A multi-scale environmental niche model for the endangered dhole (*Cuon alpinus*)

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Abstract

The dhole (*Cuon alpinus*) is a large canid at risk of global extinction. Information on the spatial distribution of suitable range areas may aid in conservation planning, but to date no range-wide distribution model exists for the dhole. We produced a multi-scale environmental niche model for dholes covering 12 current range countries. Our objectives were to quantify the spatial distribution of potential range as well as the relative probability of occurrence in identified areas. Potential dhole range were identified primarily in three regions: in western India, in central India, and across the Himalayan foothills through Southeast Asia. Most of the potential dhole range was identified in Southeast Asia, and potential range in this region also had higher relative probability of dhole occurrence than in regions. However, India was identified to harbor the highest proportion of potential dhole range among the countries within our study region. Connectivity appears to be poor both among the core regions as well as between suitable patches within each region. Dhole conservation may benefit from focusing its effort to Southeast Asia and India, and coordination of conservation action among these two regions should be a prioritized component of dhole conservation planning. We further highlight the value of improving population viability on unprotected land, especially since we there seems to be a need of improving connectivity among suitable range across different spatial scales. Finally, there seems to be a need for more monitoring activities in the northern parts of dhole's historic distribution, in particular areas within China.

Keywords: environmental niche model; maximum entropy; canidae, large carnivore; spatial conservation planning; human conflict

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Introduction

The dhole (*Cuon alpinus*, Pallas, 1811), or Asiatic wild dog, is a large, wide ranging carnivore facing global extinction. Dholes historically dominated large parts of alpine, temperate, tropical and sub-tropical forests across most of Asia (Kamler et al., 2015). However, dholes are currently confined to only 25% of their historical range, mostly within protected areas (Wolf & Ripple, 2017). The current global population is estimated to consist of 2000-2200 adults, with continued population declines projected (Kamler et al., 2015). Existing populations are small, isolated, and often exhibit severe population fluctuations (Kamler et al., 2015; Li et al., 2020). Primary reasons for the declining populations are habitat loss and fragmentation, persecution, prey depletion, interspecific competition and diseases (Davidar & Fox, 1975; Gopi et al., 2012; Kamler et al., 2015; Srivathsa et al., 2019). Given that the current threats to dhole population persistence are likely to increase in severity with increased human populations, there is a strong need for concrete conservation actions to protect the species from global extinction (Tananantayot et al., 2022).

Large carnivores, such as the dhole, are ecologically important and may function as important conservation umbrellas or as flagship species (Dalerum et al., 2008; Thinly et al., 2021). They are therefore important conservation targets (Gittleman et al., 2001). Large carnivores have large area requirements but may still adapt to human modified landscapes (Chapron et al., 2014). However, despite both past and present coexistence between humans and large carnivores, this group is highly prone to conflict (Woodroffe, 2000; Madden, 2004). Large home ranges and their generally hyper carnivorous diets frequently put them at odds with human activities, which may lead to legal or illegal persecution (Woodroffe, 2000; van Eeden et al., 2018). However, conflicts are not only caused by direct damage and threats but can also have cultural or socioeconomic dimensions (Treves & Karanth, 2003; Dalerum, 2021). Hence, carnivore conservation is a complex issue which includes both biological, physiological, economic and social aspects (Madden, 2004, Macdonald & Sillero-Zubiri, 2004). This makes carnivore conservation highly resource demanding, and prioritization is therefore necessary (e.g. Leader-Williams et al., 2010).

Considering the large area requirements of carnivores and the often spatially explicit nature of human-carnivore conflict, well informed strategies for spatial priorities may be particularly important for the success of large carnivore conservation and management (e.g., Eriksson & Dalerum, 2018). Such priorities require a comprehensive knowledge of current and potential distribution ranges of species under conservation or management concerns. Environmental niche models have proven to be particularly useful tools to identify potential distribution areas (Elith & Franklin, 2013). Using ecological knowledge of species-environment relationships, ecological niche models link species occurrences with environmental data to understand and predict species distributions (Zhu et al., 2013). Environmental niche models have been increasingly used to study a variety of topics within ecology, evolutionary biology and environmental management, including biological invasions, species' responses to climate change and spatial disease transmission (Zhu et al., 2013).

Among the multitude of proposed algorithms for environmental niche models, the MaxEnt algorithm has shown to be a robust method to predict the potential geographic distribution of species (Phillips et al., 2006; Phillips et al., 2017). The MaxEnt algorithm relies on maximum entropy to relate species occurrences to a set of environmental predictors (Elith et al., 2006), and belongs to a class of environmental niche models that only require occurrence data (Elith et al., 2011). Hence, inherent issues with logistic models based on uncertain pseudo-absences are largely removed (Ward et al., 2009). Despite a rapid development of new algorithms for occurrence only models, the MaxEnt algorithm is still among the highest performing in terms of predictive accuracy, and its output is closely correlated with empirical data (Valavi et al., 2021). Furthermore, it maintains high accuracy even with relatively low number of occurrence records (Wisz et al., 2008). However, as with other machine learning algorithms (Scowen et al., 2021), it tends to favor a level of complexity that renders it less useful for mechanistic understandings of how the environmental characteristics influence the potential for certain areas to be suitable as species ranges. For instance, many published MaxEnt models have well over 100 parameters, which limit their usefulness in terms of evaluations of mechanistic hypotheses related to how specific environmental characteristics influences potential species distributions.

In this study, we applied the MaxEnt algorithm to a data set of dhole occurrences covering a large extent of the species global distribution to create a map of potential range for the dhole, and to estimate the relative suitability for dholes within potentially suitable areas. We used the data presented in Kao et al. (2020) to adopt a multi-scale approach in which we used a coarse scale model to delineate potential dhole range, and a finer scale model to evaluate the relative probability of dhole occurrence within these areas. Our goal was to provide a quantitative assessment of the spatial distribution of potential dhole range to aid in the spatial planning and prioritization for dhole conservation (Guillera-Arroita et al., 2015). Our specific objectives were (i) to identify the spatial distribution of potential dhole range in 12 countries which all host dhole populations; and (ii) to quantify spatial variation in the relative probabilityof occurence for dholes within identified potential range. Although endangered with a high need of conservation action, previous distribution models for the species have all been done on regional to local scales (Nurvianto et al., 2015; Thinley et al., 2021 Havmøller et al 2022; Tananantayot et al., 2022). There is to date no peer-reviewed distribution model for the dhole that cover a large extent of the species current range. Such a model would allow for an informed quantification of the spatial distribution of suitable range, which is a requisite for any spatial prioritization of dhole conservation action. Hence, although we have not managed to compile data across the species full historical distribution (Kamler et al., 2015), we still regard our model to be a potentially valuable contribution towards the conservation and management of this endangered large carnivore.

Methods

Study Region

We included 12 countries in our study region. We grouped these countries into three subcontinents based on McColl (2005); China (including the mainland of People's Republic of China – hereafter referred to as "mainland China"), the Indian subcontinent (including Nepal, Bhutan, Bangladesh and India), and Southeast Asia (including Myanmar, Lao People's Democratic Republic – hereafter referred to as "Laos", Vietnam, Thailand, Cambodia, Malaysia, and Indonesia). Detailed descriptions of the environmental and socio-economic characteristics of these regions are given in Appendix 1.

