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Where will the dhole survive in 2030? Predicted strongholds in mainland Southeast Asia

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Abstract

Dhole (*Cuon alpinus*) is threatened with extinction across its range due to habitat loss and prey depletion. Despite this, no previous study has investigated the distribution and threat of the species at a regional scale. This lack of knowledge continues to impede conservation planning for the species. Here we modeled suitable habitat using presence-only camera trap data for dhole and dhole prey species in mainland Southeast Asia and assessed the threat level to dhole in this region using an expert-informed Bayesian Belief Network. We integrated prior information to identify dhole habitat strongholds that could support populations over the next 50 years. Our habitat suitability model identified forest cover and prey availability as the most influential factors affecting dhole occurrence. Similarly, our threat model predicted that forest loss and prey depletion were the greatest threats, followed by local hunting, non-timber forest product collection, and domestic dog incursion into the forest. These threats require proactive resource management, strong legal

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protection, and cross-sector collaboration. We predicted <20% of all remaining forest cover in our study area to be suitable for dhole. We then identified 17 patches of suitable forest area as potential strongholds. Among these patches, Western Forest Complex (Thailand) was identified as the region's only primary stronghold, while Taman Negara (Malaysia), and northeastern landscape (Cambodia) were identified as secondary strongholds. Although all 17 patches met our minimum size criteria (1667 km^2), patches smaller than 3333 km^2 may require site management either by increasing the ecological carrying capacity (i.e., prey abundance) or maintaining forest extent. Our proposed interventions for dhole would also strengthen the conservation of other co-occurring species facing similar threats. Our threat assessment technique of species with scarce information is likely replicable with other endangered species.

KEYWORDS

Asiatic wild dog, Bayesian Belief Network, *Cuon alpinus*, habitat prioritization, infinitely weighted logistic regression, multi-scaled species distribution model, threat assessment

1 | INTRODUCTION

Southeast Asia is one of the world's most biodiverse regions and a global carbon stabilizing zone (Estoque et al., 2019). However, much of the region's natural resources are under pressure to meet the needs of a growing human population and rapidly developing economies (Imai et al., 2018). Between 2001 and 2019, an estimated 610,000 km^2 of tropical forest, an area roughly the size of Myanmar, was cleared for agriculture and other purposes (Feng et al., 2021). Currently, less than 15% of the remaining forest cover in this region is legally protected (Estoque et al., 2019), and most protected areas have failed to mitigate negative effects from human activity (Jones et al., 2018). As a result, deforestation and overhunting threaten many of its wildlife populations (Benítez-López et al., 2019; Gray et al., 2018). For carnivores in particular, populations may suffer both directly from these threats and indirectly due to prey depletion (Benítez-López et al., 2019; Di Marco et al., 2014). Southeast Asia has thus experienced among the greatest regional declines in carnivore diversity (Wolf & Ripple, 2016). Despite these declines, most of the region's carnivores have received scarce research attention, making it difficult to assess their conservation status and mitigate key threats (Marneweck et al., 2021).

The Asiatic wild dog (*Cuon alpinus*; hereafter "dhole") is one of Southeast Asia's most threatened and least studied carnivores (IUCN Red List: Endangered; Kamler et al., 2015). Formally distributed throughout Asia, widespread changes in land use across the continent have resulted in dholes disappearing from approximately 75% of their historic range (Durbin et al., 2004; Kamler et al., 2015). Currently, Southeast Asia is estimated to support half the global dhole population (Kamler et al., 2015). However, populations in the region are threatened by habitat loss and fragmentation, prey depletion, human–wildlife conflict resulting from livestock depredation, and disease transmission from domestic animals (Chaudhary, 2016; Iyengar et al., 2005; Jenks et al., 2014; Prayoon, 2015).

Despite the potential significance of Southeast Asia for dhole conservation, available information is mostly limited to diet and prey selection, sympatric carnivore interactions, and other ecological aspects such as spatial movement and habitat selection (Charaspet et al., 2019). Few studies have examined the distribution of the species and its threats in the region (e.g., Nurvianto, Imron, & Herzog, 2015), and an assessment of both would be useful for conservation planning and for defining future research priorities. Therefore, this study had three objectives: predict suitable habitat for dhole in Southeast Asia, assess and map site-specific and regional threats to dhole populations, and identify sufficiently large areas of suitable habitat with low threat levels where the species can persist over the next 50 years ("strongholds"). To achieve these aims, we first identified potentially suitable habitats using an infinitely weighted logistic regression model (Fithian & Hastie, 2013; Hefley & Hooten, 2015) that integrated landscape and climatic information, as well as prey availability. Next, we assessed threat levels using a Bayesian Belief Network model (Marcot et al., 2006) that incorporated open access GIS data, expert opinion, available camera trap data, and information from the literature. Finally, we combine the results of our models to identify potential habitat strongholds, highlight key threats facing multiple strongholds, and discuss possible management interventions aimed at enhancing the viability of remaining populations.

