑ Positive
MODIF	0.664	0.03	1.94	1.85–2.04	< 0.001	↑ Positive
HBIOMES	0.007	0.02	1.01	0.96–1.05	0.754	↔ Non-significant
LIVESTOCK	−0.086	0.02	0.92	0.89–0.94	< 0.001	↓ Negative
FORESTLOSS	0.184	0.01	1.20	1.17–1.23	< 0.001	↑ Positive
CLIMEXTREM	−0.246	0.02	0.78	0.75–0.81	< 0.001	↓ Negative
CLIMVELOCITY	0.346	0.02	1.41	1.36–1.46	< 0.001	↑ Positive

Table 1. Binomial logistic regression model of historical local extirpation probability in leopard subspecies. β, standardized logistic regression coefficient; SE, standard error; OR, odds ratio; CI, confidence interval; p-values indicate significance of predictors in the model. *P. p. japonensis* was used as the reference category for subspecies contrasts. Direction denotes the sign of the effect on local extirpation probability (↑ = higher predictor values associated with increased probability of local extinction; ↓ = higher predictor values associated with decreased probability of local extinction; ↔ = non-significant association).

represent relative vulnerability under current environmental and human conditions and are not forecasts under future conditions.

Discussion

Our findings indicate that global patterns of leopard range contraction are strongly associated with spatial gradients of climatic displacement and anthropogenic transformation. The prominence of climate velocity and climate extremes as important predictors (Fig. 1) suggests that the impact of climatic variables on leopard persistence is so far under-recognized compared to more traditionally recognized anthropogenic pressures, being consistent with patterns reported in other apex predators[41]. Historically, conservation paradigms have emphasized habitat loss, prey depletion, fragmentation, and direct persecution as the principal threats to large carnivores[2,23,49]. Our results do not contradict these drivers but instead indicate that the pace of climatic change (measured as the velocity at which isotherms shift across the landscape) is spatially associated with habitat contraction at the global scale. This interpretation aligns with growing evidence that terrestrial mammals face increasing challenges associated with climate-driven niche displacement and dispersal constraints[38,42,48,50]. Our findings are broadly consistent with Mitchell et al.[48] and recent global analyses linking accelerated climate change with elevated extinction risk in large carnivores[41]. Collectively, these studies suggest that climate change and land-use modification may be associated with ongoing changes in habitat configuration, fragmentation dynamics, and conservation vulnerability. Although Mitchell et al.[48] focused on scenario-based projections for leopard and its subspecies incorporating dispersal assumptions, and while our analyses evaluated historical range contraction using correlative macroecological models, both studies converge in identifying climatic displacement and anthropogenic transformation as important large-scale correlates of leopard vulnerability and persistence. Similar climate-associated range dynamics and fragmentation patterns have also been reported in other felids using scenario-based modelling frameworks that explicitly incorporate dispersal assumptions and projected climatic shifts[51]. Accordingly, conservation strategies based solely on metrics of human pressure without considering potential climatic influences may overlook environmental dynamics that co-occur with anthropogenic stressors across landscapes. Integrating both human modification and climatic velocity into spatial vulnerability assessments may therefore improve spatial prioritization, although we acknowledge that correlative models cannot establish direct causality[37,52,53].

At the subspecies level, Random Forest models revealed a substantial variation in the relative ranking of predictors within subspecies-specific models (Fig. 2). In several subspecies, including *P. p. pardus* and *P. p. fusca*, variables related to human modification, livestock density, forest loss, and climate velocity ranked among the most influential predictors within their respective models, consistent with previous studies describing strong