Environmental variables and model grain

We considered 24 environmental variables associated with climate, ecological characteristics, geophysical characteristics and human environmental impact as the basis for our species distribution models (Appendix 2; Supplementary Table S1). Of these, we retained 20 uncorrelated variables ($R<0.8$) for the coarse scale and 19 for the fine scale model (Supplementary Table S2). All included variables have been regarded as important for determining the distribution of wide-ranging large carnivores (e.g. Swanepoel et al., 2013; Eriksson and Dalerum, 2018), and many have previously been used to model dhole distribution over local and regional scales (Nurvianto et al., 2015; Thinley et al., 2021; Havmøller et al 2022; Tananantayot et al., 2022).

Species distribution models, including ones fitted using the MaxEnt algorithm, are sensitive to grain sizes, i.e. the spatial scale at which environmental characteristics are linked to species observations (Gottschalk et al., 2011; Song et al., 2013). Therefore, we defined both coarse and fine scale grain sizes based on biologically meaningful information (Zarzo-Arias et al., 2019). We set the coarse scale grain size to 8 km x 8 km (64 km^2), which approximately corresponds to the average home range size reported for dholes (53.4 km^2, Acharya et. Al., 2010; Jenks et al., 2012; Srivathsa, et al., 2017). The fine scale grain size was set to 2 km x 2 km (4 km^2), which corresponds to estimated daily movement of dholes (2.2 km, Grassman et al., 2005) and similar species, e.g., Eurasian wolf (*Canis lupus lupus*) (2.5 km, Kusak et al., 2005). We outlined the coarse scale model area to contain the full study region but excluded cells with less than 50% of their area as land surface. We also excluded all islands smaller than 25,000 km^2., since we regard these islands too small to hold viable dhole populations. They could therefore be demographic sinks and not relevant from a conservation perspective. The fine scale model area was outlined as a subset of the coarse scale area, which only included areas identified as potential dhole range from the coarse scale model (see below). With these definitions, the coarse scale model region contained 240970 cells and the fine scale 390976 cells. We rescaled all environmental variables to these two resolutions (Appendix 2). The GIS processing was done with QGIS (version 3.26, http://www.qgis.org) and functions provided by the contributed package raster (version 3.5-15, Hijmans, 2022) for the statistical environment R (version 4.2.1, http://www.r-project.org, hereafter referred to as "R").

Dhole occurrence data

The dhole occurrence data was compiled during a workshop organized by the dhole working group of the IUCN SSC Canid Specialist Group, the IUCN SSC Conservation Planning Specialist Group, Smithsonian Conservation Biology Institute, Kasetsart University and the Khao Yai National Park in Thailand from 10-15 February, 2019 (Kao et al., 2020). The data set included the geographic locations of 1,604 dhole observations made from 1996 to 2018 (Appendix 2; Appendix 3; Supplementary Table S2; Supplementary Fig. S1a).

Spatial filtering of observation points has been suggested as a powerful mehtod to avoid potential sampling bias influencing the model fitting process of environmental niche models (Boria et al., 2014). We spatially filtered the raw observation data in two steps for each spatial scale before the occurrence data were used for the modeling . First, we only used one observation per cell. This filtered the 1604 raw dhole observations to 567 cells for the coarse scale model and 1011 cells for the fine scale model. Those records were further spatially filtered by only including observations at least 12 km apart, i.e., we only included one cell per each 3x3 cell neighborhood for the coarse scale and 6x6 cell neighborhood for the fine scale. We used a filtering algorithm based on finding the maximum number of observations while respecting a minimum nearest neighbor distance, implemented in the contributed R package spThin (version 0.2.0, Aiello-Lammens et al., 2015). This yielded final occurrence data consisting of 299 occurrence cells for the coarse scale (Supplementary Fig. 1b) and 291 cells for the fine scale (Supplementary Fig. 1c).

Environmental niche modeling

We used the java implementation of MaxEnt version 3.4.4 (Philips et al., 2017) called from R using the contributed packages dismo (version 1.3–3, Hijmans et al., 2021) and ENMeval (version 2.0.3, Kass et al., 2021). MaxEnt implements a maximum entropy approach to the presence only class of environmental niche models by associating species occurrences to environmental characteristics using five different feature types: linear, quadratic, product, threshold and hinge features (Phillips et al., 2006). This parameterization allows for the modeling of potentially complex relationships among environmental characteristics (Elith et al., 2011). Although machine learning algorithms, like the MaxEnt algorithm, generally favor more complex model solutions than likelihood-based algorithms, over-fitting can still be problematic (Warren & Seifert, 2011). The MaxEnt software controls over-fitting using a regularization parameter which penalizes variables with low contribution to the model. Since a MaxEnt model with any given data can have a large number of alternative parameterizations and regularization values, identification of the most parsimonious model and appropriate model tuning is an important part of MaxEnt modelling (Merow et al., 2013).

For each spatial scale, we created a model set including all types of feature combinations, each sequentially run over a set of regularization multipliers ranging from 0.1 to 10. From this set of 310 models, we identified the most parsimonious combination of feature types and regularization values using Akaike's Information Criterion corrected for small sample sizes (AICc) (Akaike, 1974). We calculated the AICc values from raw model output where the sum of the log transformed raw values were treated as equivalent to model likelihood (Warren & Seifert, 2011). Following Burnham & Anderson (2002), we regarded models within 2 AICc units of each other as having equivalent empirical support. We evaluated model performance using the AUC (Area Under a Receiver Operating Characteristic–ROC–Curve) value (Fielding & Bell, 1997) as well as three model performance metrics based on cross validation using a checkerboard method to separate our occurrence data into training and testing sets (Kass, 2021): AUC_{test} which describes the ability of testing locations to distinguish between background and presence locations), AUC_{diff} which describes the difference in the ability to distinguish between presence and background locations between training and test data (Warren & Seifert, 2011), and OR_{MTP} which is the proportion of test locations with a value below the lowest value of training locations (Kass, 2021). AUC values from 0.7 to 1 generally suggest that the model has adequate predictive ability (Araújo et al., 2005) whereas AUC_{diff} and OR_{MTP} values substantially above zero indicate over fitting.

Binary classification of potential range

We used the complementary log-log (cloglog) transformation of the raw MaxEnt values, which is bounded between 0 and 1, as the basis for summarizing the results (Phillips et al., 2017). To outline potential dhole range, we converted the cloglog output from the coarse scale model into a binary layer using the minimum cloglog score of any cell with dhole presence after the presence cells with the lowest 10% in cloglog scores had been omitted. This threshold corresponded to a cloglog score of 0.24. We therefore classified cells with cloglog scores at or above 0.24 to contain potential dhole range. The outline of these areas was used as the model region for the fine scale modeling (see above). Within potential dhole range, we evaluated the relative probability of dhole occurence directly as the cloglog values derived from the fine scale model (Phillips et al., 2017).

Estimation of variable contributions

We used three methods to evaluate the relative contribution of each environmental variable to the model of each spatial scale. First, we used a heuristic method which estimates the percent contribution of each variable to the MaxEnt solution as the proportional contribution to the model training gain for every iteration of the model fitting process (Phillips et al., 2006). Second, we calculated the regularized training gain for each variable when used by itself. This value, hence, indicated how useful a variable was for the model solution in isolation. Third, we used a jackknife procedure to evaluate how much regularized training gain was lost when each variable was omitted compared to the model including all variables. Thus, this method evaluated how much unique information each variable has among the ones included in the model.

