Department of
BIOLOGY

A17753S1 PROJECT DISSERTATION

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Title	A leopard cannot change his spots, but he's less picky about prey: Ignoring prey when modelling predators jeopardises estimates of future biodiversity.
Word Count	6896

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Abstract

Scientists have invented many types of biodiversity models to predict trends that aid in reversing biodiversity loss. Species Distribution Models (SDMs) are a diverse category of biodiversity models widely used in conservation that use climate data as the main predictor of species' occurrence. But a plethora of biotic and abiotic factors determine the ranges and abundances of species in nature. One biotic interaction of particular importance to carnivore range and abundance, as well as all species, is predator-prey relationships. But a lack of global data stifles the accurate incorporation of predator-prey relationships into SDMs. Given the limited use of ecological theory in these climate-centric, statistical biodiversity models, this begs the question, how much does this limit the predictions they make? To gauge the magnitude of this problem, I used a globally applicable biodiversity model, Glob2Loc, to test the limitations of using climate data and ignoring predator-prey relationships when modelling leopards in India. I used this case study system because while leopards are of conservational concern globally, they are reportedly adapting to urban and agricultural areas in India by changing their diets and consuming both wild and domestic prey, apparently leading to population stabilisation. First, I modelled three scenarios of leopard range and abundance, each with different assumptions on predator-prey relationships. The first scenario just accounted for climate data. The intermediate scenario matched observations most accurately by assuming leopards consume wild and domestic prey and exist in undisturbed and modified habitats to a lesser extent. The final minimum scenario echoed standard practice because it obeyed IUCN habitat classifications and removed leopards from modified habitats in their climatic range, but also constrained leopards to only coexist alongside wild prey. Next, I compared each scenario to recent field data to decide which best reflected current observations on leopard range and abundance and identify key limitations in Glob2Loc (validate). Then, I followed each scenario into 2050, assessed their differences, and reported how far standard predictions contradicted the more realistic intermediate scenario. To identify locations to which leopards may be drawn, I also mapped prey biomass across India using top prey species reported in the literature. I found my intermediate scenario, which realistically represented predator-prey relationships, best reflected current observations of leopard range. Meanwhile, my minimum scenario, which reflected a standard approach to modelling, underpredicted habitat area by two-fold. I also found that Glob2loc failed to capture leopard presence in several areas of northern central India despite leopard observations in the literature and high prey biomass in these regions. However, I also found that field measurements of abundance were flawed, which made validating Glob2Loc more challenging. Therefore, it is important to compare predator ranges to prey ranges and validate model results using field measurements to link discrepancies to the exclusion of biotic interactions. Furthermore, these results imply that considering maximum to minimum scenarios in biodiversity models can help quantify recovery potential or loss if human tolerance to wildlife increases or worsens.

Introduction

The suite of services that biodiversity provides to humanity - from enjoyable green spaces to climate regulation and food provision - are under threat because of destructive human activities (IPBES, 2019; Díaz, et al., 2019). Humanity has led one million species to the brink of extinction and cleared half the world's habitable land for agriculture (IPBES, 2019; Ellis, et al., 2010). The scale of humanity's impact on the planet is vast, and so measures have been taken to save it. To meet regional, national, and international targets for biodiversity, it is paramount that governments and industries prioritise the most effective action, and identifying such priorities can be supported by biodiversity models (Nicholson, et al., 2019).

The term 'biodiversity model' encompasses a vast range of mathematical and computational methods that either fill in gaps in biological databases (e.g., species interactions) or estimate changes to elements of biodiversity upon future or past global change (Pollock, et al., 2020). An important type of biodiversity model often used in conservation are statistical models that correlate field observations on elements of biodiversity with environmental variables to make spatially explicit predictions about future change (Guisan, et al., 2013). My research focussed on the global application of these statistical biodiversity models, where the range and abundance of thousands of species are modelled alongside land cover dynamics. These models make inferences about the global state of biodiversity and aid in assessing progress towards targets such as the Global Biodiversity Framework (Nicholson, et al., 2019).

The first step in projecting species distributions in biodiversity models is often climate centric. Climate can be easily quantified in multiple dimensions (temperature, precipitation, humidity across various scales in time and space) and is undoubtedly important in dictating where species can persist, especially if the planet exceeds 1.5°C of warming since pre-industrial times (Howard, et al., 2020). However, land-use change is currently the greatest threat to biodiversity, not climate change (Jaureguiberry, et al., 2022). Therefore, land use largely dictates where different species can be found, based on how tolerable they find modified habitats. And biotic interactions determine if species persist or not after habitat modification; if there are suitable prey or anthropogenic resources to which a species can adapt in the new landscape, then species may be able to survive (Santini, et al., 2019).

However, accounting for biotic interactions in global biodiversity models is difficult because it requires a lot of data that isn't available yet. Efforts to include biotic interactions are further complicated by unpredictable invasive alien species and that biotic interactions can change in space and time depending on climate (Srivastava, et al., 2019; HilleRisLambers, et al., 2013). Nevertheless, where it has been possible to include biotic interactions, predictive power is often significantly increased (Zhang, et al., 2022; Van der

Putten, et al., 2010; Wisz, et al., 2013). A common way to approximate biotic interactions in large biodiversity models is to clip species' initial purely climatic maximum ranges so species remain in the same ecoregions and elevations that the IUCN classifies as suitable after climate-induced range shifts (Glob2Loc; Leclère, et al., 2020; Schipper, et al., 2020). This aims to keep interacting species together. But is a *post hoc* consideration of biotic interactions enough?

To investigate the limitations of not considering biotic interactions in globally applicable biodiversity models, I quantified the differences in estimated range and abundance of a predator when accounting for prey or not, using an established biodiversity model (See section 'What is Glob2Loc?'). After a scoping review, I decided to use leopards in India as a case study system because they are recently increasing their tolerance to human-use landscapes based on adapting their prey base. They are changing their diet to include resources readily available in human-use landscapes such as dogs, cats, rodents, and livestock as well as wild prey (Athreya, et al., 2016; Prasad & Tiwari, 2009). Biodiversity models use IUCN habitat classifications to define landscapes in which species can exist, but the IUCN does not (yet) capture leopards' use of human-dominated landscapes by adapting their diet in India (Stein, et al., 2020). This creates a disconnect between on-the-ground evidence and evidence used in modelling studies.

My research question was: "What are the limitations of current approaches to biodiversity modelling given that they don't account for predator-prey relationships?". I predicted that accounting for the distributions of leopard prey (both wild and domestic), and the resultant tolerance of leopards for habitat modification, will reflect their current range and abundance better than standard, climate-centric modelling approaches and also provide a more robust prediction of their future status.

What is Glob2Loc?

Glob2Loc (**Glob**al **to Loc**al) is a biodiversity model developed by Dr. Mike Clark at the University of Oxford in collaboration with end-users in industry and non-governmental organisations. Its broad aim is to predict global biodiversity trends to identify local conservation priorities for over 20,000 terrestrial vertebrates (Figure 1).

First, it computes an ensemble of species distribution models (SDMs) accounting for climate, dispersal rate, and vegetation cover preferences to predict the maximum climate-suitable habitat per species in the future. Then, it considers how four major anthropogenic stressors (climate change, agricultural expansion, intensification, and urban expansion) will change spatially in the future based on human activity and feedbacks between the stressors. Finally, it integrates these trends with information on species tolerance to each anthropogenic stressor using data from the IUCN to remove any unsuitable habitats from the SDM predictions. This enables the prediction of future ranges for each species (biodiversity trends).

Once Glob2Loc has identified suitable habitats, it makes spatially explicit estimates of abundance across each species' habitat range. To predict abundance in unmodified habitat, observations from global databases on population density are run through a mixed effect generalised linear model with predictor variables of life history traits, Net Primary Productivity, and climate. For species that can exist in human-use landscapes (high and low-intensity cropland and pastureland), abundance from natural habitat is multiplied by a coefficient that reflects species' tolerance to that landscape based on field observations. The final output is population density per cell (2.25 km^2) for different species' habitat ranges, which can be summed up across landscapes to calculate abundance.

Glob2Loc has great flexibility in its underlying structure, which allows for more fine-scale analyses of the future of biodiversity in certain locations, the contribution of each stressor and specific species. Glob2Loc can also reproduce estimates of current range and abundance, which meant I could validate evidence in the literature with modelled scenarios based on no or various different assumptions about prey distributions (Figure 1: 'Validate'). Therefore, it is a suitable tool with which to answer my research question.

