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 that is categorized as Endangered on the IUCN Red List and at risk of global extinction. Information on the spatial distribution of suitable habitat is important for conservation planning but is largely unavailable. We quantified the spatial distribution of potential range as well as the relative probability of dhole occurrence across large parts of the species' global range. We used the MaxEnt algorithm to produce a multi-scale environmental niche model based on 24 environmental variables and dhole occurrence data from 12 countries. We identified three regions where dhole conservation should be focused: western India, central India, and across the Himalayan foothills through Southeast Asia. Connectivity between suitable areas was poor, so coordinated action among these regions should be a priority. For instance, transboundary dhole conservation initiatives across the Himalayas from southern China, Myanmar, north-east India, Nepal and Bhutan need to be

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initiated. We also highlight the value of improving dhole population viability on unprotected land and increasing monitoring in the northern parts of its historic distribution, in particular in areas within mainland China.

Keywords Canidae, *Cuon alpinus*, dhole, environmental niche model, human–wildlife conflict, large carnivores, maximum entropy, spatial conservation planning

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Introduction

The dhole or Asiatic wild dog *Cuon alpinus* is a large (10–20 kg), wide-ranging carnivore facing global extinction. In the past, dholes occurred in large areas of alpine, temperate, tropical and subtropical forests across most of Asia (Kamler et al., 2015) but they are now confined to just 25% of their historical range, mostly within protected areas (Wolf & Ripple, 2017). Existing populations are small, isolated, and often exhibit severe local population fluctuations (Kamler et al., 2015; Li et al., 2020). The current global population is estimated to be 1,000–2,200 adults, with further population declines projected as a result of continuing habitat loss and fragmentation, persecution, prey depletion, interspecific competition and disease (Davidar & Fox, 1975; Gopi et al., 2012; Kamler et al., 2015; Srivathsa et al., 2019). These threats are expected to increase in severity with human population growth, and concrete conservation action is needed to protect the species from global extinction (Tananantayot et al., 2022).

Large carnivores such as dholes are ecologically important and often act as umbrella and flagship species for conservation (Gittleman et al., 2001; Dalerum et al., 2008; Thinley et al., 2021). However, their carnivorous diet and need for large areas of suitable habitat frequently bring them into conflict with people (Woodroffe, 2000; Madden, 2004; Chapron et al., 2014). Although coexistence is possible, legal and illegal persecution sometimes happens, with associated cultural and socio-economic repercussions (Woodroffe, 2000; Treves & Karanth, 2003; van Eeden et al., 2018; Dalerum, 2021).

Carnivore conservation is a complex and resource-intensive issue where competing factors have to be prioritized (Macdonald & Sillero-Zubiri, 2004; Madden, 2004; Leader-Williams et al., 2010). Spatial prioritization should be based on a comprehensive knowledge of the current and potential distribution of the species of conservation concern (e.g. Eriksson & Dalerum, 2018). Environmental niche models are particularly useful tools that use ecological information to link occurrence and environmental data to understand and predict species distributions (Elith & Franklin, 2013; Zhu et al., 2013). They are used widely in ecology, evolutionary biology and environmental management to investigate a broad range of issues including biological invasions, the effects of climate change and spatial disease transmission (Zhu et al., 2013).

The MaxEnt algorithm is a robust method of predicting the potential geographic distribution of a species (Phillips et al., 2006, 2017). It relies on maximum entropy to relate species occurrence data to a set of environmental predictors (Elith et al., 2006), and belongs to a class of environmental niche models that require occurrence data only (Elith et al., 2011). Therefore, inherent issues with logistic models based on uncertain pseudo-absences are largely removed (Ward et al., 2009). Despite the rapid development of new algorithms for occurrence-only models, the MaxEnt algorithm is still among the best 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 a relatively low number of occurrence records (Wisz et al., 2008). However, as with other machine learning algorithms (Scowen et al., 2021), it tends to favour a level of complexity that renders it less useful for a mechanistic understanding of how specific environmental characteristics influence the potential for certain areas to be suitable habitat for the target species (many published MaxEnt models have well over 100 parameters).

We applied the MaxEnt algorithm to dhole occurrence data to create a map of potential range and to estimate the relative suitability of these areas (Kao et al., 2020). We used a coarse-scale model to delineate the potential range and a finer-scale model to evaluate the relative probability of dhole occurrence within these areas. Previous distribution models on dholes are limited to regional or local scales (Nurvianto et al., 2015; Thinley et al., 2021; Havmøller et al., 2022; Tananantayot et al., 2022). Our objective was to aid spatial planning and prioritization for dhole conservation across large parts of the global range, including areas not currently occupied (Guillera-Arroita et al., 2015). Specifically, we aimed to (1) identify the spatial distribution of potential dhole range in 12 countries within the species' known range and (2) quantify spatial variation in its relative probability of occurrence. This information is a prerequisite for effective dhole conservation management planning.