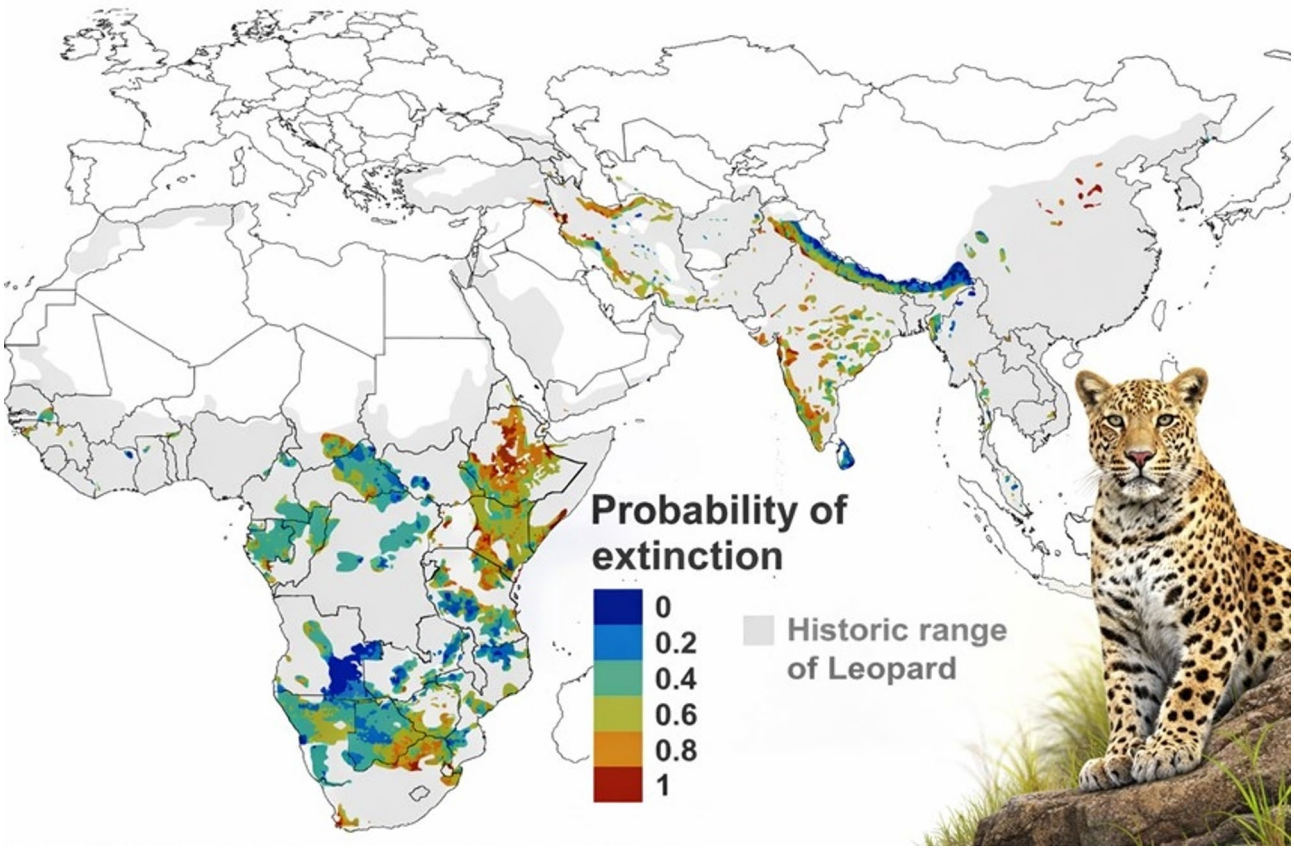


Fig. 4. Modelled relative probability of local extirpation for the leopard (*Panthera pardus*) across its current distribution. Warmer colours indicate higher model-estimated probability of local extirpation, whereas cooler colours indicate lower relative vulnerability. Grey shading represents the historical range of the species. Some subspecies with highly restricted distributions (e.g., *P. p. nimr*, *P. p. melas*, and *P. p. orientalis*) occupy small geographic areas that are difficult to distinguish at this continental scale. Values represent relative vulnerability under current conditions and are not forecasts under future conditions. Map generated using ArcGIS Desktop 10.1 (Esri Inc., Redlands, CA, USA; https://www.esri.com), with the final layout prepared using Adobe Illustrator 30.0 (Adobe Inc., San Jose, CA, USA; https://www.adobe.com/products/illustrator.html).

anthropogenic and climatic pressures across portions of Africa and the Indian subcontinent[10,11]. In contrast, geographically restricted subspecies such as *P. p. kotiya*, *P. p. delacouri*, *P. p. orientalis*, and *P. p. melas* showed comparatively less differentiated predictor-ranking patterns. These patterns may partly reflect differences in geographic extent, environmental heterogeneity, and the spatial structure of anthropogenic and climatic gradients across subspecies ranges. Because permutation-importance values were derived independently within each Random Forest model, these results should be interpreted as relative rankings within subspecies-specific models rather than directly comparable absolute differences among subspecies. Collectively, these findings indicate that leopard subspecies are associated with distinct environmental and anthropogenic contexts across their ranges, which may contribute to differences in observed predictor-ranking patterns[13,22,48].