Results

Model selection and model performance

The optimal coarse scale model included linear, product and threshold features introduced through 97 parameters and the optimal fine scale model included linear and threshold features introduced through 87 parameters. Both models had a regularization multiplier of 1.5. The models were 13.49 (coarse scale) and 5.16 (fine scale) AICc units above the model with the second lowest AICc scores (Appendix 2: Supplementary Table S3). Models of both scales showed high predictive accuracy, with AUC scores of 0.96 (Supplementary Fig. 2a) and 0.82 (Supplementary Fig. 2b), respectively, and high average AUC values based on the withheld testing data (coarse scale model: AUC_{test}=0.93; fine scale model: AUC_{test}=0.75). There were no indications of over fitting for either model, indicated by low differences between the training and testing data sets in respective AUC scores (coarse scale model: AUC_{diff}=0.03; fine scale model: AUC_{diff}=0.07), as well as minimum training presence omission rates close to zero for both models (OR_{MTP}=0.03 for both the coarse and the fine scale model, Appendix 2: Supplementary Table S3).

Distribution of potential dhole range and relative probability of dhole occurrence

Potential dhole range was identified in three general regions; one along the west coast of India, one in central east India, and one across the foothills of the Himalaya, which continued south through Southeast Asia (Fig. 1). Most of the potential dhole range were identified in Southeast Asia (56%), although a substantial part of the areas was also identified in India (33%, Fig. 2a). Bhutan had the highest proportion of its land area identified as potential dhole range (80%), and all countries within Southeast Asia had above or close to 30% of their land areas identified as potential range (Fig. 2b). Bhutan as well as several countries within Southeast Asia had among the highest average relative probability of dhole occurrence (Fig. 2c), and the relative probability of dhole occurrence was on average higher in Southeast Asia (0.38 ± 0.24) than on the Indian subcontinent (0.36 ± 0.23) and in mainland China (0.36 ± 0.17).

Variable contributions

The two variables that contributed most to both the coarse and the fine scale models were land protection status (coarse scale 37%; fine scale 59%) and temperature seasonality (coarse scale 26%; fine scale 13%), with land protection status having a substantially higher contribution to the fine scale than the coarse scale model (Fig. 3). Land protection was positively associated with dhole range suitability, for both the coarse (Appendix 2; Supplementary Fig. S3a) and the fine scale models (Appendix 2; Supplementary Fig. S3b), whereas temperature seasonality either showed a non-monotonic (coarse scale: Appendix 2; Supplementary Fig. S3a) or bimodal relationship with dhole range suitability (fine scale: Appendix 2; Supplementary Fig. S3b). Other important variables identified by the heuristic test included tree cover (12%), elevation (6%), densities of medium-sized livestock (4%) and annual mean temperature (3%) for the coarse scale (Fig. 3a), and human population density (5%), annual precipitation (5%), precipitation of the wettest month (3%) and tree cover (3%) for the fine scale (Fig. 3b). In line with these results, protected area was the most useful informative variable on its own, as well as the variable carrying most unique information when combined with all other variables, for both the coarse (Fig. 4a) and the fine scale model (Fig. 4b). Other variables identified as having a relatively high importance on their own, as well as holding a relatively high amount of unique information, included temperature seasonality and tree cover for the coarse scale model and temperature seasonality, annual precipitation, and the different live-stock densities for the fine scale model. Marginal response curves, explaining how each variable was related to the model output scores, are given in Appendix 2: Supplementary Fig. S3.

Discussion

We identified three major regions containing the majority of potential dhole range; one along the west coast of India, a second in central India, and a third across the foothills of the Himalayas which continued Southeast through Southeast Asia. These regions largely coincide with earlier studies (e.g. Thinley et al., 2021; Tananantayot et al., 2022). However, these three regions are not directly connected, and particularly the central Indian and the eastern region appear to contain heavily fragmented patches of suitable areas for the dhole. Hence, we believe that our study points to the importance of identifying and securing dispersal corridors among potential range areas for dhole range management (e.g. Rodrigues et al., 2022). Growing environmental problems coupled with a shortage of financial resources to address them require rigid and informed priorities for conservation investment (Wilson et al. 2006). While previous studies using environmental niche models for the dhole has been conducted over local to regional scales (Nurvianto et al., 2015; Thinley et al., 2021; Havmøller et al., 2022; Tananantayot et al., 2022), our model included major parts of this species range. Hence, although it may have had somewhat lower predictive accuracy on local scales compared to models trained on only a subset of the region included in this study, our approach enabled us to do large scale comparisons among regions and countries that could potentially host this endangered carnivore. Hence, our modeling approach provide important information for guiding future conservation action of this species.

We identified most of the potential dhole range in Southeast Asia, which also had slightly higher average probability of occurrence that mainland China and the Indian subcontinent. However, India contained the largest proportion of potential dhole range among any of the individual countries. The high importance of India was similarly identified by Kamler et al. (2015) and Srivathsa et al. (2020), who suggested that India is the range country that harbors the largest dhole population. On a smaller spatial scale, Cambodia, Malaysia and in particular Bhutan stand out as countries with very large parts of their territories potentially suitable for dholes. All of these countries, together with Thailand, also have among the highest relative probability of occurrence. Hence, our study partly agrees with the findings of Tananantayot et al. (2022), who identified Cambodia, Malaysia and Laos as strongholds of dhole habitat within Southeast Asia, and with Thinley et al. (2022), who found that dholes were distributed across all 20 districts of Bhutan. Historically, dholes were distributed throughout Sumatra and Java, in Indonesia (Kamler et al., 2015), but today their distribution on these islands is heavily reduced (Havmøller et al., 2022). This study found more potential range in Sumatra compared to Java, and the greater distance to the mainland populations raises further concerns for the future of dholes on Java. Our model identified a limited distribution of potential range in mainland China. Dholes have been observed in the northwest of China and occasional observations have been reported from isolated sites in the Kunlun Mountains, the Karakoram Mountains, the Qilian Mountains and the Altun Mountains during the past two decades (e.g., Riordan et al., 2015; Xue et al., 2015). These observations may represent relict populations that are adapted to arid and semi-arid deserts and alpine habitats from Central Asia to northwestern China. These are quite different habitat types from those found on the Indian subcontinent and in Southeast Asia, and the demographic responses to environmental variation ,including human persecution, may have different in these northern regions compared to more tropical areas.

Many forests in Southeast Asia are largely empty of large mammals due to human persecution (Steinmetz et al., 2014; Phumanee et al., 2020). Thus, our model may have identified potential dhole range in forests where dholes have been extirpated. For example, a snaring crisis in eastern Indochina (Laos, Cambodia, and Vietnam) has resulted in the recent extirpation of tigers and leopards from these countries despite suitable forests and prey still occurring there (Rasphone et al., 2019; Rostro-García et al., 2023). Similarly, dhole numbers and distribution in eastern Indochina are greatly reduced and fragmented in this region because of indiscriminate snaring. Therefore, dholes are absent from many areas of this region. Because our model did not consider the impacts of widespread indiscriminate snaring, the potential for dholes to inhabit potential dhole range identified in eastern Indochina may be limited, at least until the current snaring crisis has been curfed. Similarly, since we lacked reliable prey densities across appropriate spatial scales we did not include prey abundance in our analyses. We recognize that both human persecution and prey abundance are key variables determining the distribution of carnivores (Dalerum et al., 2008), including dholes (Thinley et al., 2021; Tananantayot et al., 2022). However, by not including these variables, environmental niche models can effectively be used to explicitly identify areas where carnivore distribution is limited not by habitat suitability, but by persecution of the carnivores themselves or by persecution of their prey (e.g., Eriksson and Dalerum, 2018). In particular, range limitations imposed by humans killing dholes and their prey require further quantification (e.g. Everatt et al., 2019), and we suggest that combining environmental niche models with prey abundance data may be a fruitful way of doing so (e.g., Thinley et al., 2021; Tananantayot et al., 2022).