Study area

We included 12 countries in our study, which we grouped into three subcontinents based on McColl (2005): China (including the mainland of the 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 (Lao PDR), Viet Nam, Thailand, Cambodia, Malaysia and Indonesia). Detailed descriptions of the environmental and socio-economic characteristics of these regions are available in Supplementary Material 1.

Methods

Environmental variables and spatial scale

We selected 24 environmental variables known to influence the distribution of large, wide-ranging carnivores (e.g. Swanepoel et al., 2013; Eriksson & Dalerum, 2018), many of which 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). They are associated with climate, ecology, geophysical factors and human impact. Of these, we retained 20 uncorrelated variables ($R < 0.8$) for the coarse-scale model and 19 for the fine-scale model (Table 1).

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). 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 8×8 km (64 km^2), which approximates to the mean home range size reported for dholes (53.4 km^2; Acharya et al., 2010; Jenks et al., 2012; Srivathsa et al., 2017). We set the fine-scale grain size to 2×2 km (4 km^2), which corresponds to the estimated daily movement of dholes (2.2 km; Grassman et al., 2005) and similar species such as the Eurasian wolf *Canis lupus lupus* (2.5 km; Kusak et al., 2005). We specified the coarse-scale model area as the entire study region, but excluded grid cells that were largely aquatic (i.e. where land comprised less than 50% of the area). We also excluded all islands smaller than 25,000 km^2 because we regarded these areas as too small to hold viable dhole populations. Such small islands could act as demographic sinks and would thus not be relevant from a conservation perspective. The final coarse-scale model contained 240,970 cells of 8×8 km. We specified the fine-scale model area as those cells identified as potential dhole range in the coarse-scale model, resulting in 390,976 cells of 2×2 km. We rescaled all environmental variables to the two grain sizes using *QGIS 3.26* (QGIS Development Team, 2023) and functions provided by *raster 3.5-15* (Hijmans, 2022) for the statistical environment *R 4.2.1* (R Core Team, 2023).

Dhole occurrence data and spatial filtering

We compiled a dataset of 1,604 geographical locations of dholes observed during 1996–2018 (Supplementary Material 2; Supplementary Table 2; Supplementary Fig. 1a). Data were provided by participants in a workshop co-organized by the dhole working group of the IUCN Species Survival Commission (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 in 2019 (Kao et al., 2020).

Spatial filtering is a powerful method of reducing sampling bias to improve the performance of environmental niche models (Boria et al., 2014). We filtered our raw occurrence data in two stages for each spatial scale, using an algorithm based on finding the maximum number of observations while respecting a minimum nearest-neighbour distance, implemented in *R spThin 0.2.0* (Aiello-Lammens et al., 2015). Firstly, we restricted the dataset to one observation per cell, which reduced the number of dhole observations from 1,604 to 567 cells for the coarse-scale model and to 1,011 cells for the fine-scale model. Secondly, we only included one record per 3×3 cell neighbourhood at the coarse scale and one record per 6×6 cell neighbourhood at the fine scale (i.e. if there were multiple records in such a neighbourhood, they were represented as a single data point in the centre of that neighbourhood). Therefore, the minimum nearest-neighbour distance was 12 km. The final dataset comprised 299 cells at the coarse scale (Supplementary Fig. 1b) and 291 cells at the fine scale (Supplementary Fig. 1c).

Environmental niche modelling

We ran the Java version of *MaxEnt 3.4.4* (Phillips et al., 2017), implemented in *R* using the packages *dismo 1.3–3* (Hijmans et al., 2021) and *ENMeval* v*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 occurrence with environmental characteristics using linear, quadratic, product, threshold and hinge features (Phillips et al., 2006). This parameterization allows for the modelling of potentially complex relationships among environmental characteristics (Elith et al., 2011). Although machine learning algorithms such as MaxEnt generally favour more complex model solutions than likelihood-based algorithms, over-fitting can still be problematic (Warren & Seifert, 2011). The MaxEnt software controls for over-fitting by using a regularization parameter

TABLE 1. Environmental layers used to model range suitability for the dhole *Cuon alpinus*, as well as whether or not each variable was included in a coarse- (8 × 8 km) and a fine-scale (2 × 2 km) MaxEnt model. Only variables with a correlation of 0.8 or less with any other variable were included in each model.