Clustering analyses identified three groupings of subspecies based on similarity in permutation-importance ranking patterns (Fig. 3). *P. p. pardus*, *P. p. fusca*, and *P. p. tulliana* clustered together and showed relatively stronger ranking patterns for predictors related to human modification, forest loss, and climate velocity within their respective Random Forest models. *P. p. delacouri* and *P. p. nimr* occupied intermediate clustering positions, whereas *P. p. kotiya*, *P. p. melas*, and *P. p. orientalis* formed a separate cluster characterized by comparatively less differentiated predictor-ranking patterns across variables (Fig. 3). This pattern may be associated with differences in spatial exposure and environmental variability across subspecies' ranges, rather than intrinsic biological sensitivity to specific drivers. These results are consistent with broader macroecological patterns in which species embedded in rapidly changing, human-dominated landscapes experience accelerated range contraction[9,47,48].

Operationally, these clustering patterns should not be interpreted as direct conservation-priority rankings. Instead, the clusters reflect differences in how environmental and anthropogenic predictors are represented within subspecies-specific modelling contexts. Subspecies with severely contracted or geographically restricted ranges (e.g., *P. p. melas* and *P. p. orientalis*) may exhibit lower permutation-importance values because limited spatial and environmental variability reduces the detectable influence of large-scale predictors. Consequently, conservation prioritization should integrate model-based sensitivity patterns with subspecies population size, conservation status, and regional management context.