The three identified regions of potential dhole range are geographically separated, and our models also suggest that two of the three regions appear to be internally fragmented. Similarly, Tananantayot et al. (2022) also noted a heavy fragmentation of suitable dhole range within Southeast Asia, and Rodrigues et al. (2022) made similar observations for India. For species which only remain in small populations, such a lack of population connectivity can be very detrimental for long-term population persistence (e.g. Finnegan et al., 2021). In South Africa, for instance, the poor connectivity of sub-populations of the African wild dog (*Lycaon pictus*), a species which share many characteristics with the dhole, led to the drastic decision of creating an artificial meta-population in which animals were actively translocated among carefully selected sites to maintain viable sub-populations (Mills et al., 1998). This has been at least a partial conservation success (Nicholson et al., 2020), which highlights the importance of maintaining demographic connectivity for species in fragmented landscapes. While we do not believe that an artificial meta-population approach may be realistic for the dhole across Asia, we suggest that connectivity both between and within regions containing suitable dhole habitat may be critical for the long-term survival of the species. Such connectivity must, by definition, focus largely on matrix habitats outside protected areas, which re-iterates earlier suggestions that improving connectivity among population strongholds may yield significant conservation benefits (Prugh et al., 2008).

Of the evaluated environmental variables, land protection and temperature seasonality were important for both spatial scales. While the level of complexity in our selected models, i.e. 97 parameters for the coarse scale and 87 for the fine scale model, prevents us from drawing any detailed conclusions regarding how these two variables influence dhole distribution, we still regard their importance informative. Protected land was positively associated with dhole range suitability. While we recognize that this relationship may partly have been caused by sampling bias, it does agree with previous suggestions that the persistent dhole populations are largely restricted to protected land (Kamler et al., 2015; Thinley et al., 2021). Since livestock density was also an important variable, human-dhole conflict may be a limiting factor for dhole distribution, similar to the situation for several other large carnivores (Srivestha et al 2020, Thinley et al., 2021, Ghimerey et al 2023). Preserving viable populations of wide-ranging carnivores within protected areas is usually not viable (Finnegan et al., 2021), which further highlights the necessity of focusing dhole conservation on unprotected land. Temperature seasonality also had a high influence on both scales, but with either non-monotinic or bimodal relationships with dhole range suitability. Temperature seasonality may influence almost all aspects of terrestrial ecosystems (Lisovski et al., 2017), and the observed relationships with range suitability highlight the complex effects climate may have on species distributions. However, we suggest that the importance of temperature seasonality largely reflects the optimal environmental conditions for this species, but that these optimal climate conditions may be conditioned on local factors such as prey availability and competition. The relative importance of the other environmental variables differed between the two scales. The importance of different environmental characteristics as well as the scale dependencies observed in the relative importance of different variables highlight the complexities involved with defining a species environmental niche, espetially for species with broad niche tolerances.

We recognize that our observation data was biased towards tropical areas, and that we had an extremely limited number of dhole observations from mainland China. Despite our rigid spatial filtering, this could have caused our model to discriminate against identifying potential range areas in the northern parts of the species historical distribution. We recognize that the bias in observations towards tropical regions could have been caused by prioritizing field efforts to areas where a species is most likely to be observed (Guillera-Arroita, et al., 2015). If true, we argue the observations we used to train the models may reflect at least a large portion of the current distribution of the dhole, albeit not it's full historical one. For instance, Kamler et al (2015) reported widespread and long running persecution campaigns against carnivores in the northern regions of dhole historic range, and that dholes likely disappeared from large areas of central and southern China during the 1980s and early 1990s. Hence, we suggest that our model likely represent a fair quantification of the spatial distribution of areas suitable for the dhole. None the less, we propose to use regional models for smaller scale applications. We also suggest that dynamic scale optimization, which have been used for instance for brown bear (*Ursus arctos*) and snow leopards (*Panthera uncia*) (Mateo-Sánchez et al., 2013; Atzeni et al. 2020; but see McGarigal et al., 2016), may be a useful method to further improve the spatial accuracy of range predictions for species with very broad, or even plastic, habitat tolerances such as the dhole. We also encourage further studies focusing quantifying the distribution status of dholes in the northern parts if its historical distribution, including China, as well as studies aimed at identifying the ecological requirements of dholes in these northern regions.

Apart from the potential sampling bias, we offer some additional caveats to our study. First, after appropriate spatial filtering we had a relatively limited sample sizes of dhole occurrences, which corresponded to only approximately 1 out of 1000 cells having had a dhole occurrence. However, MaxEnt has been regarded as robust to limited sample sizes (Wisz et al., 2008), and sampling biases associated with spatially un-filtered observations may decline the performance of environmental niche models more than training the models on a more limited number of filtered observations (Boria et al., 2014). Second, our observations had a large time span, including data collected over a period of more than 20 years. There may therefore have been a spatio-temporal mismatch between the observational data and some of the environmental characteristics. However, grouping the observational data into shorter periods would lead to further reductions in sample sizes, which means that models on temporally pooled data likely are the most informative. Additionally, the snaring crises in eastern Indochina has resulted in local extinctions of apex carnivores, including dholes, in the region. Therefore, dholes may not occur in seemingly suitable areas due to excessive poaching by humans. Finally, highlight that the MaxEnt algorithm, just as many other machine learning algorithms, are subject to both conceptual and data related issues which may cause problems both in model predictions and model interpretations (Araújo & Gusian, 2006; Varela et al., 2014). We have tried to minimize these issues by making biologically justified choices of the environmental variables and the model grain,. We have also used objective criteria in our a rigorous model selection approach (Warren and Siefert, 2011) and the decision of a cut off point to delineate potential range. We therefore believe that the decisions behind our models were based on biological information and objective analytical criteria, at least as far as was possible with the information at hand.

To conclude, potential dhole range were identified in three disparate regions, and connectivity appear limited both among and within these regions. Hence, we suggest that conservation action may benefit from focusing on activities in the three identified regions, but also on actions aimed to understand and improve connectivity among dhole populations. Since the majority of potential dhole range was identified in Southeast Asia, and countries within this region also had a higher proportion of their total land area identified as potential dhole range, special emphasis may be given to dhole conservation in central and Southeast Asia. However, India was identified as the country which harbors the highest proportion of potential dhole range among any of the individual countries, which agree with previous suggestions that India likely also harbors the largest proportion of the global dhole population. Coordinating conservation efforts among regions in India and Southeast Asia could subsequently be a key aspect of further dhole conservation planning. We subsequently encourage trans boundary conservation initiatives integrating areas in southern China, Myanmar, northeast India, Nepal and Bhutan. Our study also highlight the need for more monitoring and assessments of dhole population status and restoration potential in the northern parts of its historic distribution, including in mainland China. Finally, we suggest that focusing dhole conservation on population persistence on un-protected land may be key to the long-term population viability of this species, both by improving connectivity among highly suitable patches but also by avoiding issues of maintaining viable populations of wide-ranging species within restricted protected areas.