Variables	Description	Units	Resolution	Source	Coarse scale	Fine scale
Climate						
Annual mean temperature (B01)	Annual daily mean air temperatures averaged over 1 year	°C	30 arc sec	Karger et al. (2021)	Yes	Yes
Temperature seasonality (B04)	Standard deviation of the monthly mean temperatures	°C	30 arc sec	Karger et al. (2021)	Yes	Yes
Maximum temperature of warmest month (B05)	Highest daily mean temperature of any month	°C	30 arc sec	Karger et al. (2021)	No	No
Minimum temperature of coldest month (B06)	Lowest daily mean temperature of any month	°C	30 arc sec	Karger et al. (2021)	Yes	No
Annual Precipitation (B12)	Accumulated precipitation amount over 1 year	mm	30 arc sec	Karger et al. (2021)	Yes	Yes
Precipitation seasonality (B15)	Monthly precipitation expressed as % of the annual mean	%	30 arc sec	Karger et al. (2021)	Yes	Yes
Precipitation of wettest month (B13)	Precipitation of the wettest month	mm	30 arc sec	Karger et al. (2021)	Yes	Yes
Precipitation of driest month (B14)	Precipitation of the driest month	mm	30 arc sec	Karger et al. (2021)	Yes	Yes
Isothermality (B03)	Ratio of diurnal to annual variation in temperatures	NA	30 arc sec	Karger et al. (2021)	No	No
Ecology						
Biome	Areas with similar habitat conditions	Categorical[1]	Vector	Olson et al. (2001)	Yes	Yes
Land cover	Discrete land cover classed using both supervised & unsupervised algorithms	Categorical[2]	300 m	Arino et al. (2012)	Yes	Yes
Tree cover	Canopy closure for all vegetation taller than 5 m	%	1 arc sec	Hansen et al. (2013)	Yes	Yes
Normalized difference vegetation index (NDVI)	An index of primary productivity	Continuous, no unit	250 m	Jenkerson et al. (2010)	Yes	Yes
Geophysical characteristics						
Elevation	Obtained from global multiscale terrain elevation data	m	30 arc sec	Danielson & Gesch (2011)	Yes	No
Aspect	Aspect calculated from 225 m resolution digital elevation model (DEM)	Northness (-1 to 1)	7.5 arc sec	Danielson & Gesch (2011)	Yes	Yes
Slope	Slope calculated from 225 m resolution DEM	° (degrees)	7.5 arc sec	Danielson & Gesch (2011)	No	No
Terrain ruggedness	Terrain ruggedness calculated from 225 m resolution DEM	Continuous, no unit	7.5 arc sec	Danielson & Gesch (2011)	Yes	Yes
Soil	Global soil categorization	Categorical[3]	Vector	FAO (2015)	Yes	Yes
Human impact						
Large livestock	Density of horses, cattle, buffaloes	Animals/km^2	5 arc sec	Gilbert et al. (2018)	Yes	Yes
Medium-sized livestock	Density of goats, pigs, sheep	Animals/km^2	5 arc sec	Gilbert et al. (2018)	Yes	Yes
Domestic fowl	Density of ducks, geese, chickens	Animals/km^2	5 arc sec	Gilbert et al. (2018)	Yes	Yes
Human footprint	Index of the human pressure on the environment	Continuous, no unit	30 arc sec	Gilbert et al. (2018)	Yes	Yes
Human population density	Density of the human population resident in the area	Persons/km^2	30 arc sec	CIESIN (2016)	Yes	Yes
Land protection status	Land protection status	Categorical[4]	Vector	UNEP-WCMC & IUCN (2022)	Yes	Yes

[1]Biomes: tropical & subtropical moist broadleaf forests; tropical & subtropical dry broadleaf forests; temperate broadleaf & mixed forests; tropical & subtropical coniferous forests; temperate conifer forests; boreal forests/taiga; tropical & subtropical grasslands, savannahs and shrublands; temperate grasslands, savannahs and shrublands; flooded grasslands & savannahs; montane grasslands & shrublands; deserts & xeric shrublands; mangroves & snow.
[2]Land-cover classes: cultivated terrestrial areas and managed lands; woody trees; herbs; shrubs; natural and semi-natural aquatic vegetation; artificial surfaces; bare areas.
[3]Soil categories: soils with clay-enriched subsoils; soils with little or no profile differentiation, pronounced accumulation of organic matter in the mineral top soil; soils distinguished by Fe/Al chemistry; soils with thick organic layers; soils with limitations to root growth; soils formed from the arid climate; shallow soils rich in humus formed from carbonates; soils with depth surface.
[4]Protected area classes: protected; not protected.

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that penalizes variables with low contribution to the model. As 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 important (Merow et al., 2013).