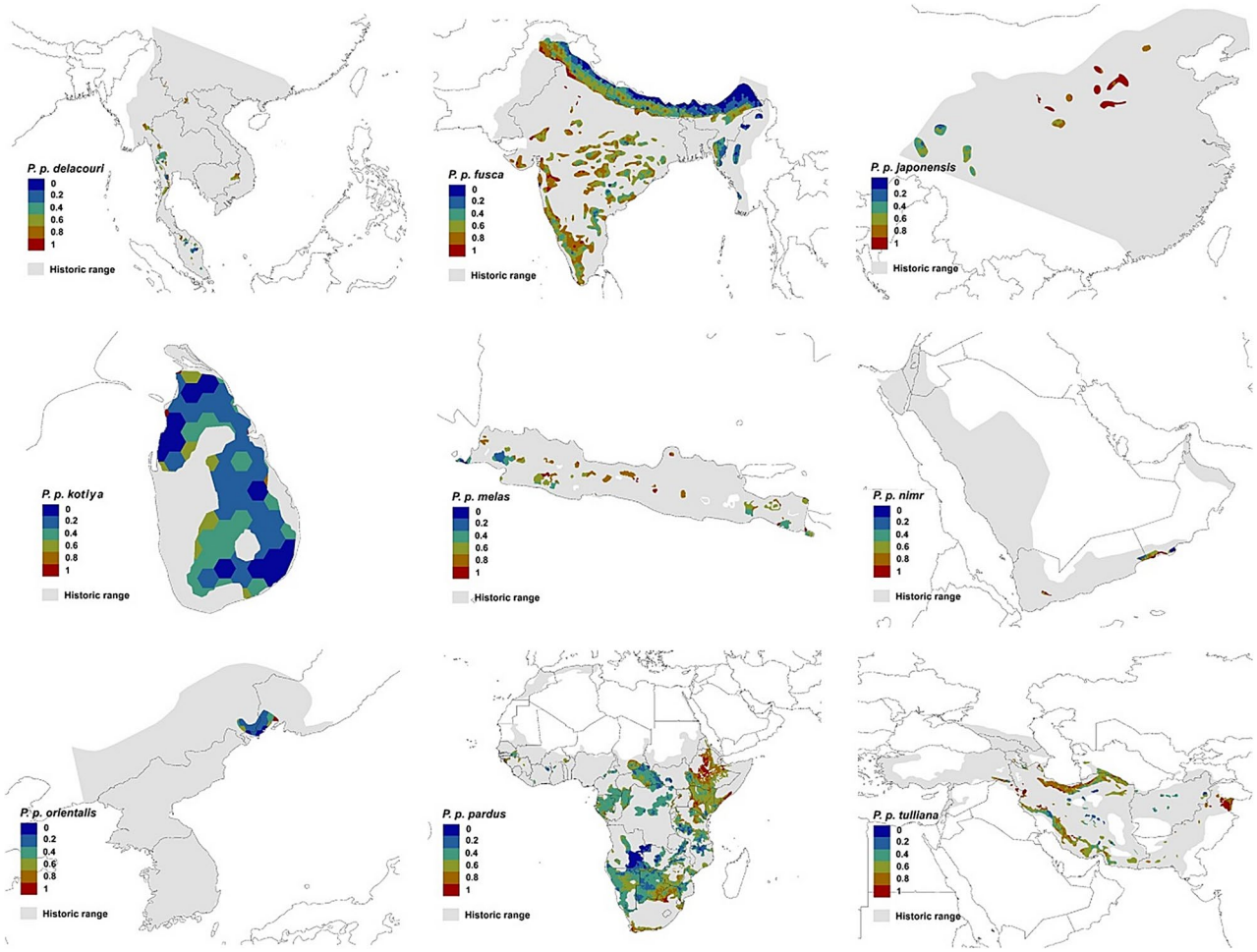


Fig. 5. Model-estimated probability of local extirpation (0–1) for the nine leopard subspecies (*P. p. delacouri*, *P. p. fusca*, *P. p. japonensis*, *P. p. kotiya*, *P. p. melas*, *P. p. nimr*, *P. p. orientalis*, *P. p. pardus*, and P. *p. tulliana*) across their current distributions. Predictions are displayed on a ~ 2500 km^2 equal-area hexagonal grid. Grey shading indicates historical range boundaries. Note that scales are different for each subspecies. Map generated using ArcGIS Desktop 10.1 (Esri Inc., Redlands, CA, USA; https://www.esri.com), with the final layout prepared using Adobe Illustrator 30.0 (Adobe Inc., San Jose, CA, USA; https://www.adobe.com/products/illustrator.html).

Anthropogenic variables such as human modification and forest loss were positively associated with contraction probability (Table 1), indicating a strong statistical relationship between land-use change and contraction patterns. Climate velocity emerged as a strong spatial correlate of historical contraction patterns within the modelling framework, indicating spatial coincidence between rapid climatic displacement and areas of historical range loss. For example, regions experiencing rapid climatic shifts in arid and semi-arid systems often spatially overlap with areas characterized by reduced prey biomass, altered vegetation structure, and increased drought frequency[37,40,47]. These conditions may also increase the spatial overlap among leopards, livestock, and humans, in patterns consistent with changes in carrying capacity and conflict dynamics[37,40,47]. However, these associations are not spatially uniform across all leopard subspecies or regions, and some mountainous or climatically heterogeneous landscapes may exhibit comparatively lower projected contraction patterns. Under this framework, climate velocity can co-occur spatially with anthropogenic stressors (e.g., habitat modification, prey depletion, infrastructure expansion), reinforcing its interpretation as a spatial correlate rather than an independent driver of extinction[37,52,53]. In marginal environments—such as arid regions of sub-Saharan Africa and West Africa, drylands of the Middle East, or cold-temperate systems near the northern distributional limit—climatic displacement co-occurs with already constrained ecological conditions, increasing sensitivity to further environmental change[47,48]. Evidence from other large carnivores indicates that elevated ambient temperatures can reduce reproductive success and limit behavioral compensation under sustained heat stress[54–56]. Although comparable demographic studies are limited for leopards at continental scales, similar mechanisms—particularly reduced recruitment or juvenile survival in small and isolated populations—are consistent with patterns observed in regions experiencing habitat fragmentation and prey depletion. Under this interpretation, climate velocity reflects spatial coincidence with regions experiencing multiple stressors rather than a singular climatic trigger[9,37,47].