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Author contributions

MPK, FD, KK and WW conceptualized the study and drafted the manuscript. MPK and FD conducted GIS processing and spatial analyses. All other authors contributed data and provided comments on the manuscript.

Conflicts of interest

None.

References

Acharya, B.B., Johnsingh, A.J.T. & Sankar, K. (2010) Dhole telemetry studies in Pench Tiger Reserve, central India. *Telemetry in Wildlife Science*, 13, 69–79.

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B. & Anderson, R.P. (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography*, 38, 541-545.

Akaike, H. (1974) A new look at the statistical model identification. IEEE *Transactions on Automatic Control,* 19, 716–723.

Araújo, M.B., Thuiller, W., Williams, P.H. & Reginster, I. (2004) Downscaling European species atlas distribution to a finer resolution: implications for conservation planning. *Global Ecology and Biogeography,* 14, 17–30.

Atzeni, L., Cushman, S.A., Bai, D., Wang, J., Chen, P., Shi, K. & Riordan, P. (2020). Meta-replication, sampling bias, and multi-scale model selection: A case study on snow leopard (*Panthera uncia*) in western China. *Ecology and Evolution*, 10, 7686–7712.

Boria, R.A., Olson, L.E., Goodman, S.M. & Anderson, R.P. (2014) Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling,* 275, 73–77.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multi-model Inference: A practical information-theoretic approach.* Springer-Verlag, New York.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M. & Huber, D. (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science,* 346, 1517–1519.

Dalerum, F., Somers, M.J., Kunkel, K.E. & Cameron, E. Z. (2008) The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodiversity and Conservation,* 17, 2939–2949.

Dalerum, F. (2021) Socioeconomic characteristics of suitable wolf habitat in Sweden. *Ambio,* 50, 1259–1268.

Davidar, E.R.C. & Fox, M.W. (1975) Ecology and behavior of the dhole or Indian wild dog *(Cuon alpinus).* In *The wild canids: their systematics, behavioral ecology and evolution* (eds. M.W. Fox), pp. 109-119. Van Nostrand Reinhold Company, New York.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M. & Ferrier, S. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography,* 29, 129–151.

Elith, J. & Franklin, J. (2013) Species distribution modeling. In *The Encyclopedia of Biodiversity* (eds. S.A. Levin), pp. 692-705. Elsevier, Amsterdam.

Eriksson, T. & Dalerum, F. (2018) Identifying potential areas for an expanding wolf population in Sweden. *Biological Conservation,* 220, 170-181.

Everatt, K.T., Moore, J.F. & Kerley, G.H. (2019) Africa's apex predator, the lion, is limited by interference and exploitative competition with humans. *Global Ecological Conservation,* 20, e00758.
Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence-absence models. *Environment Conservation,* 24**,** 38–49.
Finnegan, S.P., Galvez-Bravo, L., Silveira, L., Tôrres, N.M., Jácomo, A.T.A., Alves, G.B. & Dalerum, F. (2021) Reserve size, dispersal and population viability of wide-ranging carnivores: the case of jaguars in Emas National Park, Brazil. *Animal Conservation,* 24**,** 3-14.
Ghimirey Y, Acharya R, Yadav K, et al. (2024) Challenges and possible conservation implications of recolonizing dholes Cuon alpinus in Nepal. *Oryx*, online early. Doi:10.1017/S003060532300073X
Gittleman, J.L., Funk, S.M., MacDonald, D.W. & Wayne, R.K. (2001) *Carnivore Conservation*. Cambridge University Press, Cambridge.
Gopi, G., Habib, B., Lyngdoh, S. & Selvan, K.M. (2012) *Conservation of the endangered asiatic wild dog (Cuon alpinus) in western Arunachal Pradesh: linking ecology, ethics and economics to foster better coexistence.* Wildlife Institute of India, Dehradun.
Grassman, L.I., Tewes, M. E., Silvy, N. J., Kreetiyutanont, K. (2005) Spatial ecology and diet of the dhole (*Cuon alpinus*) in north Central Thailand. *Mammalogy,* 69**,** 11–20.
Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., McCarthy, M.A., Tingley, R. and Wintle, B.A. 2015. Is my species distribution model fit for purpose? Matching data and models to applications. Global Ecology and Biogeography 24: 276-292.
Havmøller, L. W., Havmøller, R. W., Nawangsari, V.A., Pratiwi, A., Møller, P.R. & Træholt, C. (2022). Status and conservation of dholes in Indonesia. *Canid Biology and Conservation,* 24, 4-12.
Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2021) *dismo: Species Distribution Modeling*. R package version 1.3-5. https://CRAN.R-project.org/package=dismo.
Hijmans, R.J. (2022) *raster: Geographic Data Analysis and Modeling*. R package version 3.5-15. https://CRAN.R-project.org/package=raster.
Jenks, K.E., Songsasen, N. & Leimgruber, P. (2012) Camera trap records of dholes in Khao Ang Rue Nai Wildlife Sanctuary, Thailand. *Canid News,* 15, 1–5.
Kamler, J.F., Songsasen, N., Jenks, K., Srivathsa, A., Sheng, L. & Kunkel, K. (2015) *Cuon alpinus*. The IUCN Red List of Threatened Species. Version 2015: e.T5953A72477893. http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T5953A72477893.en. Accessed 7 March 2023.
Kao, J., Songsasen, N., Ferraz. & Traylor-Holzer, K. (2020) *Range-wide population and habitat viability assessment for the Dhole, Cuon alpinus*.IUCN SSC Conservation Planning Specialist Group, Apple Valley.
Kass, J.M., Muscarella, R., Galante, P.J., Bohl, C.L., Pinilla-Buitrago, G.E., Boria, R.A., et al. (2021) ENMeval 2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. *Methods in Ecology and Evolution,* 12, 1602-1608.
Kusak, J., Skrbinšek, A.M. & Huber, D. (2005) Home ranges, movements, and activity of wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. *European Journal of Wildlife Research,* 51, 254-262.
Leader-Williams, N., Adams, W.M. & Smith, R.J. (eds.) (2010) *Trade-offs in Conservation*: *Deciding what to save.* Chichester: Wiley-Blackwell, Oxford.
Li, S., McShea, W.J., Wang, D., Gu, X., Zhang, X., Zhang, L. & Shen, X. (2020). Retreat of large carnivores across the giant panda distribution range. *Nature Ecology and Evolution,* 4, 1327-1331.