We created a set of 310 models including combinations of all five types of feature (i.e. linear, quadratic, product, threshold and hinge features), each sequentially run over a set of regularization multipliers ranging from 0.1 to 10 for each spatial scale. We then identified the most parsimonious combination of feature types and regularization values using the Akaike information criterion corrected for small sample sizes (AICc; Akaike, 1974). We calculated the AICc values from raw model output where the sums of the log transformed raw values were treated as equivalent to model likelihood (Warren & Seifert, 2011). Following Burnham & Anderson (2002), we regarded models within two AICc units of each other as having equivalent empirical support. We evaluated model performance using the value of the area under the receiver operating characteristic curve (AUC; 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 et al., 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 (minimum training presence omission rate; Kass et al., 2021). AUC values from 0.7 to 1.0 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 the 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% of cloglog scores had been omitted. This corresponded to a cloglog score of 0.24 and we classified cells at or above this threshold as potential dhole range. The outline of these areas was used as the model region for the fine-scale modelling. We evaluated the relative probability of dhole occurrence as equivalent to 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 at each spatial scale. Firstly, we used a heuristic method that estimates the percentage 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). Secondly, we calculated the regularized training gain for each variable when used by itself, indicating how useful each variable was for the model solution. Thirdly, we used a jackknife procedure to evaluate how much regularized training gain was lost when each variable was omitted compared to when all variables were included in the model, indicating how much unique information was contributed by each variable.

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 (Supplementary Table 2). Models at both scales showed high predictive accuracy, with AUC scores of 0.96 for the coarse-scale model (Supplementary Fig. 2a) and 0.82 for the fine-scale model (Supplementary Fig. 2b), and high mean 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 (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; Supplementary Table 2).

Distribution of potential dhole range and relative probability of dhole occurrence

We identified potential dhole range in three regions: along the west coast of India, in central east India, and across the foothills of the Himalaya and continuing south through Southeast Asia (Fig. 1). The largest area was in Southeast Asia (56% of the total potential dhole range identified) with a further 33% in India (Fig. 2a). We identified 80% of Bhutan as potential dhole range, the highest proportion of any country, and $\geq$ 30% of land as potential dhole range in all countries in

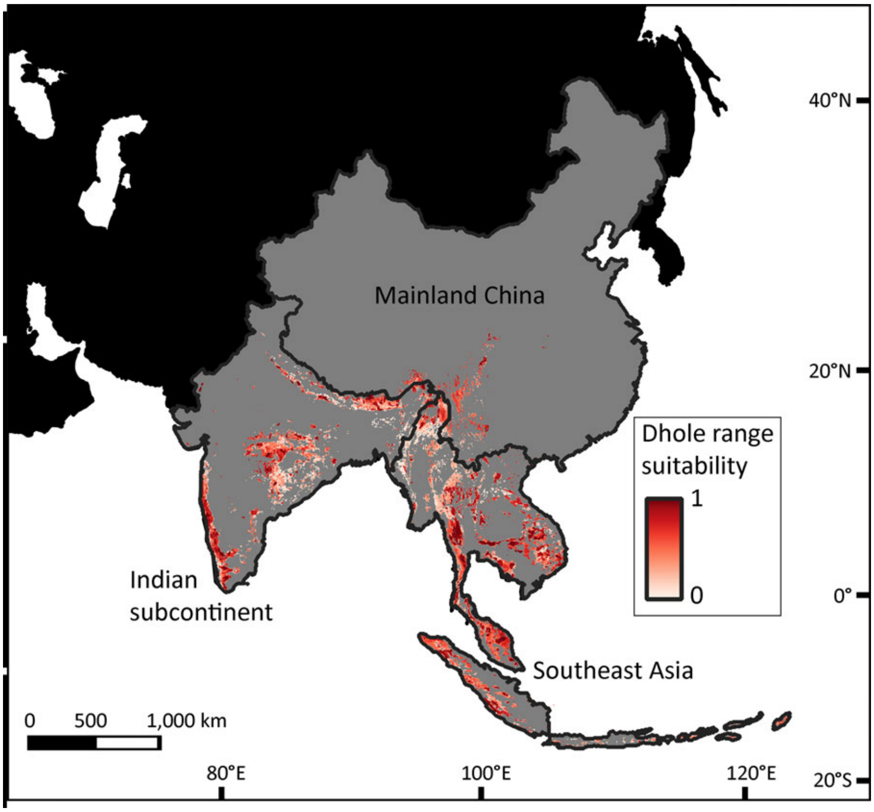

FIG. 1 Distribution of potential dhole range and the relative probability of dhole *Cuon alpinus* occurrence for 12 countries across the Indian subcontinent, Southeast Asia and mainland China. We estimated the distribution of the potential range across the study area from a binary classification of the output from a MaxEnt model with 8 × 8 km resolution, and the relative probability of occurrence as the complementary log–log transformation of the output from a MaxEnt model with 2 × 2 km resolution.