Figure 1: The Inputs and Outputs of the Biodiversity Model, Glob2Loc

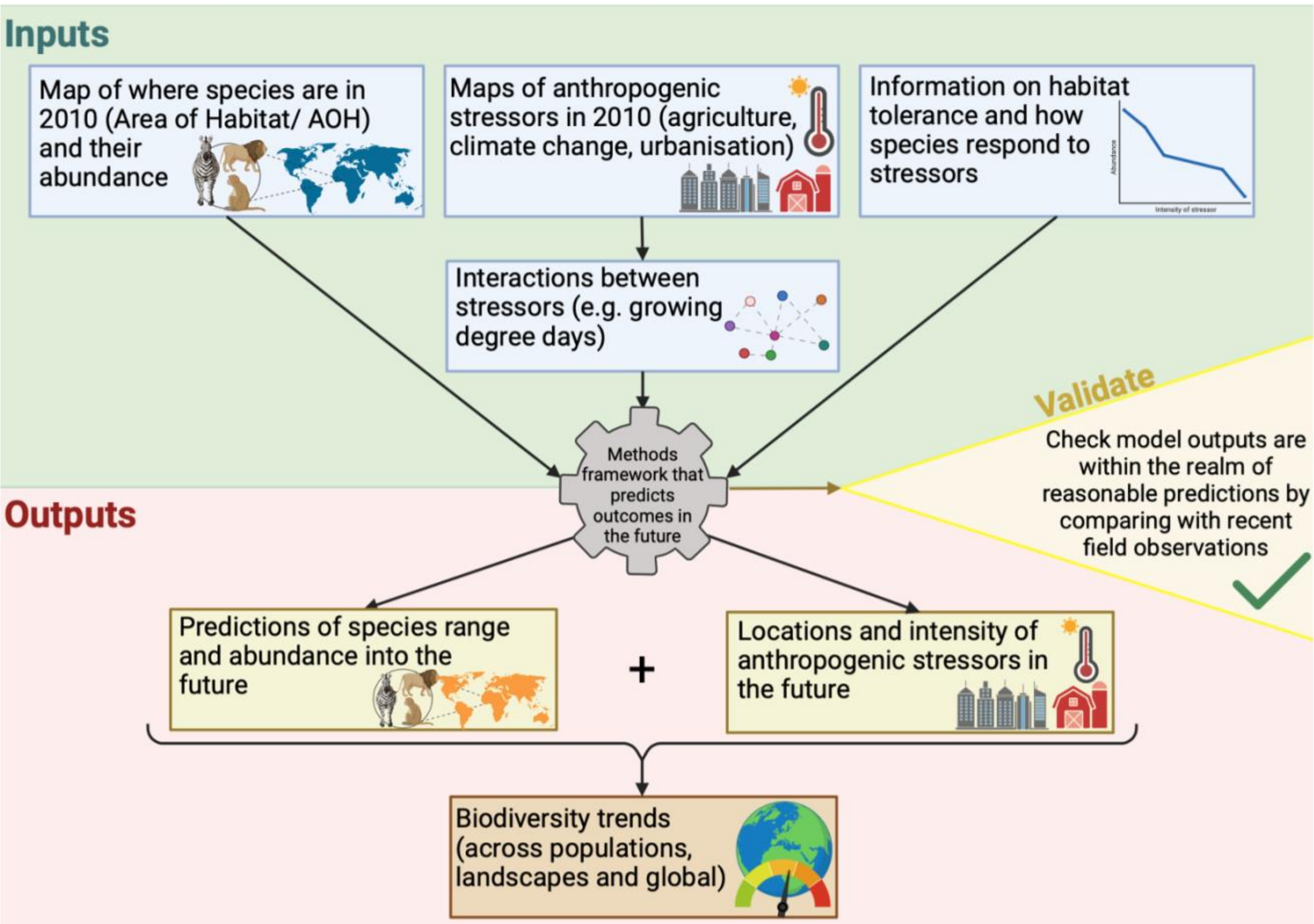

Figure 1: This schematic represents how the data inputs of Glob2Loc are computed into the outputs that predict biodiversity trends into the future. The inputs describe where species are currently found (Rondini, et al., 2011) and relate that to the location and intensity of anthropogenic stressors and species' tolerance to those stressors (blue boxes). The first model output comes from the ensemble model and describes the range and abundance of species after climate change, habitat preferences, elevation tolerance, and dispersal distance have been accounted for; the second output projects to location and intensity of anthropogenic stressors into the future, accounting for interactions between them as well (yellow boxes). These two primary outputs are then combined to give the final estimates of biodiversity trends into the future that account for human activities and how species range and abundance respond to them at 2.25 km^2 resolution (brown box). Glob2Loc can also be used to check modelled outputs against field observations to ensure predictions are reasonable (See 'Validate' triangle on the right). Figure created using BioRender.com

Methods

Overview

Figure 2 simplifies my research process into five steps. To understand the current literature around predator-prey relationships in human-use landscapes, I began with a scoping review of how predator-prey interactions change with agriculture and urbanisation (Figure 2; 1). Then, I decided on a research question, formed expectations, and planned the rest of my methodology. Next, using the biodiversity model Glob2Loc, I created three scenarios to represent current leopard range and abundance with different assumptions about predator-prey relationships (Figure 2; 2). The first scenario represented a maximum potential range and abundance, whereby only climate was considered, and leopards were not constrained by other species. The second was an intermediate, which assumed leopards ate wild and domestic prey and existed in wild and modified habitats at lower abundance. The final minimum scenario represented the typical modelling approach whereby all unsuitable habitat as defined by the IUCN was removed but additionally, leopards were constrained to exist only where top wild prey species did as well. I ran and validated each scenario with recent field data to decide which best reflected current observations on leopard range and abundance and to identify key limitations in Glob2Loc (Figure 2; 3). Then, I followed each prey scenario into 2050, given the projected climate and land-use change assumed by Glob2Loc (Figure 2; 4). Finally, I assessed the differences across each scenario's predictions and the uncertainty within each scenario to determine how significant the limitations of not accounting for predator-prey relationships are in standard biodiversity models (Figure 2; 5). I also explored what my results mean for leopard conservation as well as wider modelling of trends in biodiversity.

Figure 2: Flow Diagram to Illustrate Methodology

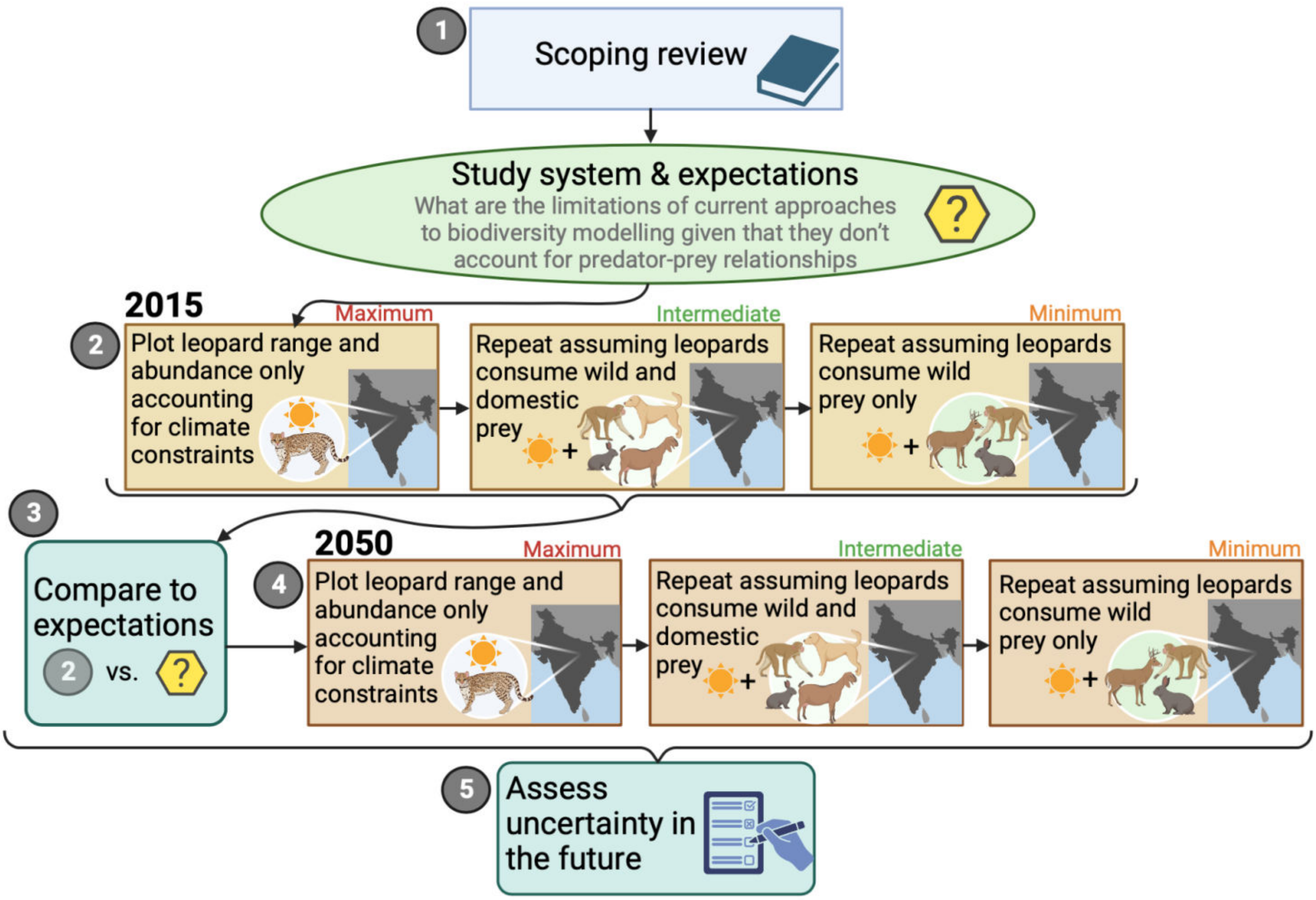

Figure 2: A flow diagram to show my research process where numbered steps correspond to sections in the 'Methods'. The icons in each step represent what I did. Light blue boxes refer to literature-based reading stages (1); Light brown boxes represent the 2015 scenario generation (2); and darker brown boxes represent when I ran the same scenarios generated in 2015 forward to the year 2050 (4); Darker blue boxes with curves edges represent steps where graphical results were compared to my expectations to evaluate model uncertainty and gauge which scenario is most realistic (3 & 5). Figure created using BioRender.com

Scoping Review: How predator-prey relationships change with agriculture and urbanisation and choosing a case study system

To fully understand the current literature around predator-prey relationships in and out of agricultural and urban areas, I began by carrying out a scoping review (Figure 2; 1). I used the search engine Google Scholar to look up keywords and phrases in scientific literature. These included: "predator" OR "predator-prey" AND "agricultur[]" OR "urban[]" OR "climate change". I also used snowballing methods to locate studies with obscure titles that were missed by my keyword search.

I ensured the studies I read were relevant using inclusion criteria. To minimise the chance of including weak science, studies had to be original peer-reviewed research papers or commentaries. Studies also had to be experimental or observational and set in a clearly described location. To also ensure as many confounding variables as possible were controlled for, studies had to compare urban or agricultural land to a nearby undisturbed site either along a gradient or via patches. Studies also had to measure the range and/or abundance of predators and their prey, or predation rate (directly or indirectly using prey decoys or measuring anti-predator behaviour). To make sure trends and case study systems were reproducible in Glob2Loc, the species studied were limited to terrestrial vertebrates that have been assessed for their threat status by the IUCN.

My scoping review resulted in 32 usable papers describing possible study systems, which included leopards in India. I decided to pursue this as a case study because their unique habitat tolerance and high abundance in India is underpinned by changing predator-prey relationships (Athreya, et al., 2013). Leopards are exhibiting generalist behaviour and including a wide diversity of prey in their diets, which is helping them persist in natural and modified landscapes (Athreya, et al., 2016). While the consumption of livestock is causing conflict in some places, in others, their consumption of disease-carrying pests is providing a health benefit to people (Kshettry, et al., 2018; Braczkowski, et al., 2018).

I then read deeper into my case study system to learn about the best current estimates of the abundance and range of leopards and their prey in India. I expanded my literature search to include technical reports by governments and conservation organisations as well as primary research papers and meta-analyses. The objective was to collect the best current evidence of leopard range and abundance rather than gather data linked to a specific year. This was because sampling effort differs greatly year-on-year and updates in ranges and abundance estimates in the literature may represent a progression of our understanding, rather than changes in leopard status.

Modelling Three Scenarios of 2015 Leopard Range and Abundance with Different Assumptions on Predator-Prey Relationships

Now that I had a concrete study system and contextual information about the current state of leopards, I used Glob2Loc to reproduce three versions of current leopard range and abundance, covering each assumption of prey availability (Table 1 & Figure 2; 2). While expectations from the literature represented the best current evidence, they varied in how old the population estimates were. The modelled baseline had to be linked to leopard status in a specific year, so I chose 2015 because it matched closely with the publication dates of several major studies on leopard range and abundance. Furthermore, Glob2Loc's 2015 estimate of range and abundance in this year was not significantly different from estimates for the surrounding years (2010, 2020, and 2025) (Appendix; Figure S1).

Table 1: Summary of Assumptions in my Maximum, Intermediate and Minimum Scenarios of Leopard Range and Abundance

Scenario	Prey Assumptions	Habitat Assumptions	Additional notes
Maximum	Not considered	Persist in entire climatic niche regardless of prey and human activities	Describes potential range and abundance without human activity
Intermediate	Constrained by wild and domestic prey	Persist in unmodified habitat at regular abundance but exists in human-modified landscapes at lower abundances to reflect lower tolerance (agriculture and urbanised areas)	Represents the most ecologically accurate prey base for leopards in India
Minimum	Constrained to wild prey only	Only persist in unmodified landscapes deemed suitable according to IUCN habitat classifications (such as forests, grasslands, and desert)	Reflects the typical approach to biodiversity modelling using IUCN habitat classifications, but additionally constrained leopard to coexist with wild prey only

Table 1: Summary of the assumptions behind each scenario I created and additional notes on what each scenario described. Scenarios were names 'Maximum', 'Intermediate' and 'Minimum' to reflect the size of the estimates of range and abundance they compute relative to each other.