Interestingly, livestock density and human population density were inversely correlated with the extinction risk. This pattern should be interpreted as a statistical association rather than evidence of reduced anthropogenic pressure, which likely reflects the persistence of leopards within traditional agro-pastoral mosaics. This is well documented in parts of India and sub-Saharan Africa, where a combination of alternative prey sources and landscape heterogeneity enables leopard survival despite high human and livestock densities[9,16,30,31,57–59]. Rather than indicating stable or intentional coexistence systems, this pattern may indicate opportunistic persistence facilitated by prey subsidies (e.g., livestock in rural landscapes), local tolerance, and patchy habitat cover in human-dominated landscapes. This pattern likely reflects a spatial filtering effect, where leopards persist in heterogeneous human-modified landscapes but are absent from areas that have undergone complete habitat transformation, which may currently exhibit low human population density but no longer support viable leopard populations. Nonetheless, these benefits are transient; chronic climatic stress, infrastructure expansion and human-wildlife conflict may be associated with reduced long-term stability of these coexistence dynamics.

The comparatively weaker influence of climate extremes suggests that persistent spatial climatic displacement, rather than isolated short-term anomalies, may better capture the geographic signature of contraction within this modelling framework. This interpretation is broadly consistent with the literature highlighting the cumulative effects of chronic climatic pressure, climate-associated demographic instability, and reduced behavioral compensation capacity in large carnivore populations[10,37,40,43,47,48,55,56]. However, as historical range contractions span multiple decades but climate velocity reflects more recent climatic trends, these associations should be interpreted cautiously and not as evidence of direct temporal causation. Moreover, subspecies that experienced substantial historical range contractions driven by persecution or overexploitation prior to the satellite era may exhibit weaker associations with contemporary anthropogenic layers, as current spatial covariates may not fully capture legacy pressures that predate modern geospatial datasets. This temporal mismatch may partially contribute to the heterogeneity observed among subspecies-specific importance patterns. Future work should explicitly test fine-scale interactions among climate velocity, habitat modification, human density, livestock and conflict to better resolve synergistic mechanisms underlying range contraction, which cannot be captured by main effects alone.

Three broad conservation implications emerge from this study. First, areas identified by the vulnerability models to exhibit elevated relative vulnerability may warrant increased conservation attention. These areas include portions of Southwest Asia, East Africa, and South Asia (Figs. 4 and 5)[33,53,60,61]. Second, climate velocity emerged as one of the most influential predictors in both the global and several subspecies-specific analyses, indicating a consistent spatial association between climatic displacement and contraction patterns across multiple regions[37,39,42,53,62]. This result suggests that climatic variables may provide important complementary information to anthropogenic indicators when evaluating relative vulnerability patterns within the leopard's extant range[43]. Third, substantial variation in predictor-ranking patterns among subspecies (Figs. 2 and 3) suggests that conservation planning may benefit from incorporating subspecies-specific environmental contexts rather than assuming a uniform threat structure across the species' range[54]. The sensitivity patterns identified here should therefore be interpreted as complementary information rather than a prescriptive prioritization framework.

We acknowledge several methodological limitations of our study. Random Forest models provide measures of variable importance, whereas logistic regression estimates the direction and magnitude of predictor effects (i.e., effect sizes), but both remain correlative and subject to residual multicollinearity despite the variance-inflation screening we used[63–66]. Therefore, these models do not allow direct inference of causal mechanisms. Furthermore, the absence of globally consistent datasets on prey availability, trophic interactions, and predator–prey dynamics limits the explicit incorporation of biological drivers of extinction processes. The use of a 2500 km^2 hexagonal grid balanced computational feasibility and global coverage but may obscure finer processes such as prey dynamics, conflict intensity, or micro-refugia, and may further constrain the detection of variable effects in insular or small-range subspecies, where limited spatial extent and reduced environmental gradients dampen model sensitivity to large-scale drivers. Although this resolution reduces excessive spatial dependence, residual spatial autocorrelation may still be present and should be considered when interpreting model outputs. Additionally, our predictors do not capture temporal dynamics of mitigation efforts or adaptive behaviour, which could moderate contraction trajectories. Furthermore, the modelling framework does not explicitly incorporate interaction terms among predictors, and therefore may not capture synergistic or antagonistic effects between climatic and anthropogenic drivers. Moreover, the temporal mismatch between historical range contractions—often spanning multiple decades—and contemporary environmental layers may further limit inference regarding direct temporal causation. Also, globally consistent, spatially explicit datasets capturing direct persecution, poaching intensity, and retaliatory killing are currently unavailable at the global scale, which may result in these pressures being indirectly captured by correlated anthropogenic predictors such as human modification, road density, and human footprint[9]. Importantly, the spatial predictions presented in Figs. 4 and 5 are derived exclusively from model-based environmental and anthropogenic covariates and do not incorporate demographic parameters such as population size, genetic isolation, or metapopulation connectivity, all of which may substantially exacerbate realized extinction risk. The comparability of absolute permutation-importance magnitudes across subspecies-specific Random Forest models may be limited by differences in sample size, range extent, and environmental heterogeneity. Accordingly, the clustering analyses are intended to compare overall multivariate ranking patterns among subspecies rather than absolute predictor-importance magnitudes directly across models. Future research integrating proxies for persecution/conflict, genomic resilience indices, and socio-ecological variables could refine predictive resolution and management relevance[35,54,67]. Our conservative classification of IUCN distribution categories represented a modelling trade-off between false positives and false negatives. This trade-off should be interpreted as prioritizing high-confidence occupancy, thereby reducing overestimation of occupied range and strengthening the detection of large-scale spatial contraction patterns.