Southeast Asia (Fig. 2b). The highest mean relative probability of dhole occurrence was in Bhutan, Thailand, Cambodia and Malaysia (Fig. 2c), and the relative probability of dhole occurrence was on average higher in Southeast Asia (0.38 ± SD 0.24) than on the Indian subcontinent (0.36 ± SD 0.23) or in mainland China (0.36 ± SD 0.17).

Contributions made by environmental variables

Land protection status (coarse-scale 37%; fine-scale 59%) and temperature seasonality (coarse-scale 26%; fine-scale 13%) contributed most to the models at both spatial scales, with land protection status contributing substantially more to the fine-scale model (Fig. 3). Land protection was positively associated with dhole range suitability for both models (Supplementary Figs 3 & 4), whereas temperature seasonality showed a non-monotonic relationship with dhole range suitability in the coarse-scale model (Supplementary Fig. 3) and a bimodal relationship in the fine-scale model (Supplementary Fig. 4). Other important variables were tree cover (12%), elevation (6%), density of medium-sized livestock (4%) and annual mean temperature (3%) for the coarse-scale model (Fig. 3a), and human population density (5%), annual precipitation (5%), precipitation of the wettest month (3%) and tree cover (3%) for the fine-scale model (Fig. 4). Overall, land protection status was the most informative variable individually and carried the most unique information when combined with all other variables (Fig. 4a,b). Temperature seasonality and tree cover were important individually and contributed high levels of unique information to the coarse-scale model and, likewise, temperature seasonality, annual precipitation and livestock density contributed to the fine-scale model. Marginal response curves showing how the predicted probability of dhole presence changes as each environmental parameter is varied while keeping all other predictors constant are provided in Supplementary Figs 3 and 4.

Discussion

Most areas identified as potential dhole range were located in three major regions; one along the west coast of India, a second in central India, and a third across the foothills of the Himalayas and continuing through Southeast Asia. These regions largely coincide with those identified in earlier studies (Thinley et al., 2021; Tananantayot et al., 2022). However, these three regions are not directly connected, and dhole habitat is heavily fragmented particularly in the central Indian and the eastern regions. Hence, it is important to identify and secure dispersal corridors between areas of potential dhole habitat (Rodrigues et al., 2022). As environmental problems increase and financial resources to address them are limited, robust and evidence-based approaches are required to determine priorities for