All scenarios at least accounted for climate, dispersal limitations, and natural habitat preferences. Glob2Loc's projections of land-use change were reported with estimates of their uncertainty. So, in the intermediate and minimum scenarios where land-use data was integrated, I reported 95% confidence intervals around estimates of abundance and habitat area. As my maximum scenario only accounted for the climate's influence on leopard range, 95% confidence intervals in the results couldn't be calculated.

This is a limitation in my analysis and other globally applicable biodiversity models that don't project climate change with uncertainty (Buisson et al. 2010).

Maximum Scenario (climate only)

My first scenario represented maximum leopard range by just accounting for climate data. The resultant map of range and abundance acted as a maximum threshold because leopards were not constrained by land use or prey availability. No globally applicable biodiversity model would stop here, but I included it in my analysis because it indicated what range and abundance could be without anthropogenic interference.

Intermediate Scenario (wild and domestic prey)

Next, I created the intermediate scenario, which still assumed leopards could exist across much of the habitat that climate constraints allowed, but at a lower abundance in modified landscapes (such as agriculture or urban areas). This reflected the fact that leopards could consume wild and domestic prey. Having a middle-ground scenario as well as a maximum and minimum also gave me an idea of the skew in the range of estimates for abundance and habitat area.

I calculated abundance in the intermediate scenario differently in unmodified, agricultural, and urban landscapes. In unmodified habitat, leopard abundance was at its maximum as defined by the regression model built into Glob2Loc (See 'What is Glob2Loc?'). In agricultural landscapes, abundance was adjusted based on the intensity of given croplands (high or low) and pasturelands. As leopards only exist in the outskirts of cities in the literature, I removed 50% of urbanised land was removed from their range, and abundance was adjusted in the remainder of urban areas to reflect lower tolerance. However, it is noteworthy that many generalist predators tend to be overabundant in cities despite lower wild prey numbers due to the abundance of anthropogenic resources (rubbish, domestic and commensal animals like dogs and rats) (Eötvös, et al., 2018; Gámez, et al., 2022). This is known as the Predator-prey Paradox, but it is not known if leopards obey it due to lack of data (Fischer, et al., 2012).

Minimum Scenario (wild prey only)

Finally, I created the minimum scenario, which constrained leopard distribution, so they only existed where wild prey species were also present. I also restricted leopard habitat to natural areas by removing agricultural or urbanised land from their range where insufficient wild prey was available. This scenario reflected the assumption that leopards are intolerant of human activities and restricted to consuming wild prey with the same low tolerance for human activity. It also reflects the typical approach to modelling taken by other major biodiversity models (Leclère, et al., 2020; Schipper, et al., 2020).

To obtain estimates of wild prey availability with which to constrain leopard distribution, I made prey meat availability maps using top prey species reported in the literature (Appendix; Table S1). I also used this map to identify areas that leopards may be drawn to due to high diversity and mass of prey. First, I overlaid the habitat ranges of all prey species to make a map of prey species richness. Then, I combined the species richness map with each prey species' estimated abundance across its range and body mass to create a heatmap that depicted regions of high and low prey biomass. To constrain leopard range by wild prey species, I cropped leopard range so they could only exist where at least one top prey species was present. It wasn't possible to constrain leopard range by a threshold weight of available prey because I could not capture all prey species in my review.

Due to the restrictions in Glob2Loc, I could only include prey that were terrestrial vertebrates and assessed by the IUCN, i.e. those deemed worth including in the IUCN Red List. In particular, highly abundant, and common species have not been assessed. Therefore, wild boar (*Sus scrofa*) could not be included because it is highly abundant, and the IUCN does not assess two relevant sub-species present in India. However, this limitation won't cause a significant problem because the prey species I have already included cover 97.6% of India, and adding another species would not likely change the trend. Also, there was limited input data on the habitat extents of two langurs (*Semnopithecus hypoleucos* and *Semnopithecus priam*), which meant they weren't modelled in Glob2Loc to avoid overfitting (less than 57 km^2). However, I was able to include five other *Semnopithecus* species, so the exclusion of two was not likely to be a large limitation.

Comparing my Three Scenarios to Field Observations (Validate)

Next, I assessed how my three scenarios compared to up-to-date field observations (Figure 2; 3). This step checked how well the model predicted 2015 range and abundance since it was built on data from 2010 (See Figure 1: 'Inputs'). This revealed which modelled scenario's predictions best reflected observed reality to gauge if omitting predator-prey relationships in current approaches to biodiversity modelling is a significant limitation.

Projecting my Three Scenarios of Leopard Range and Abundance into 2050

Finally, I looked at the range of estimates of leopard range and abundance in the future by running the same scenarios I created in 2015 forward to the year 2050 (Figure 2; 4). I used 2050 to characterise the future because it is a crucial year for international carbon and biodiversity targets (Mace, et al., 2018). It is also currently the furthest away year projected by Glob2Loc, which is still in development.

Following this procedure and comparing 2015 to the current literature before looking forward to 2050 meant that I knew which specific differences in the future were due to limitations in Glob2Loc's construction or to climate and land use change. If I compared range and abundance in 2050 directly to expectations from the current literature, I wouldn't have been able to identify if discrepancies were because of an error in the model or climate change. Therefore, I compared the best current evidence to a point in time that was closer to when new data was published (2015) and then followed each scenario into 2050.

I compared each 2050 scenario to the outcomes of my baseline analysis from 2015, where I deduced nuances between my scenarios and the literature (Figure 2; 5). I compared my three estimates for future leopard range and abundance to see if any large differences were a cause for concern. I also predicted which 2050 scenario was most likely to occur based on which one most closely matched the evidence in 2015. All models and statistical analyses were run in R version 4.1. and my code is available at https://doi.org/10.6084/m9.figshare.22794107.v3

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Results

Scoping Review: Expectations of Leopard Range and Abundance from Field Observations

Range: The best estimate of leopard range in India is displayed in Figure 3, panel A (889,000 km^2; adapted from Jacobson, et al., 2016). The authors carried out a meta-analysis by identifying recent presence and absence data of leopards across all wild and modified landscapes and estimated their current distribution in QGIS 2.10.1-Pisa. Other estimates available only considered leopard range in unmodified forests and computed far smaller ranges (Appendix; Figure S2) (Jhala, et al., 2015; Jhala, et al., 2020).

Figure 3: Leopard Range from the Literature Compared to Glob2Loc Scenarios (2015)

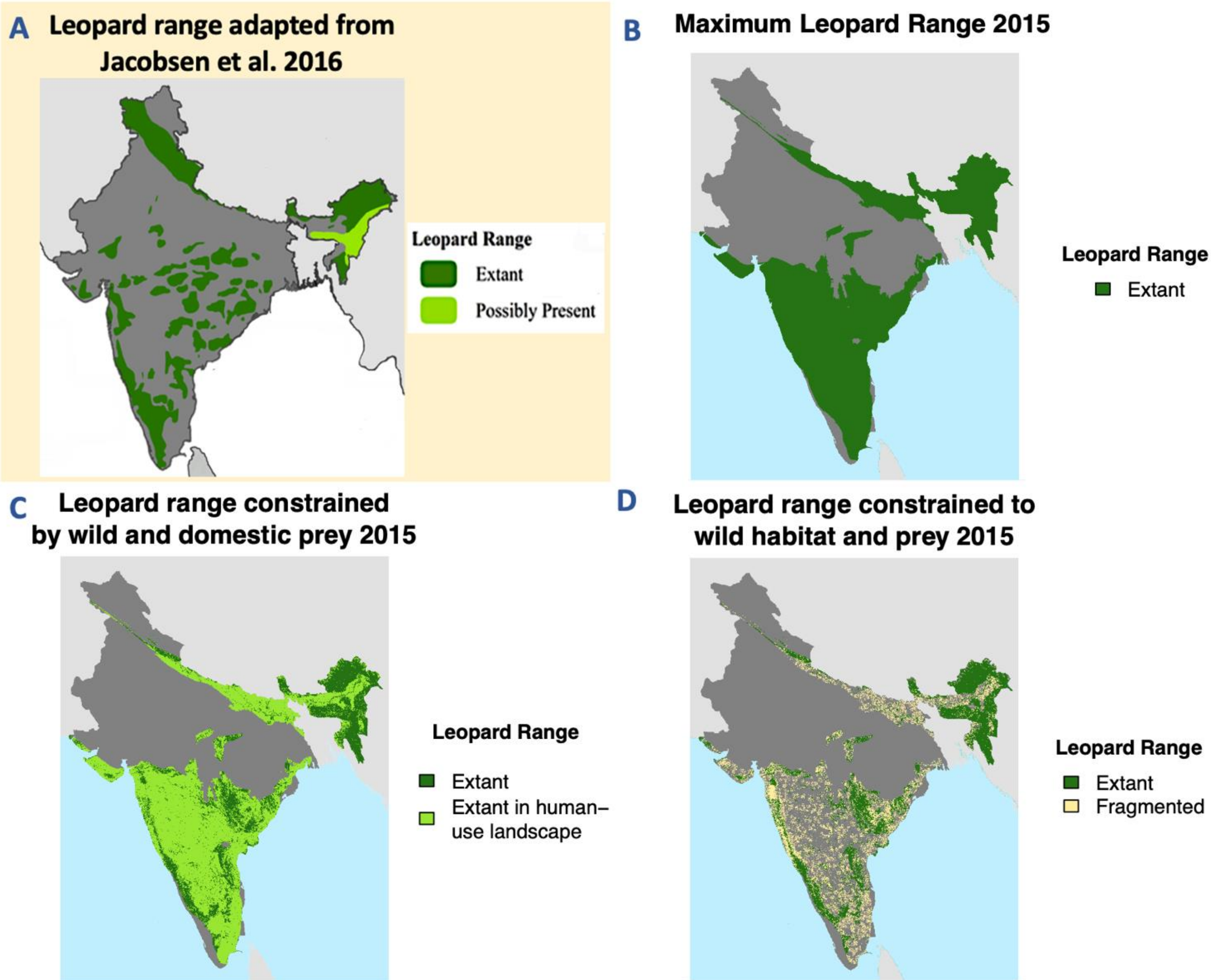

Figure 3: Comparison of the best current evidence on leopard range from the literature (Panel A, yellow background; 889,000 km^2) and my modelled scenarios each based on integrating prey types and availability to different extents (Panels B to D). ‘B’ describes leopard range only accounting for climate (1,524,700 km^2). ‘C’ describes leopard range constrained by climate, domestic, and wild prey. ‘Extant’ (dark green) habitat describes cells with at least 50% undisturbed habitat. ‘Extant in human-use landscape’ (light green) describes habitat where leopards are present, but at lower abundances than in undisturbed habitat because at least 50% of the cells contain modified land. ‘D’ describes leopard range constrained to wild habitat and prey (450,351 km^2). ‘Fragmented’ (yellow) represents cells with 1-50% undisturbed habitat as the remainder is modified and unsuitable. Cells that were completely modified by agriculture/urbanisation with 0% natural habitat were assumed to be unsuitable for leopard occupancy and were removed from leopard range (grey).

Abundance: India is estimated to contain a population of at least 12,800 adult leopards according to the government's most recent report (Jhala, et al., 2020). To estimate leopard abundance, the authors used likelihood-based spatially explicit capture recapture methods in a joint distribution framework with habitat quality, prey abundance, and human footprint as covariates. Specifically, observations of how leopard abundance in 2018 correlated with each covariate in camera-trapped locations were extrapolated to other forested landscapes, based on how the covariates changed.