Despite these caveats, our multi-model, spatially-explicit framework constitutes a comprehensive quantitative assessment of potential range contraction for the leopard as a wide-ranging apex carnivore at the global scale.

In conclusion, our study advances a spatially explicit understanding of range contraction potential in leopards under the accelerating constraints of the Anthropocene, offering a framework that can be extended to other apex carnivores. By integrating climate velocity, anthropogenic pressures, and subspecific differentiation, we show that climate velocity represents a strong spatial correlate of global range contraction within the modelling framework applied here, operating alongside established human pressures. These findings suggest that climatic displacement may represent an underappreciated spatial correlate of relative vulnerability patterns in wide-ranging carnivores. These findings suggest that climatic displacement and anthropogenic pressures should be jointly considered when evaluating relative vulnerability patterns across the remaining leopard range. Our findings highlight the importance of incorporating both climatic and anthropogenic correlates into spatial assessments of vulnerability in wide-ranging carnivores.

Materials and methods

Data compilation and pre-processing

To investigate the global predictors of range contraction in the leopard, we compiled a spatially-explicit database integrating IUCN-based historical and current distribution data for all nine extant subspecies (Indochinese, Indian, North Chinese, Sri Lankan, Javan, Arabian, Amur, African, and Persian), with all datasets standardized to a common spatial resolution, coordinate system, and spatial extent. Range contraction was operationalized as local extirpation (1) versus persistence (0) at the grid-cell level. We obtained historical and present-day range maps from the IUCN[14], which provides expert-reviewed, georeferenced estimates of subspecies distribution boundaries. In this study, "historical" refers to the IUCN-based baseline distribution representing cumulative range contraction over recent decades, rather than a uniformly defined historical time interval across all subspecies and regions.

We projected all environmental and anthropogenic predictor layers into a global equal-area hexagonal grid (~2500 km^2 per cell) to minimize spatial distortion and ensure balanced sampling across biogeographic regions[14,68]. We selected a 2500 km^2 hexagonal resolution to balance global computational feasibility with ecological interpretability while limiting excessive spatial autocorrelation that may arise at finer resolutions. Range map data represent the extent of occurrence rather than true occupancy and may therefore overestimate species presence at fine spatial resolutions[69,70]. However, at coarse spatial grains (e.g., ≥ 100 × 100 km), patterns derived from range maps tend to converge with those obtained from point-locality data, providing reliable representations of large-scale biodiversity gradients[70,71].

The leopard status was classified at the hexagon level as persistent (0) or historically extirpated (1) based on IUCN occurrence categories. Only cells overlapping historical polygons classified as Extant (category 1) were treated as confirmed persistence. All other categories—Probably Extant (2), Possibly Extant (3), Possibly Extinct (4), Extinct (5), and Presence Uncertain (6)—were conservatively coded as historical local extirpation to minimize false-positive classification of persistence across large-scale spatial analyses, including areas containing reintroduced populations and regions with uncertain occupancy status (e.g., Russian North Caucasus). While this approach may increase false-negative classifications by excluding areas with uncertain or low-confidence presence, it ensures that cells classified as persistent represent high-confidence occupancy, thereby improving the robustness of detected spatial patterns in a global macroecological framework. Subspecies-specific sample sizes ranged from 101 to 23,724 grid cells, with "historically extirpated" cells representing approximately 58% to 98% of observations across subspecies (see Supplementary Table S1). We took subspecies boundaries directly from the IUCN taxonomic shapefiles and used them without modification to avoid subjective delineation. We overlaid predictor layers onto the hexagonal grid to extract mean values per cell, producing a standardized dataset for modelling extirpation probability.