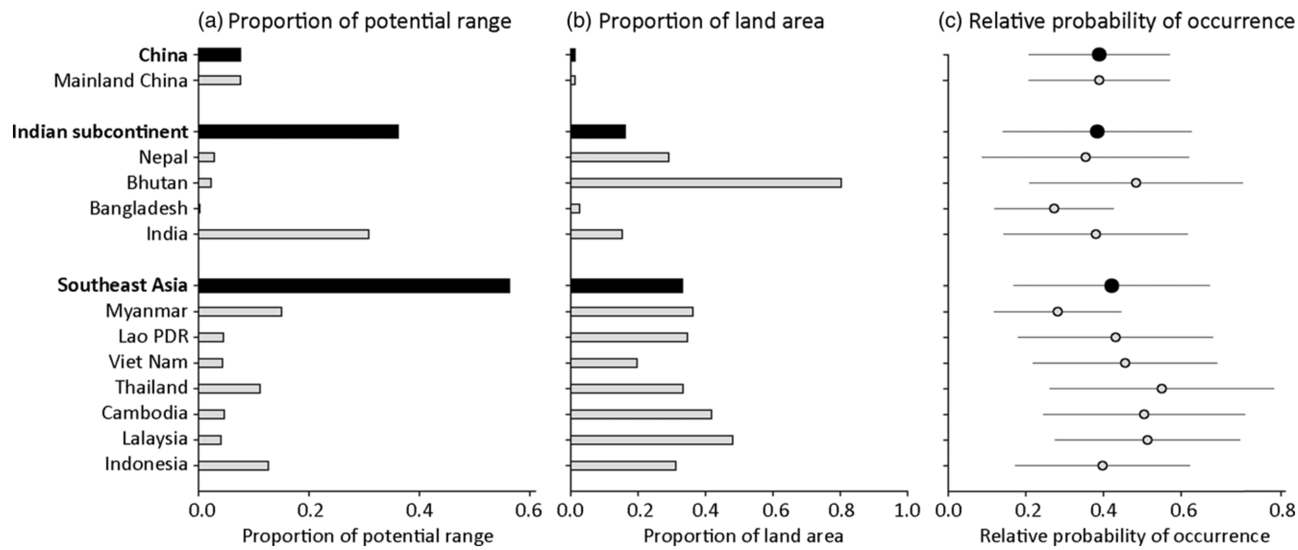

FIG. 2 Results of our analysis of the dhole's potential range and relative probability of occurrence for 12 countries across three regions: (a) proportion of potential dhole range per region and country, (b) proportion of land area within each region and country identified as potential dhole range, (c) mean ± SD relative probability of occurrence across the regions and counties. We estimated the potential dhole range across the study area from a binary classification of the output from a MaxEnt model with 8 × 8 km resolution, and the relative probability of occurrence as the complementary log–log transformation of the output from a MaxEnt model with 2 × 2 km resolution.

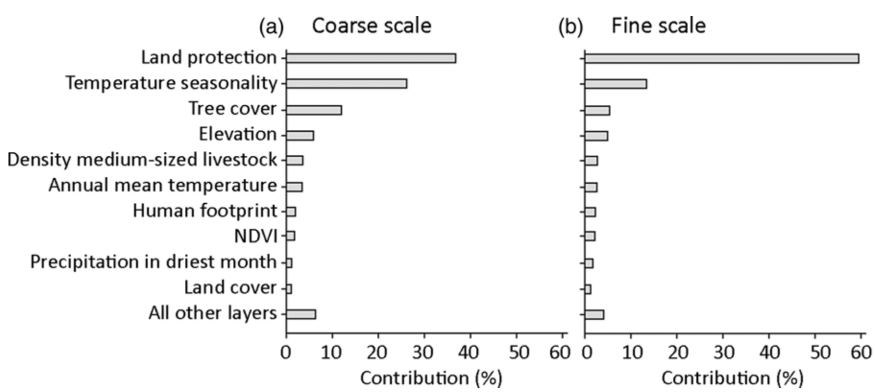

FIG. 3 Per cent contribution of selected environmental variables to MaxEnt models of potential dhole range: (a) coarse scale (8 × 8 km), (b) fine scale (2 × 2 km). The contribution was based on a heuristic method that estimates the proportional contribution of each variable to the model training gain for every iteration of the model-fitting process. NDVI, normalized difference vegetation index.

conservation investment (Wilson et al. 2006). In contrast to previous studies using environmental niche models for the dhole at local to regional scales (Nurvianto et al., 2015; Thinley et al., 2021; Havmøller et al., 2022; Tananantayot et al., 2022), our model encompassed the majority of the species' range. Although this approach may result in lower predictive accuracy at local scales compared to models trained on more localized data, it enabled us to make large-scale comparisons among regions and countries that could potentially harbour dholes, thus providing important information for guiding future conservation actions for this Endangered carnivore.

We identified most of the potential dhole range in Southeast Asia, which also had a slightly higher average probability of occurrence than mainland China and the Indian subcontinent. However, India contained the largest proportion of potential dhole range amongst the individual countries. India has previously been identified as important for dhole conservation. Kamler et al. (2015) and Srivathsa et al. (2020) suggested that the country harbours the largest dhole population. On a smaller spatial scale, large parts of Cambodia, Malaysia and Bhutan are potentially suitable for dholes. These countries, together with Thailand, also have a high relative probability of dhole 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. (2021), who found that dholes were distributed across all 20 districts of Bhutan. In Indonesia, dholes were historically distributed throughout Sumatra and Java (Kamler et al., 2015), but their distribution on these islands is now much reduced (Havmøller et al., 2022). We found larger areas of potential range in Sumatra compared to Java, where the greater distance to the mainland populations raises further concerns for dhole