The only other country-wide estimate was published five years earlier and reported a far lower abundance of approximately 8000 leopards in 2014 (Jhala, et al., 2015). While this apparent increase in abundance from 2014 to 2018 was reported as a conservation success by some news outlets, it is important to note that the assessment published in 2020 had almost three times the sampling effort as did the 2015 study. So, it is difficult to conclude if the population did increase or if the latter study was more thorough (Vaidyanathan, 2019).

Conversely, 12,800 may be an absolute minimum abundance estimate as the authors only surveyed undisturbed forests in major tiger conservation landscapes (Jhala, et al., 2020). In fact, leopards exist outside forests and are also known to exhibit lower abundances in tiger territory, so the abundance of leopards is likely to be higher (Harihar, et al., 2011; Odden, et al., 2010). After the 2015 study, the lead authors acknowledged this and stated in a conference that although they measured abundance to be 8000, true abundance could be 12-14,000 (Bhattacharya, 2015). Assuming the same proportional limitation existed in the 2018 study could mean true abundance was 19,200-22,400 leopards, but this hasn’t been verified. Furthermore, data deficiencies meant camera-trap information from northeast India could not be included in their model and estimate of country-wide abundance.

Comparing my Three Scenarios of Range and Abundance from Glob2Loc with Field Observations

Range

The geographical maps of India from Glob2Loc and the literature were not identical, meaning I couldn't carry out a direct, quantifiable, spatially explicit comparison of differences in range. Specifically, the maps of India from Glob2Loc and the literature defined the boundary between northwest India and Pakistan differently, and the shape of India differed (Athreya & Kulkarni, in conversation 2023). Furthermore, the methods employed in the literature and Glob2Loc were very different, making it impractical to conduct an explicit comparison. So, I compared country-level habitat area and also completed a qualitative visual comparison of range.

Total habitat area: The best estimate from the literature lay approximately halfway between my modelled maximum and minimum scenarios, which indicated that an intermediate habitat area would best match observations (Figure 4). The habitat area predicted by the wild habitat and prey-only scenario (minimum) was approximately half that of the observed habitat area estimate from the literature (450,000 km^2 vs 889,000 km^2). The habitat area predicted by the climate-only scenario (maximum), assuming leopards occupy their entire climatic niche regardless of human activity, was almost twice as large as the literature's best estimate (1,500,000 km^2 vs 889,000 km^2). This confirmed my prediction that the intermediate scenario best matches observations because leopards are adapting to human-use landscapes but are not completely tolerant.

The habitat area predicted by the intermediate scenario (accounting for wild and domestic prey) could not be included in Figure 4 because its area was the same as the maximum scenario. But a large amount of this habitat is of a lower quality that will inevitably be fragmented (centre of cities, roads, impenetrable agriculture). But its total area could be approximated as halfway between the maximum and minimum scenarios (987,525 km^2) because observations from the literature indicated that total leopard habitat was an intermediate area (Figure 4). So, the best way to capture leopard range in a model is to acknowledge they do exist in human-use landscapes, but not all, and not necessarily at the same density as in natural habitat.

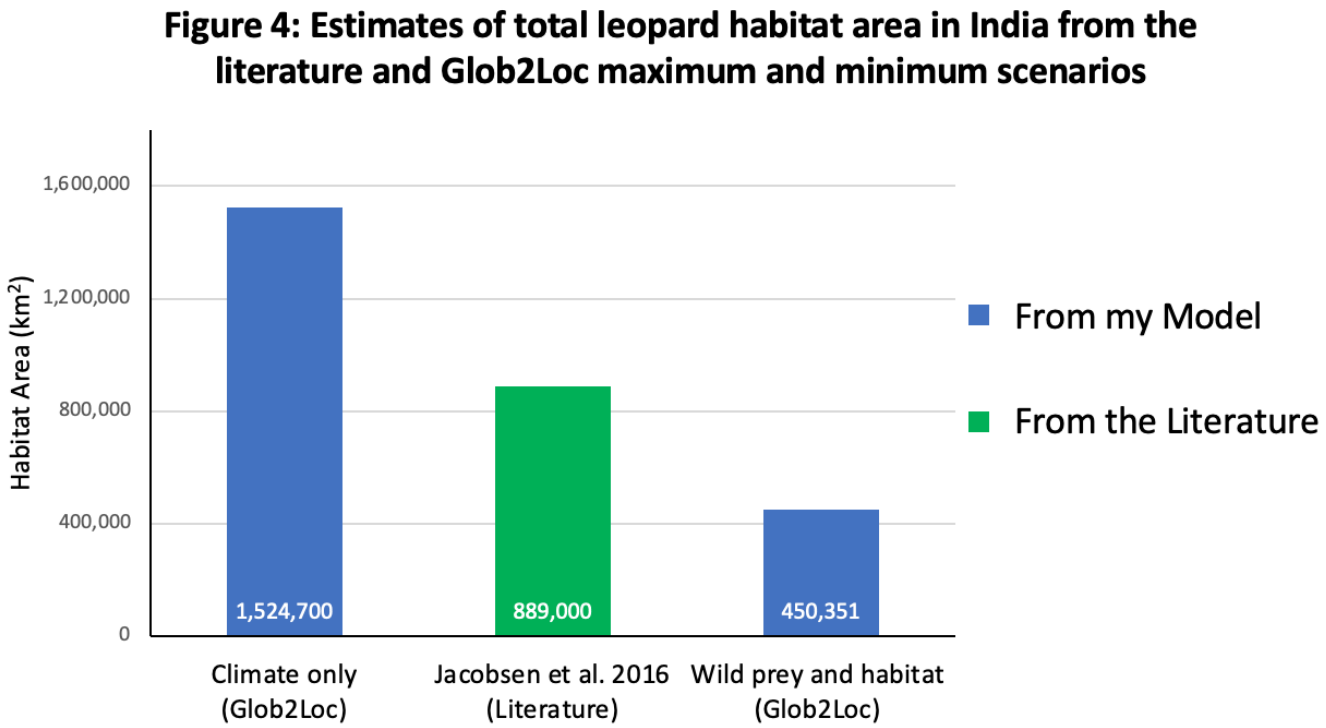

Figure 4: Comparison of total leopard habitat in India from the literature's best estimate and the maximum and minimum scenarios generated in Glob2Loc. Blue bard represent my modelled thresholds, and the green bar reflects habitat area from the Jacobsen et al 2016 meta-analysis. Confidence intervals were not reported in the literature and were not available for Glob2Loc's maximum estimate as they were derived from confident in land-use estimates which wasn't considered in the climate-only scenario. Glob2Loc's intermediate scenario, accounting for wild and domestic prey has the same habitat area as the maximum scenario. The figure shows that an intermediate habitat area may best match field observations.

Qualitative visual comparison: As the evidence from the literature shows that leopard habitat is fragmented but still covers a significant portion of India, a scenario between my modelled minimum and intermediate may best represent observations. Figure 3 depicts the expectations from the literature (Panel A) and my three modelled scenarios using Glob2Loc (Panels B, C, and D).

The range predicted by my minimum scenario was too fragmented to represent an adaptable species such as leopards (Figure 3D). If I changed the assumptions behind my minimum scenario and artificially increased leopard tolerance to human-use landscapes, the resulting range map became more similar to observations from the literature (Appendix; Figure S3). I achieved this by halving the threshold proportion of natural habitat per cell required to classify it as 'Extant', 'Fragmented', or unoccupied by leopards. This confirmed that leopards should be modelled with a higher tolerance to modified landscapes and that an intermediate range scenario is most realistic. It is common practice to fine-tune models to match observations to get a good fit because no model perfectly replicates reality, so long as any ex-ante adjustments are made for all species

The maximum scenario failed to identify that leopard populations are fragmented across central India and exist in two bands along the west coast and north of the country. Therefore, assuming leopards exist continuously along their climatic niche is a large limitation and removes Glob2Loc's predictions far from observed reality. But it highlighted that land-use change has significantly impacted leopard range because total habitat area fell by 70.5% ± [67.0, 74.0] between my maximum and minimum scenarios.

A three-way comparison of leopard range in Glob2Loc, the literature, and prey range in Glob2Loc indicated that prey availability should be considered alongside climate to model generalists like leopards. Firstly, constraining leopard range to wild prey after their maximum habitat was defined only reduced the population by an estimated 52 leopards. Secondly, several leopard populations exist in northern central India, as evidenced by my literature search, but this wasn't captured in Glob2Loc (Figure 3). However, Glo2Loc predicted there may be a significant biomass of prey species in this region (Figure 5). Therefore, leopard populations may exist in northern central India because of ample prey availability, despite climate variables being just below the threshold to define the habitat as suitable in Glob2Loc.

Figure 5: Prey Biomass in Leopard-free Areas in 2015

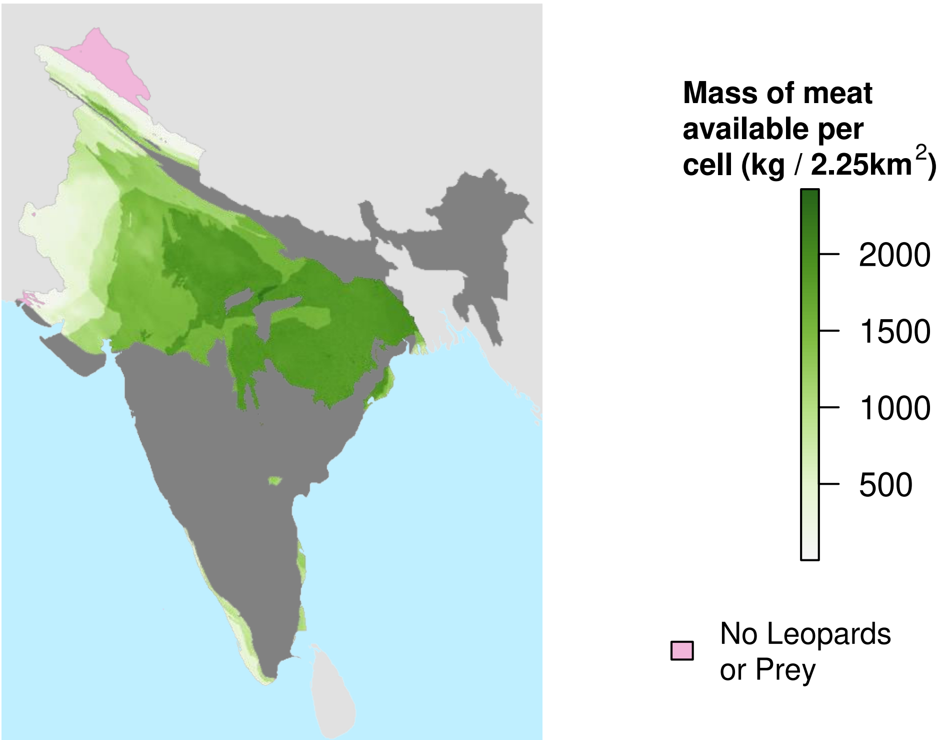

Figure 5: A map to show the biomass of the top 16 wild prey species in leopard-free regions of India in 2015 according to Glob2Loc (species listed in Appendix; Table S1). Darker green regions indicate areas with the highest prey biomass. The map was constructed by combining the range, abundance, and body mass of each top prey species. Then, habitat that overlapped with leopards' maximum habitat scenario was removed. Light pink regions depict areas that are free from both leopards and their top prey. Appendix Figure S4 Panel A illustrates the total prey biomass in India.