Selection and standardization of predictor variables

We selected 11 continuous predictors describing multidimensional anthropogenic and climatic pressures following integrative extinction-risk frameworks[9,72]. We obtained all raster layers from Branco et al.[44], who standardized global datasets into a unified ~ 1-km resolution grid through consistent reprojection, resampling, and masking of non-terrestrial areas. Anthropogenic predictors included: (1) human population density (HPD) from the Global Human Settlement Layer, expressed as inhabitants per km^2[73]; (2) built-up area (BUILT) derived from Landsat-based global surface classifications[74]; (3) road density (ROADS) from the Global Roads Inventory Project[75], expressed as total road length per km^2; (4) the Human Footprint Index (FOOTPRINT), a composite measure integrating population density, land use, infrastructure, and energy proxies[76]; (5) Impact Areas (IMPACT), mapping low- and high-impact terrestrial zones from infrastructure and land-use overlap[77]; (6) Human Modification Areas (MODIF), a cumulative index integrating 13 anthropogenic stressors, including settlement, agriculture, transportation, mining, and energy infrastructure[78]; (7) Human Biomes (HBIOMES), representing the degree of human transformation of the terrestrial biosphere through activities such as agriculture, urban development, forestry, and other land uses[79]; (8) livestock biomass density (LIVESTOCK) from FAO datasets[80], expressed as head-equivalent biomass per km^2 across cattle, sheep, goats, pigs, and poultry; and (9) forest loss (FORESTLOSS) representing proportional forest cover loss between 2007 and 2017 derived from ALOS PALSAR L-band SAR mosaics, using region-specific backscatter thresholds to consistently detect forest canopy change at the global scale[81]. This layer was included as a spatial indicator of habitat transformation.

Climatic predictors were: (10) climate extremes (CLIMEXTREM) from the CRU TS dataset[82], defined as the largest absolute trend in mean monthly minimum or maximum temperature (°C per decade); and (11) climate velocity (CLIMVELOCITY), calculated as the ratio between temporal temperature trends derived from MODIS-based land surface temperature data (2000–2020) and the local spatial gradient of mean annual

temperature[83], expressed in km per decade and representing the displacement required for organisms to track their climatic niche. Although IMPACT, MODIF, and FOOTPRINT all quantify anthropogenic pressure, they represent different dimensions and spatial formulations of human influence—including direct infrastructure overlap, cumulative landscape modification, and broader composite measures of human pressure—and were therefore evaluated separately.

To evaluate potential multicollinearity, we assessed variance inflation factors (VIFs) for all predictors. All variables fell below the predefined threshold (VIF < 5), indicating moderate but acceptable levels of multicollinearity (Supplementary Table S3), consistent with widely used thresholds in ecological modelling frameworks[65]. The categorical factor representing subspecies identity exhibited comparatively higher VIF values, which is expected given its association with geographic and environmental gradients, but remained within acceptable limits. We standardized all variables using z-scores to improve numerical stability, facilitate model convergence, and enable direct comparison of effect sizes across variables with different units and scales[84,85]. All predictor variables, definitions, units, and data sources are summarized in Supplementary Table S2.

Modelling framework for global and subspecies-specific historical probability of extirpation risk

We implemented a dual-modelling framework combining generalized linear models (GLMs) and Random Forest (RF) classifiers to quantify both linear and nonlinear drivers of leopard range contraction. Within this framework, the global GLM and subspecies-level RF analyses served complementary but distinct purposes. The GLM was used to estimate broad-scale statistical associations and estimate the direction and magnitude of predictor effects across the extant distribution, whereas RF models were used to evaluate nonlinear relationships and relative predictor importance within subspecies-specific datasets. We used RF models to capture complex interactions and high-order nonlinearities that cannot be accommodated by parametric GLMs[63,64].