Lisovski, S., Marilyn, R. & John, C. W. (2017) Defining the degree of seasonality and its significance for future research. *Integrative and Comparative Biology,* 57, 934-942.
Macdonald, D. W. & Sillero-Zubiri, C. (2004) Conservation: From theory to practice, without bluster. In *The Biology and Conservation of Wild Canids:* (eds. D.W. MacDonald & C. Sillero-Zubiri), pp. 353-372. Oxford University Press, Oxford.
Madden, F. (2004) Creating coexistence between humans and wildlife: global perspectives on local efforts to address human–wildlife conflict. *Human Dimensions of Wildlife,* 9, 247–257.
Mateo-Sánchez, M., Cushman, S., & Saura, S. (2013). Scale dependence in habitat selection: The case of the endangered brown bear (*Ursus arctos*) in the Cantabrian Range (NW Spain). International *Journal of Geographical Information Science*, 28, 1531–1546.
McColl, R.W. (2005) *Encyclopedia of World Geography.* Facts on File Inc, New Yorks, USA.
McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., & Cushman, S. A. (2016). Multi-scale habitat selection modeling: A review and outlook. *Landscape Ecology*, 31, 1161–1175.
Mills, M.G.L., Ellis, S., Woodroffe, R., Maddock, A., Stander, P., Rasmussen, G., et al. (1998) *Population Habitat and Viability Assessment for the African Wild Dog (Lycaon pictus) in Southern Africa.*IUCN/SSC Conservation Breeding Specialist Group, Pretoria.
Ngoprasert, D., Gale, G.A., & Tyre, A. J. (2019) Abundance estimation from multiple data types for group-living animals: An example using dhole (*Cuon alpinus*). *Global Ecology and Conservation*, 20, e00792.
Nicholson, S.K., Marneweck, D.G., Lindsey, P.A., Marnewick, K. & Davies-Mostert, H.T. (2020) A 20-year review of the status and distribution of African wild dogs (*Lycaon pictus*) in South Africa. *South African Journal of Wildlife Research,* 50, 8-19.
Nurvianto, S., Imron, M.A. & Herzog, S. (2015) The influence of anthropogenic activities and availability of prey on the distribution of dholes in a dry deciduous forest of East Java, Indonesia. *Asian Journal of Conservation Biology,* 4, 26–36.
Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modelling of species geographic distributions. *Ecological Modelling,* 190, 231–259.
Phillips, S.J., Anderson, R.P., Dudík, M., Shapire, R.P. & Blair, M.P. (2017) Opening the black box: an open-source release of Maxent. *Ecography,* 40, 887–903.
Phumanee, W. Steinmetz, R., Phoonjampa, R., Bejraburnin, T., Grainger, M. & Savini, T. (2020) Occupancy-based monitoring of ungulate prey species in Thailand indicates population stability, but limited recovery. *Ecosphere,* 11, e03208.
Prugh, L., Hodges, K.E., Sinclair, A.R.E. & Brashares, J.S. (2008) Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences,* 105, 20770-20775.
Rasphone, A., Kéry, M., Kamler, J. F. & Macdonald, D. W. (2019) Documenting the demise of tiger and leopard, and the status of other carnivores and prey, in Lao PDR's most prized protected area: Nam Et-Phou Louey. *Global Ecology and Conservation,* 20, e00766.
Riordan, P., Wang, J., Shi, K., Fu, H., Dabuxilike, Z., Zhu, K. & Wang, X. (2015) New evidence of dhole *Cuon alpinus* populations in north-west China. *Oryx,* 49, 203-204.
Rodrigues, R.G., Srivathsa, A. & Vasudev, D. (2022) Dog in the matrix: envisioning countrywide connectivity conservation for an endangered carnivore. *Journal of Applied Ecology,* 59, 223–237.

Rostro-García, S., Kamler, J. F., Sollmann, R., Balme, G., Augustine, B. C., Kéry, M., et al. (2023) Population dynamics of the last leopard population of eastern Indochina in the context of improved law enforcement. *Biological Conservation,* 283, e110080.

Scowen, M., Athanasiadis, I. N., Bullock, J. M., Eigenbrod, F. & Willcock, S. (2021) The current and future uses of machine learning in ecosystem service research. *Science of The Total Environment*, 799, e149263.

Srivathsa, A., Narayanarao, K. & Karanth, K. (2017) Field report: Home range size of the dhole estimated from camera- trap surveys. *Canid Biology and Conservation,* 20, 1-4.

Srivathsa, A., Karanth, K.U., Kumar, N.S. & Oli, M.K. (2019) Insights from distribution dynamics inform strategies to conserve a dhole (*Cuon alpinus)* metapopulation in India. *Scientific Reports,* 9, 3081.

Srivathsa, A., Sharma, S., Singh, P., Punjabi, G.A. & Oli, M.K. (2020) A strategic road map for conserving the Endangered dhole (*Cuon alpinus)* in India. *Mammal Review*, 50, 399-412.

Steinmetz, R., Srirattanaporn, S., Mor-Tip, J. & Seuaturien, N. (2014) Can community outreach alleviate poaching pressure and recover wildlife in Southeast Asian protected areas? *Journal of Applied Ecology*, 51,1469-1478.

Swanepoel, L.H., Lindsey, P., Somers, M.J., va Hoven, W. & Dalerum, F. (2013) Extent and fragmentation of suitable leopard habitat in South Africa. *Animal Conservation,* 16, 41-50.

Tananantayot, J., Agger, C., Ash, E., Aung, S.S., Baker-Whatton, M.C., Bisi, F. et al. (2022) Where will the dhole survive in 2030? Predicted strongholds mainland Southeast Asia. *Conservation Science Practice,* 4, e12831.

Thinley, P., Rajaratnam, R., Kamler, J.F. & Wangmo, C. (2021) Conserving an endangered canid: assessing distribution, habitat protection, and connectivity for the Dhole (*Cuon alpinus*) in Bhutan. *Frontiers in Conservation Science,* 2, 654976.

Treves, A. & Karanth, K.U. (2003) Human–carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology,* 17, 1491–1499.

van Eeden, L.M., Eklund, A., Miller, J.R.B., López-Bao, J.V. & Chapron, G. (2018) Carnivore conservation needs evidence-based livestock protection. *PLoS Biology,* 16, e2005577.

Valavi, R., Elith, J., José, J., Lahoz-Monfort. & Guillera-Arroita, G. (2021) Modelling species presence-only data with random forests. *Ecography,* 44, 1731-1742.

Ward, G., Hastie, T., Barry, S., Elith, J. & Leathwick, J.R. (2009) Presence-only data and the EM algorithm. *Biometrics,* 65, 554– 563.

Warren, D.L. & Seifert, S. (2011). Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications,* 21, 335-342.

Wilson, K.A., McBride, M.F., Bode, M., & Possingham, H.P. (2006) Prioritizing global conservation efforts. *Nature*, 440, 337–340

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., Elith, J. et al. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions,* 14, 763-773.

Wolf, C. & Ripple, W.J. (2017). Range contractions of the world's large carnivores. *Royal Society Open Science*, 4, 170052.

Woodroffe, R. (2000) Predators and People: using human densities to interpret declines of large carnivores. *Animal Conservation,* 3,165-173.

Xue, Y., Li, D., Xiao, W., Zhang, Y., Feng, B. & Jia, H. (2015) Records of the dhole (*Cuon alpinus*) in an arid region of the Altun Mountains in western China. *European Journal of Wildlife Research*, 61, 903-907.

Zarzo-Arias, A., Penteriani, V., Delgado, M.D.M., Peón Torre, P., Garcia-Gonzalez, R., Mateo-Sánchez, M.C., et al. (2019) Identifying potential areas of expansion for the endangered brown bear (*Ursus arctos*) population in the Cantabrian Mountains (NW Spain). *PLoS One,* 14, e0209972.