TABLE 1 Infinitely weighted logistic regression model selection table for relative probability of dhole occurrence in Southeast Asia included eight different variables at optimal scales: annual precipitation (32 km), closed canopy cover (4 km), elevation (32 km), forest cover (2 km), open canopy cover (32 km), poaching threat (4 km), prey index (1 km), and roughness (0.25 km)

Model	K	ΔAIC_c	w_i
Forest cover + Prey index	2	0.00	0.167
Forest cover + Prey index + Roughness	3	0.34	0.140
Forest cover + Prey index + Elevation	3	1.43	0.082
Prey index	1	1.56	0.076
Forest cover + Prey index + Elevation + Roughness	4	2.04	0.060
Forest cover + Roughness + Threat	3	2.21	0.055
Forest cover + Roughness + Elevation + Poaching threat	4	2.28	0.053
Forest cover + Roughness + Annual precipitation	3	2.48	0.048
Prey index + Close canopy	2	2.63	0.045
Prey index + Open canopy	2	2.92	0.039
Prey index + Roughness	2	3.27	0.033
Prey index + Elevation	2	3.39	0.031
Forest cover + Elevation + Roughness + Annual precipitation	4	3.39	0.031
Prey index + Close canopy + Roughness	3	3.78	0.025
Prey index + Elevation + Close canopy	3	4.43	0.018
Prey index + Opened canopy + Roughness	3	4.51	0.017
Prey index + Opened canopy + Elevation	3	4.83	0.015
Prey index + Elevation + Roughness	3	5.18	0.013
Prey index + Closed canopy + Elevation + Roughness	4	5.71	0.010
Prey index + Opened canopy + Elevation + Roughness	4	6.45	0.007

Note: K is number of parameters included in the model; AIC_c is Akaike's Information Criteria corrected for small sample size; ΔAIC_c is the absolute difference of AIC_c score; w_i is a measure of relative support for each model.

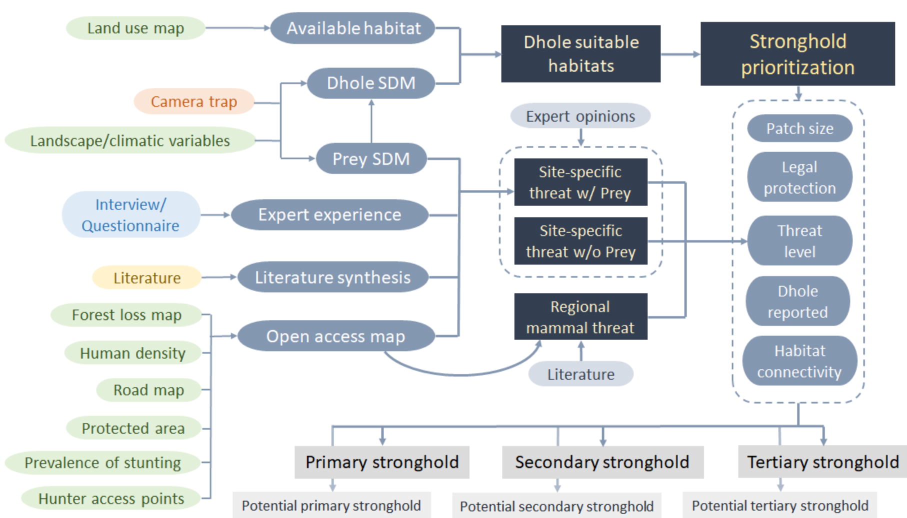

FIGURE 1 The framework of the status assessment of dhole included three principal sections: Suitable habitat, threats, and stronghold prioritization. Suitable habitat was derived from presence-only camera trap data incorporated with landscape and climatic variables, while threat considered several factors from four data sources (Table S5). Strongholds were identified based on dhole presence-absence, suitable habitat patch size, threat level, percent legal protection, as well as habitat connectivity for patches that were smaller than the minimum requirement of a stronghold (3333 km^2)

2 | MATERIALS AND METHODS

We present our study's conceptual framework in Figure 1. We reviewed the literature, including publications, reports, and photographs from online media to confirm dhole presence (records after 2010 only) and collated camera trap bycatch data from independent studies throughout mainland Southeast Asia.