At the global scale, we fitted a binomial GLM using glmmTMB[86], modelling historical local extirpation (1 = extirpation, 0 = persistent) as a function of all standardized predictors, with subspecies identity included as an additive fixed effect to account for baseline differences among subspecies, using treatment contrasts (*P. p. japonensis* as the reference category). A single global model including all predictors was retained to estimate independent associations while controlling for potential confounding effects of anthropogenic and climatic variables. In contrast, RF models were used to detect nonlinear relationships and assess relative predictor importance, but were not used for spatial projection due to their limited interpretability and well-documented instability when extrapolating beyond the environmental domain represented in the training data. We did not include higher-order (e.g., quadratic) terms in the GLM to maintain model parsimony, particularly given the large number of covariates included in the model[65]. We assessed multicollinearity adopting VIF < 5 as a threshold for acceptable collinearity[65,87].

We extracted regression coefficients, odds ratios (OR), 99.5% confidence intervals, and Tjur's R^2, and evaluated statistical significance using a conservative threshold of $p < 0.005$[88]. We conducted model diagnostics using DHARMa, which employs simulation-based standardized residuals to assess model fit through the tests of dispersion, residual uniformity, and outliers, complemented by graphical diagnostics. Diagnostic tests did not detect significant overdispersion, deviation from residual uniformity, or outliers, indicating adequate model fit. At the subspecies scale, we fitted RF classifiers using the R randomForest package with 1,000 trees and default hyperparameters (mtry = $\sqrt{p}$, nodesize = 1). Models were fitted using extinction status (1/0) as the response variable. Default settings were used to ensure consistency and comparability of variable importance estimates across subspecies[64,89].

We quantified predictor importance using permutation importance, which measures a variable's contribution by calculating the decrease in model performance when the values of that variable are randomly permuted, thereby disrupting its relationship with the response (mean decrease in accuracy[63,90]). Permutation importance reflects relative influence on predictive accuracy rather than direct causal contribution. Because permutation-based accuracy reduction is expressed in raw accuracy units (which typically range from 0 to 200 under moderate class imbalance[66]), we report unnormalized scores. We assessed model performance using out-of-bag (OOB) accuracy. Permutation-importance values were calculated independently for each subspecies-specific RF model. These values were used to characterize within-subspecies variation in predictor importance (Fig. 2). To obtain a global estimate of predictor importance (Fig. 1), we averaged permutation-importance values across all subspecies-specific models. Because permutation-importance values are derived independently within each subspecies-specific model, they were interpreted as relative rankings within models rather than directly comparable absolute values among subspecies. Subspecies-specific sample sizes (number of hexagonal grid cells per subspecies), class balance information ("persistent" vs. "historically extirpated" cells), and out-of-bag performance metrics are reported in Supplementary Table S1. We visualized importance patterns using bar plots and heatmaps (*ggplot2*, *pheatmap*). To further summarize similarities among subspecies, we performed hierarchical clustering based on permutation-importance values. RF models do not explicitly account for spatial autocorrelation unless spatial predictors are included. Residual spatial autocorrelation may still be present in the data and could influence model performance and variable importance estimates.

Spatial estimation of current relative vulnerability

We estimated relative vulnerability across the extant distribution of each leopard subspecies by applying the fitted global binomial GLM to hexagons classified as currently occupied (range-actual = 1; corresponding to cells defined as "persistent"). This classification ensures that predictions are restricted to areas of confirmed present-day occupancy. Instead, predicted probabilities were obtained using the parameter estimates (β coefficients) from the previously fitted global model and applying them to the standardized predictor values of currently occupied hexagons. The model incorporated all uncorrelated anthropogenic and climatic predictors as fixed

effects and included subspecies identity as an additive fixed effect to account for baseline differences among subspecies. We generated extirpation probabilities for each occupied hexagon and expressed them on the response scale as continuous values from 0 to 1. We quantified model-based uncertainty using frequentist 99.5% confidence intervals derived from parameter standard errors. Predictions are based exclusively on environmental and anthropogenic covariates and do not incorporate demographic processes such as population size, genetic structure, dispersal limitation, or prey availability. We performed all spatial pre-processing and analyses in R version 4.3.1 (R Core Team, 2024) using the packages *tidyverse*[91], *dplyr*[92], *glmmTMB*[86], raster[93], *sf*[94], and *terra*[95].

Data availability

All data used in this study are publicly available from the IUCN Red List (https://www.iucnredlist.org) and the SPECTRE database. Processed data and code will be made available upon request.

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Declarations

Competing interests
The authors declare no competing interests.

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