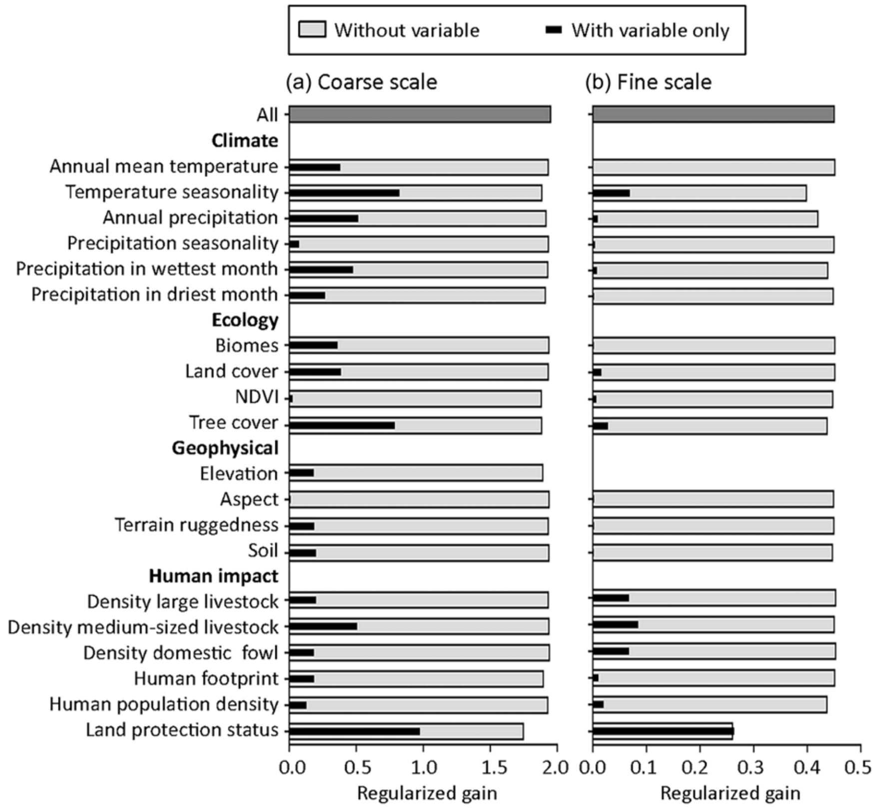

FIG. 4 Jackknife tests of contributions of selected environmental variables to MaxEnt models of potential dhole range: (a) coarse scale (8 × 8 km), (b) fine scale (2 × 2 km). Each graph shows the regularized gain when a variable is used on its own (black bars) as well as the loss in regularized gain when it is removed from the full model (grey bars). NDVI, normalized difference vegetation index.

conservation. Our model identified a limited potential range in mainland China. Dholes have been observed in the north-west of China and occasionally in isolated sites in the Kunlun Mountains, the Karakoram Mountains, the Qilian Mountains and the Altun Mountains during the past 2 decades (e.g. Riordan et al., 2015; Xue et al., 2015). These observations may represent relict populations that are adapted to arid, semi-arid and alpine habitats from Central Asia to north-west China. Environmental conditions in these habitat types differ greatly from those on the Indian subcontinent and in Southeast Asia, and the demographic responses of dholes to environmental variation, including human persecution, may have differed in these northern regions compared to more tropical areas.

Many forests in Southeast Asia are largely depleted of large mammals because of human persecution (Steinmetz et al., 2014; Phumanee et al., 2020). Our model may therefore have identified potential dhole range in forests where the species has been extirpated. For example, a snaring crisis in eastern Indochina (Laos, Cambodia and Viet Nam) 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). Dhole numbers and distribution in eastern Indochina are also greatly reduced and fragmented because of indiscriminate snaring, and dholes are absent from many parts of this region. Because our model did not consider the impacts of widespread snaring, the potential for dholes to inhabit the potential dhole range identified in eastern Indochina may be limited, at least until the snaring crisis has been resolved. Similarly, because no reliable data are available on 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 direct persecution or lack of prey (Eriksson & Dalerum, 2018). Such range limitations require further quantification (Everatt et al., 2019), and we suggest that combining environmental niche models with prey abundance data may yield valuable insights (Thinley et al., 2021; Tananantayot et al., 2022).

The three regions identified as potential dhole range are geographically separated, and our models suggest that habitat in two of the three regions is fragmented. 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 persisting only in small, isolated subpopulations, lack of population connectivity can be detrimental in the long term (Finnegan et al., 2021). In South Africa, for instance, it has been recognized that the poor connectivity of subpopulations of the African wild dog *Lycaon pictus*, which shares many characteristics with the dhole, needs to be addressed to safeguard the species' future. Consequently, a decision was made to translocate individuals between carefully selected sites to maintain viable subpopulations and create an artificial meta-population (Mills et al., 1998). This conservation intervention has been at least partially successful (Nicholson et al., 2020), highlighting the importance of maintaining demographic connectivity for species in fragmented landscapes. Although we do not believe that an artificial meta-population approach would 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 species' long-term survival. Such connectivity must, by definition, focus largely on matrix habitats outside protected areas, which reiterates 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 at both spatial scales. Although 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 as informative. Protected land was positively associated with dhole range suitability, and although this relationship may partly have been caused by sampling bias, it does agree with previous suggestions that persisting dhole populations are largely restricted to protected areas (Kamler et al., 2015; Thinley et al., 2021). As livestock density was also an important variable, human–dhole conflict may be a limiting factor for dhole distribution, similar to the situation for other large carnivores (Srivastha et al., 2020; Thinley et al., 2021; Ghimirey et al., 2024). Preserving viable populations of wide-ranging carnivores within protected areas is usually not feasible (Finnegan et al., 2021), which further highlights the necessity of focusing dhole conservation on unprotected land. Temperature seasonality also had a strong influence at both scales, but with either non-monotonic 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. The importance of temperature seasonality suggests that dholes are sensitive to climatic conditions, but the non-monotonic relationship between temperature seasonality and range suitability suggests that local factors such as prey availability and interspecific competition also play a role. The relative importance of the other environmental variables differed between the two spatial 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 in defining a species' environmental niche, especially for species with broad niche tolerances.