2.1 | Study area

Our study focused on six countries in mainland Southeast Asia: Cambodia (KH), Laos (LA), Myanmar (MM), Peninsular Malaysia (MS), Thailand (TH), and Vietnam (VN). Indonesia was not included in this study due to the differences in habitat.

2.2 | Dhole suitable habitats

We determined dhole habitat suitability using infinitely weighted logistic regression, a presence-only species distribution modeling technique (Fithian & Hastie, 2013), which incorporated variables relating to prey occurrence, climate, topography, and vegetation. The suitability was only projected to the area within the map of available habitat, which was generated from a 2019 land cover map provided by Copernicus Global Land Service (Buchhorn et al., 2020). The dhole is a habitat generalist (Johnsingh, 1985), thus available habitat included forests (including evergreen, deciduous, coniferous, and degraded), grasslands, and other types of natural land cover.

2.2.1 | Prey distribution model

We generated an index of dhole prey availability by creating distribution maps of five dominant prey species, gaur *Bos gaurus*, muntjac *Muntiacus* sp., sambar *Rusa unicolor*, serow *Capricornis* sp., and wild boar *Sus scrofa*, using presence-only data from available camera trap studies (2010–2021). These five species have been identified as the main components of the dhole diet, and widely distributed across Southeast Asia (see Table S4). Other prey species (banteng *Bos javanicus*, hog deer *Axis porcinus*, and Eld's deer *Rucervus eldii*; Charaspet et al., 2020; Hayward et al., 2014; Kamler et al., 2020) were not included in the model due to their restricted distributions. Unfortunately, records in Laos and Vietnam were either unavailable or insubstantial, so we excluded these two countries from the distribution model (see Figure S1). In total, data from 4470 survey locations (>395,730 trap nights) from four countries (Cambodia, Malaysia, Myanmar, Thailand) were included in the analysis. Prey species presence points were thinned using the diameter of their average home ranges to reduce the clustering of data. We thinned dhole by 5.86 km (Charaspet et al., 2019; Grassman Jr. et al., 2005; Jenks et al., 2015; Nurvianto, Muhammad, & Herzog, 2015), gaur by 4.0 km (Sankar et al., 2013), muntjac by 2.0 km (Mccullough et al., 2017), sambar by 3.4 km (Chatterjee et al., 2014; Chundawat et al., 2007; Sankar, 1994), serow by 1.0 km (Wanghongsa, 1993), and wild boar by 4.0 km (Friebel, 2009; Gaston et al., 2008; Janoska et al., 2018; Johann et al., 2020; Keuling & Leus, 2019; Massi et al., 1997). A habitat mask of each species was generated by creating an 11.72 km buffer (double the diameter of the dhole home range) around each prey species presence point and clipping the buffered area by the available habitat. Then, background points were generated with 1-km spacing within the habitat mask of each species. These background points represented the available environmental variables.

We used seven predictors based on the ecology of the ungulate prey species: an index of mammal poaching (see dhole threat map section—*Regional threat map*, for map preparation), annual mean precipitation, terrain roughness, elevation, percent forest cover, percent closed-canopy forest (>70% canopy cover), and percent open-canopy forest (20–70% canopy cover) (Gregorio, 2005) (Table S3). Different species were likely to respond to the predictors differently, so multiscale modeling was used (McGarigal et al., 2016). Predictors were evaluated at 8 scales (0.25, 0.5, 1.0, 2.0, 4.0, 8.0, 16.0, and 32.0 km) using focal statistics prepared in ArcGIS Pro 2.4.0. The multi-scaled modeling was performed in R 4.0.4. (R Core Team, 2021). All predictors were standardized by subtracting the mean and dividing by the standard deviation to make predictors comparable (Gelman & Hill, 2007). Since model validation required a completely unfamiliar dataset, we randomly divided our presence points into training and testing datasets (70% and 30%, respectively) to check model fit (Franklin, 2015). Only training presence points were used in the model. We extracted the values of 56 predictors (7 predictors in 8 scales) to presence and background points for individual prey species, then used Monte Carlo simulations to confirm that the number of background points was enough to represent the environmental values (based on stabilized beta coefficients) (Hefley & Hooten, 2015). The optimal scale of seven predictors was initially defined by univariate selection based on AIC values (Akaike, 1973). This step ensured that the most optimal scale of each predictor for each species was applied to the global model. The optimal scales of the seven predictors were then tested using Spearman's correlations (r_s) and modeled using infinitely weighted logistic regression (Fithian & Hastie, 2013; Hefley & Hooten, 2015). We fit the global models using the "dredge" function with the MuMIn package (Bartoń, 2020). The function evaluates all predictor combinations but allowed us to select subsets of predictors that were highly correlated ($r_s \geq 0.5$) for exclusion from the same models. We averaged the beta coefficients of predictors of the models with delta AIC <6 (Burnham & Anderson, 2002; Richards, 2008) to check the trend and significance of each predictor on recent occurrence species records. Then we averaged the predictions of these models to generate final predictions which we used to extrapolate as relative occurrences of individual prey species in each of the four countries with available data (i.e., Cambodia, Malaysia, Myanmar, and Thailand).