Zhu, G, Liu, G., Bu, W. & Gao, Y. (2013) Ecological niche modeling and its applications in biodiversity conservation. *Biodiversity Science,* 21, 90–98.

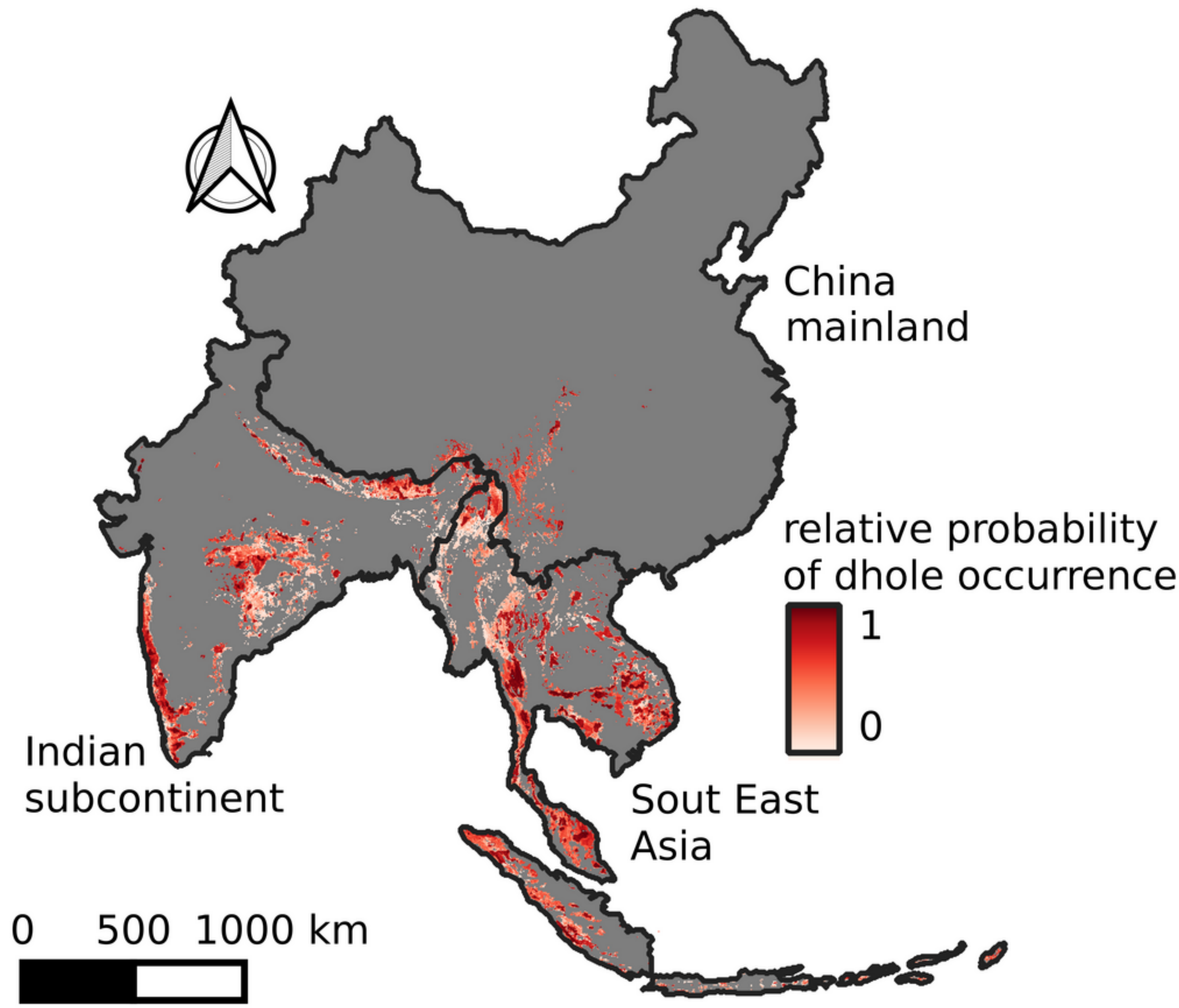

Fig. 1 Distribution of potential dhole range and the relative probability of dhole occurrence for 12 countries within three sub-continents of Asia. The distribution of potential range was estimated from a binary classification of the output from a MaxEnt model with a 8 km x 8 km resolution conducted across the whole study region, and relative probability of occurrence within these areas was estimated as the complementary log-log transformation of a MaxEnt model with 2 km x 2 km resolution conducted within potential range.

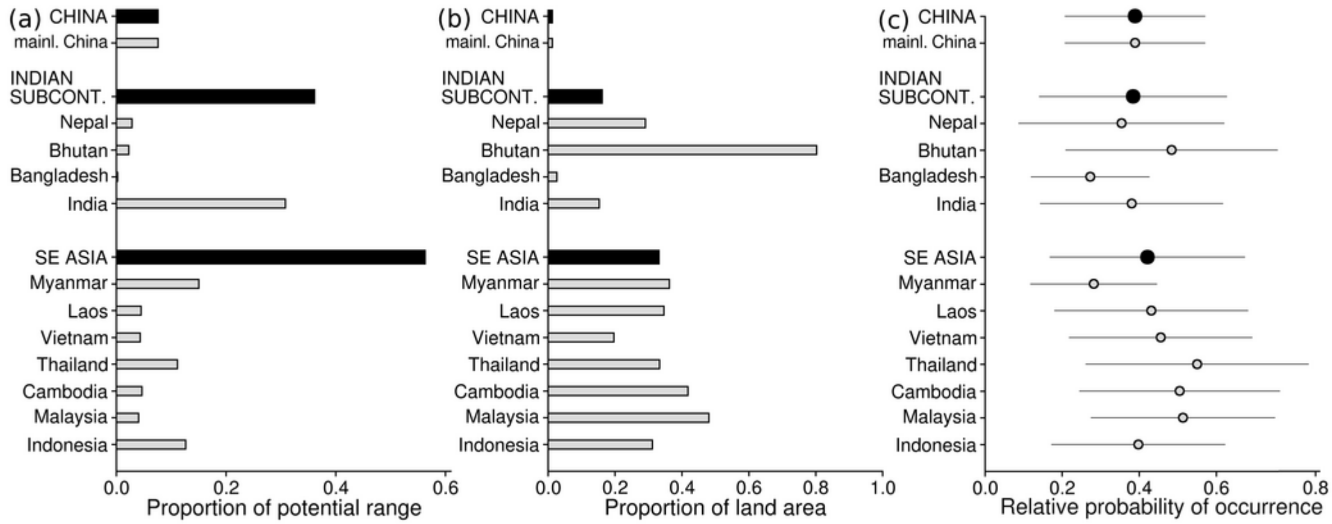

Fig. 2 Proportion of potential dhole range (a), proportion of land area identified as potential dhole range (b) and average (± sd) dhole range suitability (c) within three major Asian subcontinents as well as within each country. Potential dhole range was estimated from a binary classification of the output from a MaxEnt model with a 8 km x 8 km resolution conducted across the whole study region, and relative range suitability was estimated as the complementary log-log transformation of the output from a MaxEnt model with 2 km x 2 km resolution conducted within identified potential range.