Abundance

Overall, an estimate of leopard abundance between my minimum and intermediate scenarios in Glob2Loc would accurately reflect observations (14,900-27,000 leopards). Accounting for a wide habitat tolerance and consumption of a broad range of prey (wild and domestic) best predicts leopard status now and possibly into the future. Figure 6 compares the abundance estimates from the literature (green) to my modelled scenarios covering each prey assumption (blue).

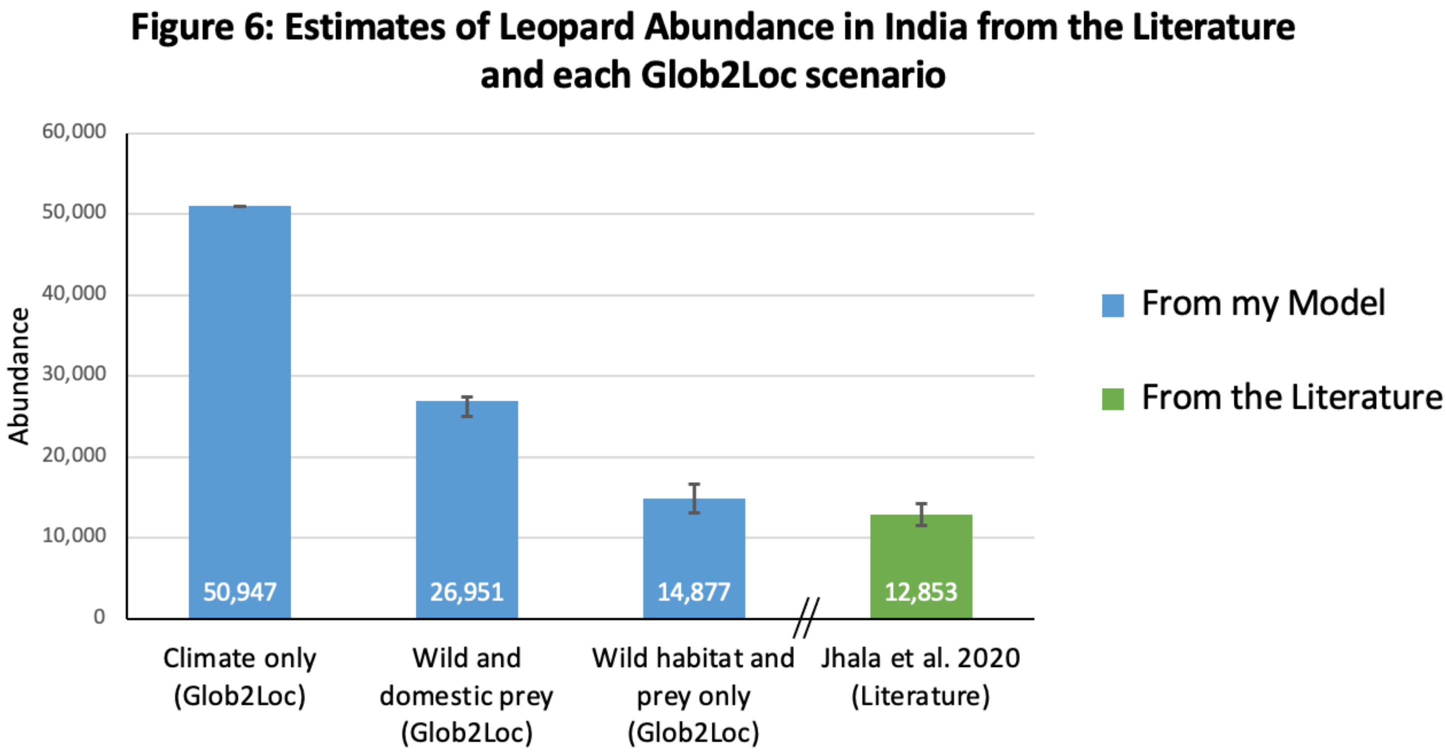

Figure 6: Comparison of abundance estimates from the literature (green) and my modelled scenarios in Glob2Loc (blue). The estimate from Jhala et al. 2020 (12,853 95% CI [11,491, 14,215]) represents a minimum estimate that only accounted for leopard abundance in forested habitat where tigers were also present. Therefore, my modelled minimum scenario (wild habitat and prey only; 14,877 95% CI [13,120, 16,623]) is most similar to the literature in terms of habitat coverage. Abundance in reality may possibly be higher and closer to the intermediate scenario (wild and domestic prey; 26,951 95% CI [25,013, 27,435]). No confidence interval is available for the maximum leopard abundance estimate (climate only; 50,947) because confidence was derived from uncertainty in land cover estimates.

Although the literature and Glob2Loc used different methods to estimate abundance, the model accurately reflected observations. The literature calculated a minimum possible abundance estimate because it only monitored leopards in undisturbed forests coinhabited by tigers and did not cover all states in India. Therefore, the literature is most similar and comparable to my minimum scenario (considering wild habitat and prey only). Estimates of abundance from the literature and my minimum scenario were not significantly different (95% confidence intervals overlap; Figure 6). Therefore, my intermediate and maximum scenarios may have accurately reconstructed abundance given their assumptions about prey. Uncertainty in the literature's best estimate of leopard abundance in India confounded my validation which sought to identify which modelled scenario was most realistic. But leopard abundance could be approximated to lie between the minimum and intermediate estimates in Glob2Loc (14,900-27,000). However, Glob2Loc didn't account for all stressors to leopards, such as poaching, which would mean the realised abundance is lower than what Glob2Loc predicted (Stein, et al., 2020).

Assessing my Three Scenarios of Leopard Range and Abundance in 2050

Change from 2015 to 2050

Climate change and human-induced land-use change did not significantly affect leopards by 2050 in Glob2Loc because the 95% confidence intervals of leopard minimum habitat area, which accounted for all stressors, overlapped (Appendix; Figure S1). Furthermore, leopards persisted in much of their range from 2015 to 2050 (Figure 7D). By 2050, habitat area increased overall by 2.56% in the maximum, climate-only scenario. However, reporting the overall change in range masks the finding that habitat loss and gain occurred to roughly equal extents in different locations at range edges (Figure 7D). Habitat area decreased overall in the minimum scenario by 0.833% due to urbanisation and agricultural expansion.

Range

My intermediate scenario is likely to provide the most robust estimate of the future since it best matched observations in 2015 (Figure 7B). Without considering the diets of leopards and their range expanding to human-use landscapes, a typical biodiversity model may underestimate future range by 2.25-fold (intermediate scenario: 1,005,100 km^2, minimum scenario: 446,600 km^2) (Figure 7). My climate-only, maximum scenario predicted habitat area was 3.50 times higher than my minimum scenario, which constrained leopards to wild habitat and prey (maximum: 1,563,600 km^2, minimum: 446,600 km^2). This difference highlights that land use has a large impact on leopard range and so acknowledging how species respond to agriculture and urbanisation in models is important to get accurate results.

Figure 7: Glob2Loc's Estimates of the Maximum, Intermediate and Minimum Range of Leopards in 2050

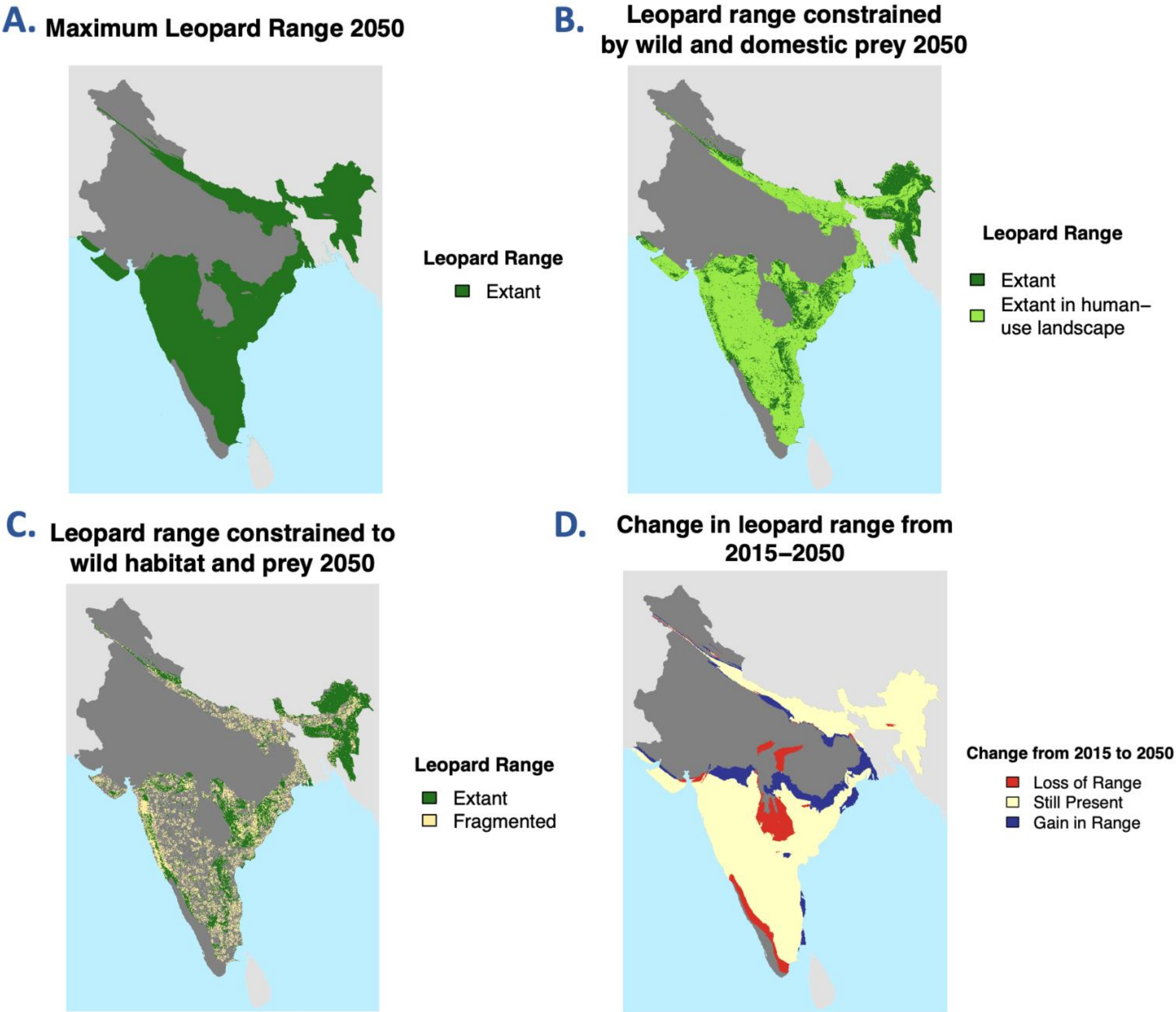

Figure 7: The range of predictions of leopard habitat area in 2050 from the maximum to minimum scenarios as continued from 2015 using the same thresholds to classify occupancy as Figure 3; B to D. Panel A is the maximum climate-only scenario with prey and land-use not accounted for (1,563,600 km^2); Panel B is the intermediate scenario accounting for wild and domestic prey in wild and modified habitat (approximately 1,005,100 km^2, halfway between A and B); Panel C represents leopard range constrained to wild habitat and prey only (446,600 km^2). From the baseline analysis in 2015, it is most likely that the intermediate scenario (B), accounting for wild and domestic prey and habitat, is most likely to represent the future. Panel D illustrates the difference in range from 2015 to 2050 according to the intermediate scenario which accounted for the most realistic prey base (wild and domestic prey; difference between Figure 3C & Figure 7B). Most range is unchanged (yellow) but there are gains and losses around the range edges (red and blue).