We recognize that our observation data were biased towards tropical areas, with only a limited number of dhole observations from mainland China. Despite our spatial filtering, our model may thus have under-represented potential range areas in the northern parts of the species' historical distribution. The bias of observations towards tropical regions could have been caused by field efforts being prioritized in areas where the species is most likely to be observed (Guillera-Arroita et al., 2015). The observations we used to train the models may thus reflect at least a large portion of the current dhole distribution, albeit not its full historical range. For instance, Kamler et al. (2015) reported widespread and long-running persecution campaigns against carnivores in the northern regions of dhole's historical range, and suggested that dholes probably disappeared from large areas of central and southern China during the 1980s and early 1990s. Hence, although our model probably represents a fair quantification of the spatial distribution of areas suitable for the dhole, we propose using regional models for smaller-scale applications. We also suggest that dynamic scale optimization, as used for the brown bear *Ursus arctos* and snow leopard *Panthera uncia* (Mateo-Sánchez et al., 2013; Atzeni et al. 2020; but see McGarigal et al., 2016), may be useful to further improve the spatial accuracy of range predictions for species with broad and plastic habitat tolerances, such as the dhole. We also encourage further studies to quantify the distribution status of dholes in the northern parts of their historical distribution, including China, as well as identifying their ecological requirements in these northern regions.

Apart from the potential sampling bias, some additional caveats apply to our study. Firstly, after appropriate spatial filtering we had a relatively limited sample size, with only c. 1 out of 1,000 cells containing a dhole occurrence. However, MaxEnt has been regarded as robust to limited sample sizes (Wisz et al., 2008), and sampling biases associated with spatially unfiltered observations may depress the performance of environmental niche models more than training the models on a more limited number of filtered observations (Boria et al., 2014). Secondly, our observations included data collected over a period of > 20 years, and there may 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

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pooled data are probably the most informative. Additionally, snaring in eastern Indochina has resulted in local extinctions of apex carnivores, including dholes. Therefore, dholes may not occur in seemingly suitable areas because of poaching. Finally, we highlight that the MaxEnt algorithm, just as many other machine learning algorithms, is subject to both conceptual and data-related issues that may cause problems both in model predictions and model interpretations (Araújo & Gusian, 2006; Varela et al., 2014). We tried to minimize these issues by making biologically justified choices regarding the environmental variables and the model grain. We also used objective criteria in our rigorous model selection approach (Warren and Siefert, 2011) and in the definition of the cut-off point in the MaxEnt cloglog output that delineated potential range. We therefore believe that our modelling process was based on biologically relevant information and objective analytical criteria, as far as this was possible with the information available.

To conclude, we identified potential dhole range in three disparate regions, and connectivity appeared limited both between and within these regions. Hence, we suggest that conservation actions should be focused on activities within each of these three regions, and on improving connectivity amongst dhole populations. As the majority of the 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, this region should be a priority for dhole conservation. However, amongst individual countries, India harbours the highest proportion of potential dhole range, which agrees with previous suggestions that the country probably also harbours the largest proportion of the global dhole population. Coordinating conservation efforts between regions in India and Southeast Asia could thus be a key aspect of future dhole conservation planning. We encourage transboundary conservation initiatives integrating areas in southern China, Myanmar, north-east India, Nepal and Bhutan. Our study also highlights 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 in unprotected areas may be key to ensure the long-term viability of this species, both by improving connectivity amongst highly suitable habitat patches but also by avoiding problems associated with efforts to maintain viable populations of wide-ranging species within restricted protected areas.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards.

Data availability The predicted rasters from the MaxEnt models are available in cloglog format together with the thinned observations used to train the coarse- and fine-scale models, as well as scaled and aligned environmental layers used for each model, on the Figshare platform (doi.org/10.6084/m9.figshare.29141738).

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