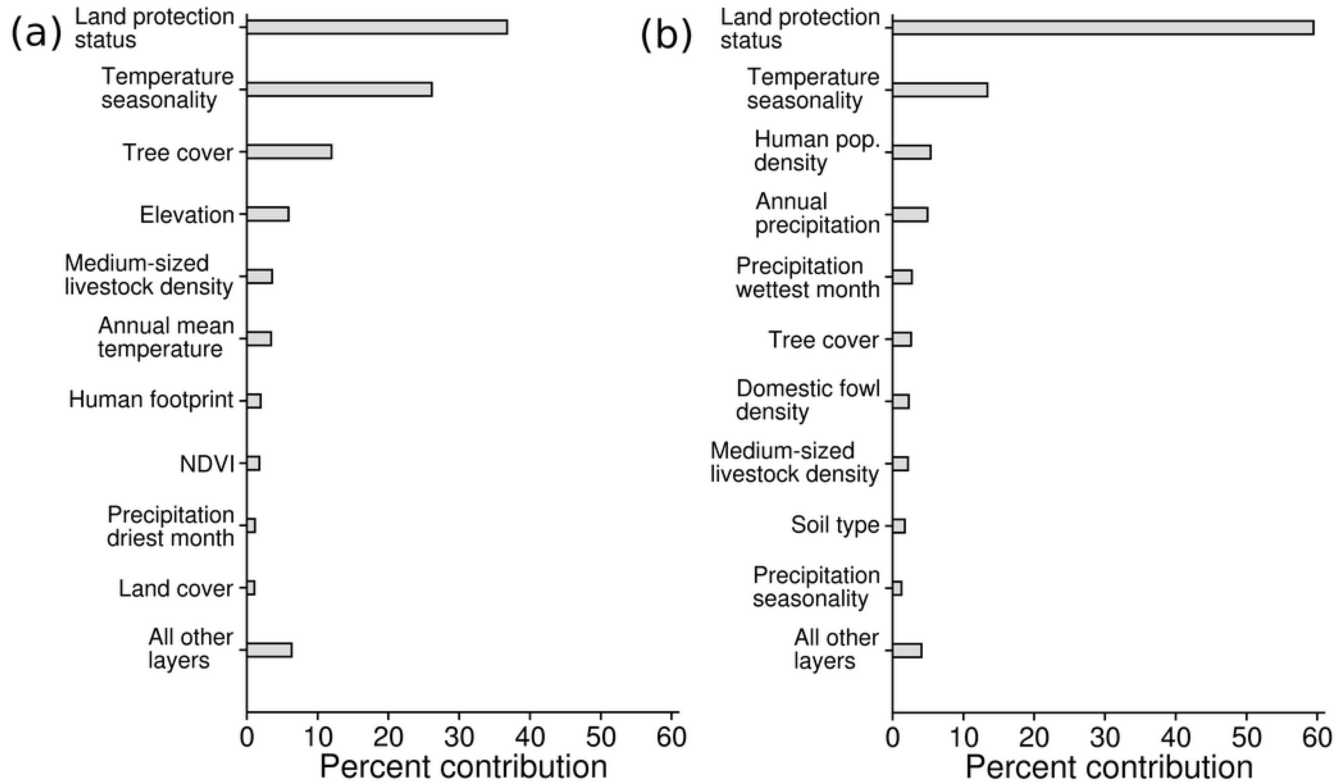

Fig. 3 Percentage contribution of environmental variables to a coarse scale (8 km x 8 km, a) and a fine scale (2 km x 2 km, b) MaxEnt model of potential dhole range. Percentage contribution was based on a heuristic method which estimates the proportional contribution of each variable to the model training gain for every iteration of the model fitting process.

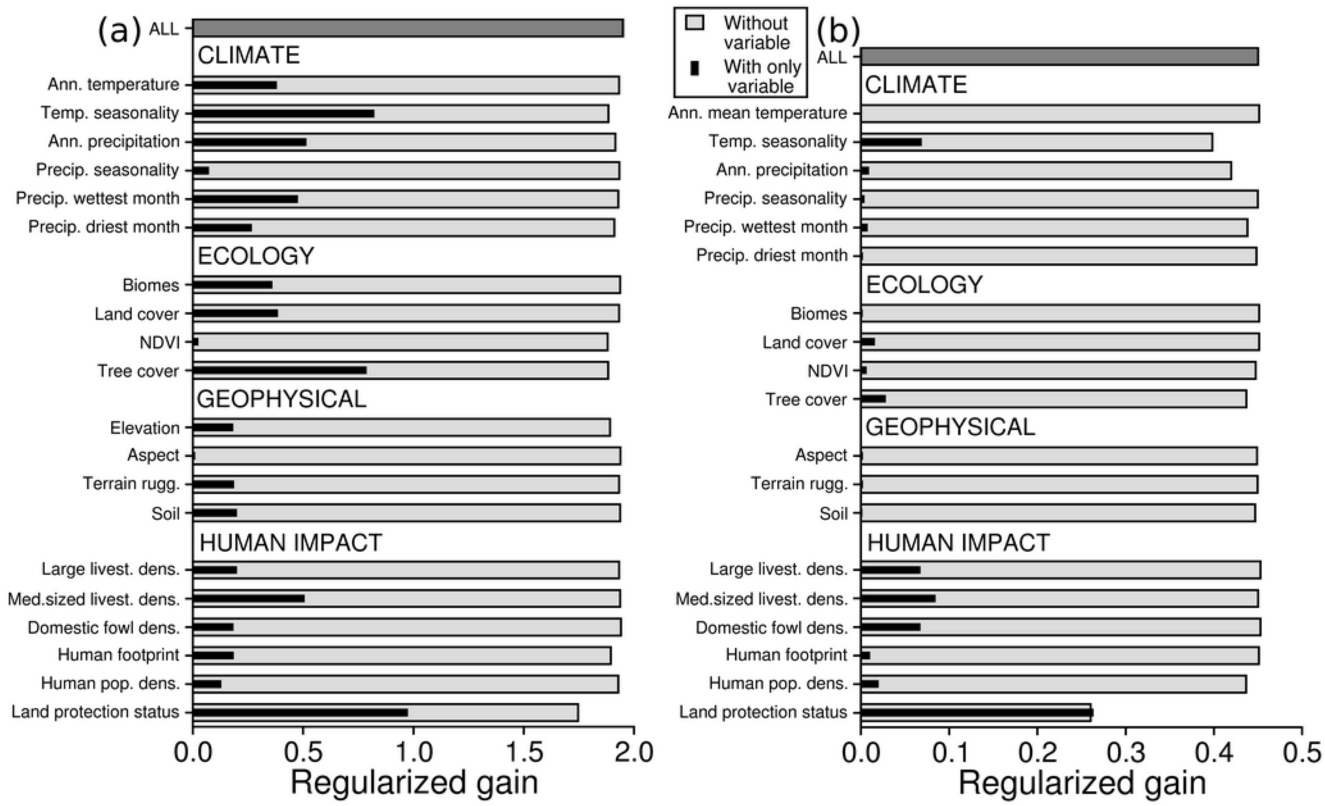

Fig. 4 Jacknife tests of variable contributions to a coarse (8 km x 8 km, a) and a fine (2 km x2 km, b) scale MaxEnt model of potential dhole range. Each graph shows the regularized gain when a variable is used on its own (black bars) as well as the loss in regularized gain when it is removed from the full model (grey bars).