I found that to define leopard range, considering prey availability after climate may cause Glob2Loc to underpredict range again in 2050. Firstly, constraining leopards by wild prey availability did not significantly affect leopard range, which was reduced by just 1.35% (which equated to approximately 194 leopards). Secondly, top prey biomass is still highest in northern central India, which is still unoccupied by leopards in 2050 (Figure 8). Therefore, it is likely that in 2050, there will be a concentration of leopard populations in northern India as they are facilitated by prey availability, even though Glob2Loc classified this region as containing an unsuitable climate.

Figure 8: Prey Biomass in Areas without Leopards in 2050 According to Glob2Loc

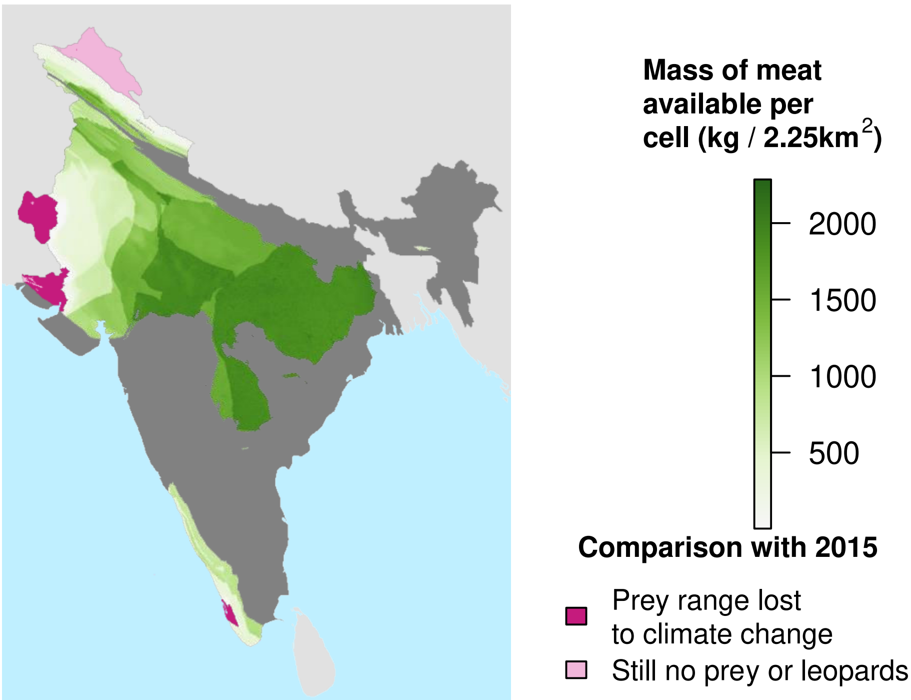

Figure 8: A map to show the biomass of the top 16 wild prey species in leopard-free regions of India in 2050 and a comparison with 2015. Darker green regions represent areas with more/heavier prey species. Hot pink regions in west India highlight areas which contained top wild prey in 2015, but not in 2050 due to climate change. Light pink regions depict areas that are predicted to be unoccupied by leopards and their top prey in 2015 and 2050. The gain in prey range due to climate change by 2050 was negligible and occurred outside leopard habitat, and so is reported elsewhere (Appendix; Figure S4).

Abundance

Glob2Loc's estimates of leopard abundance increased in my intermediate and maximum scenarios from 2015 to 2050 because climate change increased maximum habitat by 2.56%. But in the minimum scenario, abundance decreased because projections of urban and agricultural expansion removed more habitat by 2050 than was gained due to climate change (Figure 9).

Leopard abundance in 2050 may be between 14,600-27,400 adults (minimum-intermediate scenario) if nuances between current observations and Glob2Loc carry forward into the future (Figure 10). This suggests the impact of climate, agriculture, and urbanisation on the leopard population in India won't change from 2015 to 2050. But leopard populations globally are decreasing overall due to poaching, which isn't accounted for in Glob2Loc (Stein, et al., 2020). The upper and lower bounds of leopard abundance defined by my maximum and minimum scenarios also quantify loss or recovery potential for leopard populations if habitat is rewilded or if human-wildlife conflict worsens.

To not validate model outputs with observations or consider predator-prey relationships could mean that typical approaches to modelling trends in biodiversity underpredict leopard abundance by almost 2-fold in the future (Figure 9: A and B). This problem will continue unless IUCN data is updated. Instead reporting upper and lower thresholds for leopard abundance in models and accepting uncertainty may be more truthful (e.g., 2050: 14,500-27,400 leopards). My maximum scenario predicted leopard abundance was 3.6 times greater than my minimum scenario in 2050 (Figure 9: A & C). So, assumptions about prey consumption and habitat tolerance greatly affect predictions in biodiversity models.

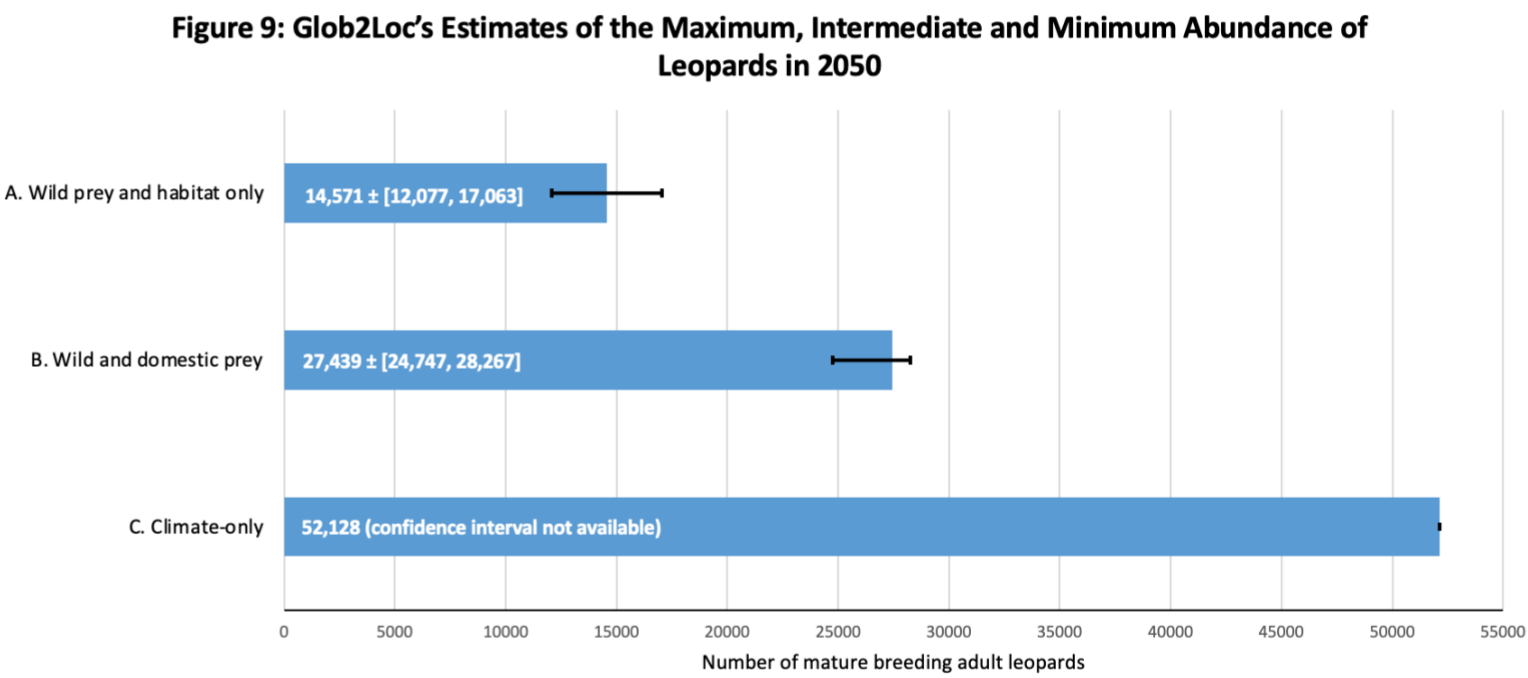

Figure 9: Visualisation of the range of estimates of leopard abundance based on no (climate only) or two different assumptions of what prey leopard eat and hence where they roam (wild only or wild and domestic). Without considering an intermediate scenario and understanding how modelled results compare to observations, there is a 3.6-fold difference between the maximum and minimum estimates of leopard abundance (14,571 - 52,128). However, when you report a range after considering how the model compared to the literature in 2015, this uncertainty is almost halved (14,571 - 27, 439 and a 1.9-fold difference).

Discussion

We need to represent carnivore ecology appropriately in models if they are to be useful in projecting biodiversity trends. Leopard distribution and abundance, as with many generalists, is largely determined by prey availability (Sutton, et al., 2023). I assessed the limitations in current approaches to biodiversity modelling when predator-prey relationships are not accounted for, using the biodiversity model, Glob2Loc. I found that my modelled intermediate scenario which most closely approximated leopard diet, as evidenced by a literature search, also matched field observations most accurately (Figure 3; Figure 6). Validating Glob2Loc with real observations helped identify uncertainty in the model and the literature and allowed me to link imperfections in the model's predictions to not accounting for how prey influence range. I found that reporting ranges rather than one number when estimating abundance better represents the uncertainty in the literature and biodiversity models. Furthermore, a scenario-based approach to biodiversity modelling, as reported here, can quantify possibilities in terms of recovery potential or loss if human tolerance to wildlife increases or worsens in the future

Validating biodiversity model outputs as a way to identify limitations of excluding biotic interactions

Species distribution models (SDMs) are limited when they only consider how climate affects habitat ranges or are adjusted *post hoc* to account for habitat preferences. To overcome this, comparing the predicted range of focal species with recent data and other species with which it is known to interact identifies where the model is inaccurate and why. For example, Glob2Loc failed to capture a cluster of leopard populations in northern central India (Figure 3). But comparing modelled outputs to field observations identified that this may be because Glob2Loc doesn't account for prey availability, which is shown to be high in this region (Figure 5). One could conversely argue that the ensemble SDMs in Glob2Loc did not accurately define climate suitability, leading to fallacious extrapolation of leopard range. But no SDM can perfectly capture climate tolerance of a species because of the biotic and topographic factors that also influence observed ranges from which we define climate suitability. This is especially true for generalists such as leopards which live in warm climates and whose range is strongly determined by biotic interactions (Paquette & Hargreaves, 2021; Galiana, et al., 2023). With more time, I would investigate the climatic characteristics of northern central India to gauge if Glob2Loc poorly defined climatic suitability of leopards or if prey facilitates leopard presence in areas with typically unsuitable climate. But in the meantime, validating model outputs identifies limitations caused by approximating reality.

Glob2Loc and individual SDMs cannot fully capture the plethora of biotic and abiotic factors that come together to determine if and to what extent species exist in nature (Peterson & Soberón, 2015). This is instead conceptualised in ecology as the fundamental niche, which is an abstract, n-dimensional hyperspace with axes for every condition and resource that affects a species (Hutchinson, 1957). But species distribution modelling and the concept of niches are separate (Colwell & Rangel, 2009). SDMs are built on data from observations in nature which at best reflect the realised potential of the current gene pool, and not their true potential (Jiménez-Valverde, et al., 2008). Moreover, Buisson et al. 2010 found that of all the sources of uncertainty in ensemble species distribution models (e.g., initial data inputs, type of SDM, and climate change scenarios), SDMs were the greatest source of uncertainty in forecasts (Buisson, et al., 2010). Therefore, validating model outputs with recent data is an important step in using SDMs, which are inherently limited in their applications.

Methods exist to include biotic interactions in SDMs, and this has led to improved predictive power, especially in landscape-level case studies where inter-species relationships can be parameterised (Sutton, et al., 2023; Giannini, et al., 2013). However, data limitations stifle the incorporation of biotic interactions into biodiversity models that operate on a global scale, such as Glob2Loc (Wisz, et al., 2013). A recent advance however has been the use of random forest models to predict predator-prey relationships to build up the database computationally (Llewelyn, et al., 2022). As a next step, it would be beneficial to use computationally constructed interaction databases such as this in SDMs and use prey ranges as covariates that explain predator range to see if new outputs better reflect observations.

It would also be useful to include a joint species distribution model (jSDM) into Glob2Loc's ensemble, which uses co-occurrence data to identify associations between species that cannot be explained by shared climate preferences alone and project communities under climate change (Pollock, et al., 2014). However, best practice currently recommends that when focussing on predator-prey relationships, trophic interaction distribution models are optimal (Dormann, et al., 2018). These models, which require information on predator and prey range as well as the specific location of hunts can identify 40% more of a species' true range than individual SDMs (Trainor, et al., 2014). But data requirements for more accurate models such as these are too large for globally applicable biodiversity models. This confirms it is important in the meantime to validate outputs from models in the meantime with real observations to identify and understand limitations

Overall, my results indicate potential limitations of global biodiversity models and caution their potential use. There is a need to develop a framework to validate globally applicable biodiversity models. Centralised methods that allow model outputs to be swiftly and efficiently checked against real data would identify if projections of future biodiversity trends are reliable. This could be commenced by expanding this analysis to more species and countries to see if the discrepancies identified between observations and model outputs of leopards in India are upheld in other study systems.

Considering scenarios in biodiversity modelling can allude to recovery potential or loss if tolerance to wildlife changes

An approach to scenario-based biodiversity modelling may also indicate the potential loss of leopards in India if human tolerance of wildlife decreases. The extent to which large carnivores coexist alongside humans in urban and agricultural settings is a product of human-wildlife conflict and the effectiveness of management strategies that are in place (Linnell, et al., 2001). However, Glob2Loc is limited in that it doesn't account for the effect poaching and retaliatory killing have on leopard populations, when these activities are recognised as the biggest threats to leopards by the IUCN (Stein, et al., 2020). While leopards are reportedly persisting in human-modified landscapes in India recently, this may change in the future and Glob2Loc, like other biodiversity models, cannot capture this unless IUCN data is updated. But a scenario-based approach to modelling, as reported in this study, can help to overcome this limitation by reporting the best and worst outcomes for biodiversity. If retaliatory killings in India drive leopards out of landscapes co-occupied by humans by 2050, then their maximum possible abundance could be defined by the minimum scenario in Glob2Loc rather than the intermediate scenario (Figure 10). This could coincide with a population decrease of 46.9%.

Conversely, recovery potential can be quantified by scenario-based modelling if land is rewilded (taken out of agriculture and given back to nature). For example, a decrease in meat consumption and the rewilding of agricultural land has been proposed as a solution to the biodiversity crisis (Wang, et al., 2023). To quantify the impact of this, Glob2Loc can project future biodiversity trends under different human diet scenarios and their associated land-use change (e.g., business as usual or increase in plant-based foods). This analysis would especially help inform recovery potential for specialist species that are completely intolerant to human-use landscapes.

Conclusions: No biodiversity model is perfect, but that doesn't mean they are not useful. To gauge uncertainty in current models and to understand the reasons for their errors, authors should emphasise validating outputs with real data and checking how interacting species are projected together. It may be imperative to scale up bias-testing in other globally applicable biodiversity models as recently, there have been calls to move on from global mapping exercises given they have little more left to uncover (Wyborn., et al., 2021). If discrepancies between models and recent data are a common occurrence, then this could shift the research community's next steps.

Acknowledgements

I would like to thank Dr Vidya Athreya for giving her thoughts on the research topic and highlighting the need to explicitly mention disputed country boundaries in my thesis to be sensitive to different people. I would also like to thank Apoorva Kulkarni and Trisha Gupta for their opinions about leopards in India and their benefits as well as conflicts. Finally, I would like to thank Dr Joseph Poore and Dr Sophus zu Ermgassen for their interest and the useful questions they asked me during a lab group meeting.

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Management Report

I first emailed my supervisors in August of the summer vac to discuss a new project as the one I completed a proposal on fell through. I first met with them to discuss this at the end of September, and we came up with ideas for a new project then, so I avoided losing time planning when I returned to Oxford. After this, I began reading up on Glob2Loc and the previous modelling papers it expands on.

Then in mid-October, I met with MC where I explained I had become interested in the fact that Glob2Loc doesn't account for biotic interactions in its projection of range and abundance. For the rest of Michaelmas, I began my scoping review of how predator-prey relationships change with climate change, agriculture, and urbanisation and how that affects species range/abundance in these areas. I drafted mini-proposals and figured out a rough research path to pursue once I knew specific case study system to investigate from my reading.

I originally wanted to add another model into the Glob2Loc ensemble that accounted for biotic interactions and test if the new ensemble predicted range and abundance better than the original. So, I spent a significant amount of time doing another scoping review and online tutorials of how predator-prey interactions have been accounted for in species distribution modelling so far. But in the end, I didn't have enough time over the year to action my ideas from this step.

In 0th week of Hilary term, after completing my scoping reviews, I met with my supervisors to confirm my specific case study system which I decided was most interesting from my reading. I then solidified the rest of my methodology and spent the rest of Hilary reading more closely around leopards in India, extracting statistical results from Glob2Loc, and comparing them to ecological theory and expectations. This required me to learn Mac terminal language and access Oxford's Advanced Research Computer (ARC) to edit and run code and download results onto RStudio on my laptop for analysis.

As I completed my analysis in Hilary term, I sometimes discovered missing data or errors when I used the code from Glob2Loc. It therefore needed to be troubleshooted a few times which would delay my analysis. But I used simulated data in the meantime and carried out similar analyses on several amphibian species in Brazil to get used to how the model worked and create code for my analysis. I also used delays in this time to start writing up my methods. This meant I didn't waste time before Glob2Loc's leopard and prey code worked again.

I finished my research towards the end of the Easter Vac and finished writing up my thesis in this time too. I handed my first draft to my supervisors at the start of Week 1 Trinity term and received comments later that week. I then spent the rest of my time before the deadline editing my thesis.

Appendix

Table S1: List of all wild terrestrial vertebrate prey species used

Species (binomial)	Classification (Class, family)
Axis axis	*Mammalia, Cervidae*
Boselaphus tragocamelus	*Mammalia, Bovidae*
Hoolock hoolock	*Mammalia, Hylobatidae*
Herpestes smithii	*Mammalia, Herpestidae*
Lepus nigricollis	*Mammalia, Leporidae*
Macaca leonina	*Mammalia, Cercopithecidae*
Macaca mulatta	*Mammalia, Cercopithecidae*
Macaca radiata	*Mammalia, Cercopithecidae*
Pavo cristatus	*Aves, Phasianidae*
Semnopithecus ajax	*Mammalia, Cercopithecidae*
Semnopithecus dussumieri	*Mammalia, Cercopithecidae*
Semnopithecus entellus	*Mammalia, Cercopithecidae*
Semnopithecus hector	*Mammalia, Cercopithecidae*
Semnopithecus schistaceus	*Mammalia, Cercopithecidae*
Rusa unicolor	*Mammalia, Cervidae*
Viverricula indica	*Mammalia, Viverridae*

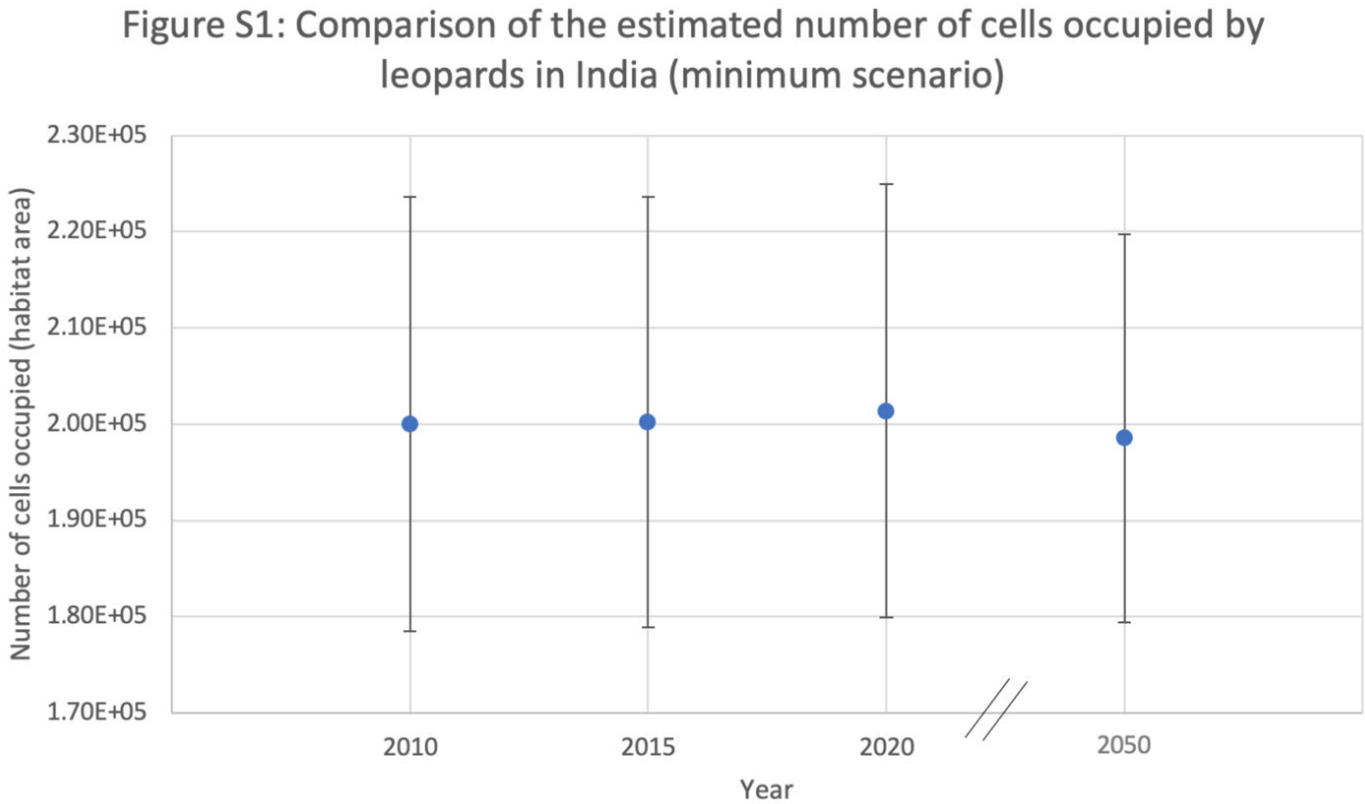

Figure S1: Comparison of habitat area in the minimum scenario in 2010, 2015, 2020 and 2050. It shows that the difference between climate, agriculture and urbanisation across each year is not estimated to significantly affect the habitat extent of leopards in India (95% confidence intervals overlap). Therefore, it was appropriate to use 2015 for my baseline analysis to approximate leopard range and abundance.

Figure S2: A Map to show the assessed leopard range estimated by Jhala et al. 2020

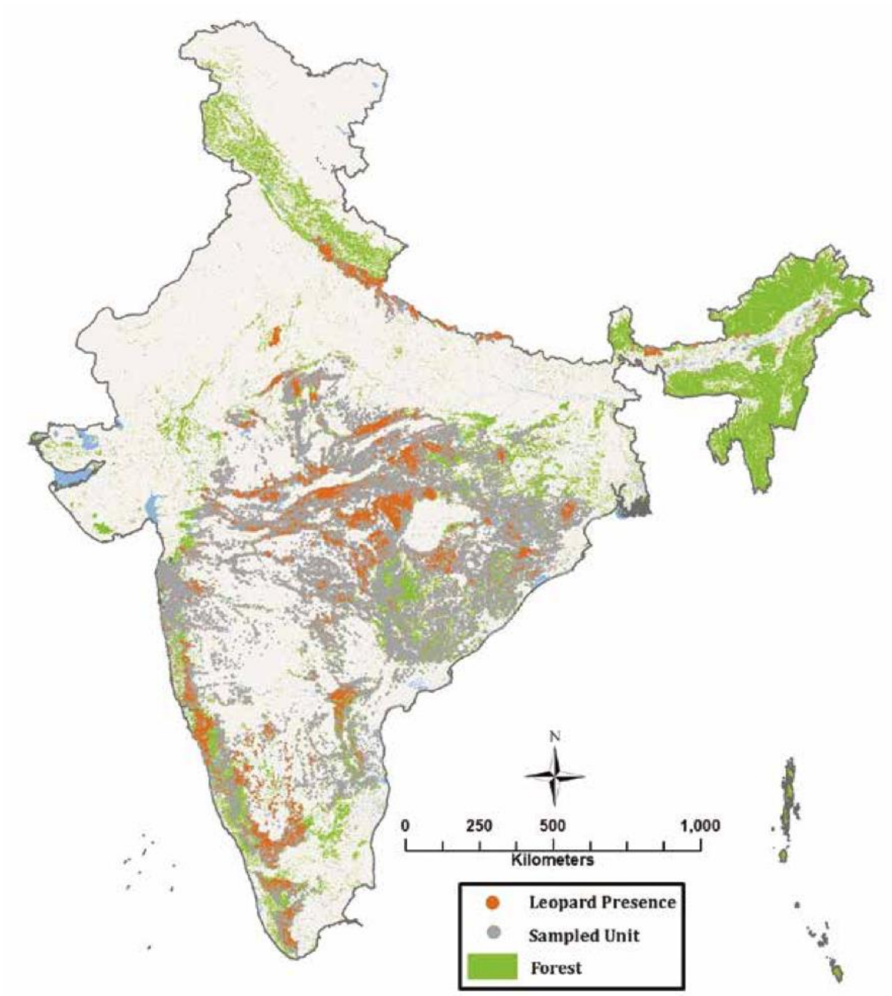

Figure S2: Leopard range map in 2018**, a**dapted from (Jhala, et al., 2020)**.** Likely leopard presence due to camera trapping and MaxEnt species distribution model outputs is shown in red. The Northeast could not be included in the abundance calculation due to lack of data. Furthermore, not all of India could be sampled (grey) so other habitat may have been missed. Analysis was only carried out in states and forests where tigers are also present. But leopards exist outside this area too (Jhala, et al., 2020). This study resulted in a less generous estimate of leopard range than (Jacobson, et al., 2016).

Figure S3: Comparison between the literature and two versions of Glob2Loc's minimum scenarios with different thresholds for leopard presence

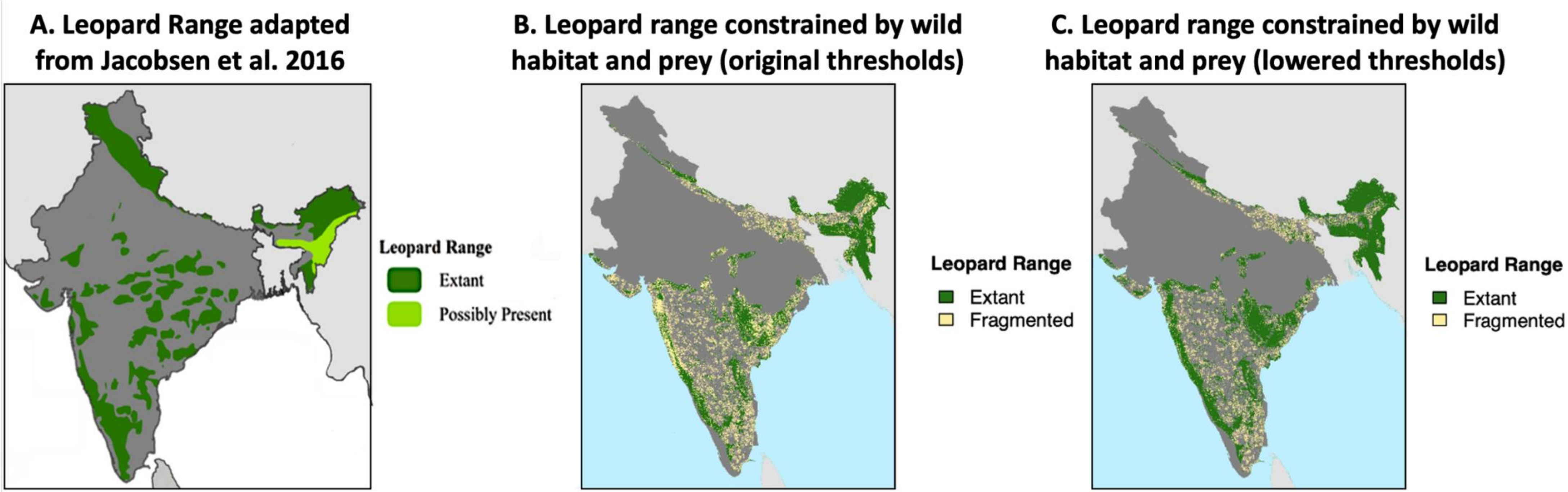

Figure S3: Comparison of observations of leopard range from the literature and my minimum scenario in Glob2Loc. Panel B is the same graph as Figure 3D ('Extant' = at least 50% natural land; 'Fragmented' = 1-50% natural land). Panel C represents a minimum scenario but modelled leopards to have a higher tolerance for human-use landscapes than Panel B. Panel C was constructed using lower thresholds for leopard presence and hence predicts more of India to contain Extant populations (green) and fewer fragmented populations (yellow) than Panel B. In Panel C, 'Extant' (green) represents cells that contain at least 25% natural habitat, and 'Fragmented' (yellow) cells represent areas with 1-25% natural habitat.

Figure S4: Comparison of Top Prey Species' Range from 2015 to 2050 in India According to Glob2Loc

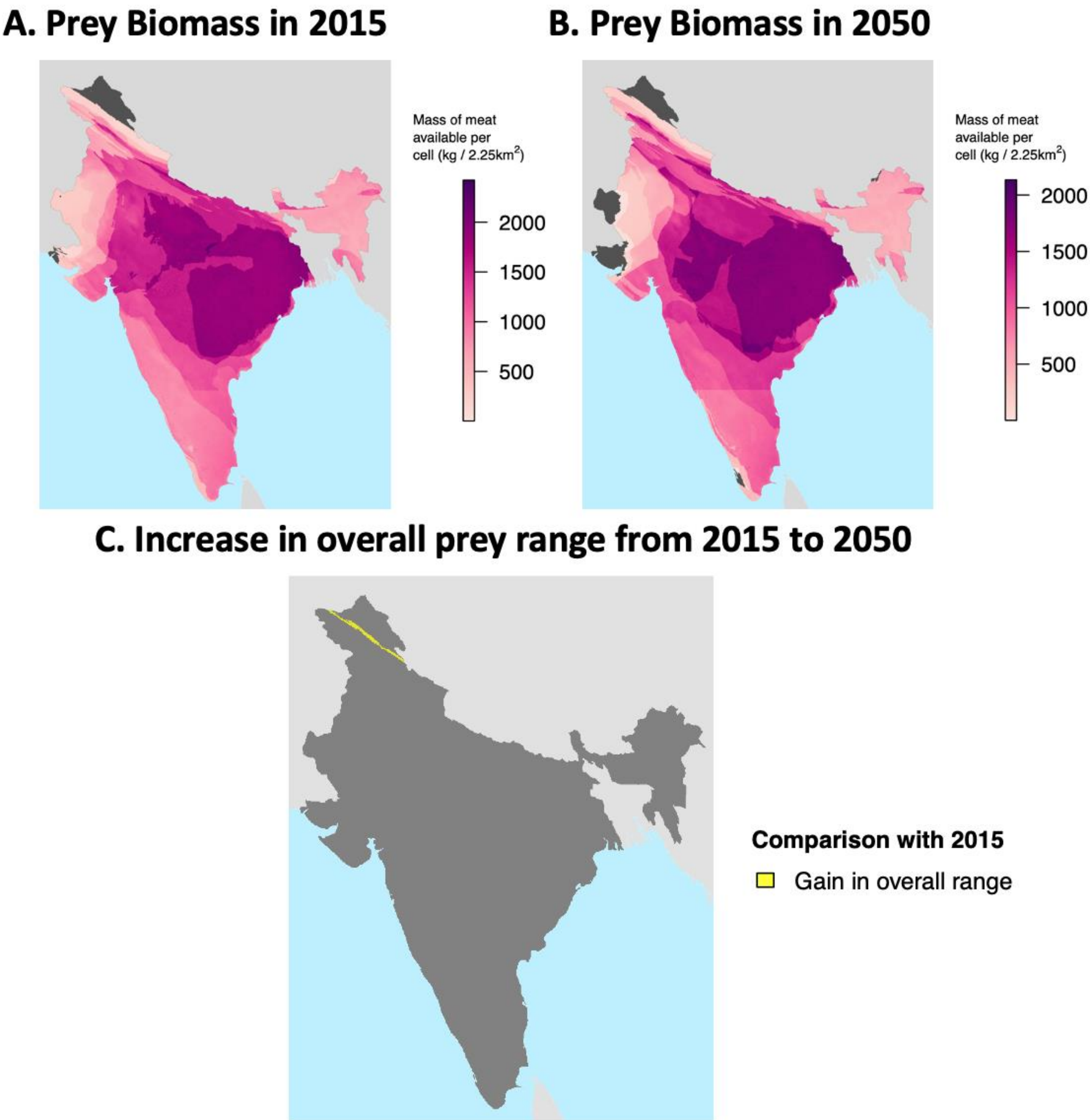

Figure S4: Glob2Loc predicted a marginal increase in overall prey range from 2015 to 2050 in North India (Panel C). Panels A and B illustrate total prey biomass in India in 2015 and 2050 by incorporating information on each species' habitat range, abundance, and body mass. Panel C only reports regions of India that Glob2Loc predicted to contain leopard prey species in 2050 that were unoccupied by prey in 2015.