We validated the models with the Boyce index (Hirzel et al., 2006) using the "ecospat" package (Broennimann et al., 2020). A testing dataset, the remaining 30% of presence points, was used to evaluate how well the occurrence predictions explained species presence points. The Boyce index ranges from −1 to 1 where stronger positive values indicate consistent prediction with anticipated model output, zero indicates random prediction, and stronger negative values indicate counter prediction.

The relative occurrence predictions of individual prey were then converted into percentages for simplicity. We generated a dhole prey index by combining the relative occurrences of the five main prey species using prey-specific weights based on estimated mean biomass percentages in the dhole diet derived from previous diet studies (Table S4):

$$\begin{aligned}\text{Dhole prey index} = {} & (\text{gaur}^{*}\,0.18) + (\text{muntjac}^{*}\,0.17) \\ & + (\text{sambar}^{*}\,0.41) + (\text{serow}^{*}\,0.12) \\ & + (\text{wild boar}^{*}\,0.11).\end{aligned}$$

The prey index was then transformed into 8 spatial scales (0.25, 0.5, 1.0, 2.0, 4.0, 8.0, 16.0, and 32.0 km), as predictors in the dhole distribution model (below).

2.2.2 | Dhole distribution model

We created our dhole distribution using the same process used to model prey occurrence. Eight scales of eight predictors were used: prey index, mammal poaching threat, annual mean precipitation, terrain roughness, elevation, percent forest cover, percent closed-canopy, and percent open-canopy forest cover (Table S3). The final prediction was a relative probability of occurrence score (from 0 to 1) of dhole in the four countries with available data. Dhole occurrence was defined as the area with a score above the threshold of the maximum of the sum of sensitivity and specificity (MaxSSS). The MaxSSS threshold is more stable for presence-only data and was suggested to be better for endangered species in terms of minimizing omission errors (Liu et al., 2015). Areas with scores under the MaxSSS were considered unsuitable. Finally, the map was overlaid on the available habitat map to generate a suitable habitat map for dhole.

2.3 | Dhole threat map

Two levels of threat map were generated and used in this study: a site-specific threat map and a regional threat map. The site-specific threat map includes only sites where we had local information from experts (and thus the threat evaluation could be more specific), while the regional threat map only considered open access data but covered all six countries of mainland Southeast Asia (and thus was less specific). For both levels, Bayesian belief networks (BBN) were used to generate threat maps. BBNs are probabilistic graphical models that contain three elements; (i) nodes that represent independent (parent) and dependent (child) variables, (ii) arrows (direction) showing the causal relationship between parent and child nodes, and (iii) conditional probability tables that specify the consequent belief of each node to be a particular state (Oliver & Smith, 1990). BBNs are commonly used in resource management and decision making (Grainger et al., 2018) because of their ability to incorporate multiple types of the data such as empirical data and expert opinion (Marcot et al., 2006; Vojkovic et al., 2021). Consequently, BBN models have been developed and used for globally threatened species with scarce information (Tantipisanuh et al., 2014) similar to dhole. We developed three models (Figure 2) based on our literature review, expert opinions, and quantitative databases. We used Netica software version 4.02 (Norsys, Vancouver, British Columbia, Canada).

2.3.1 | Site-specific threat map

The dhole threat model was based on five factors (i.e., habitat degradation, prey availability, disease transmission from livestock, human conflict, and human disturbance) which were then defined by 15 component nodes that influenced these five factors (Figure 2). The input data for these 15 nodes were obtained from four sources: (i) open access maps that is, forest loss (Buchhorn et al., 2020; Hansen et al., 2013), roads (derived from Environment Systems Research Institute, Inc.), human density (CIESIN, 2016); (ii) expert opinion that is, local hunting, carnivore competition, presence of domestic dog, human attitudes toward dhole, the distribution of livestock inside the forest, the distribution of livestock outside the forest,

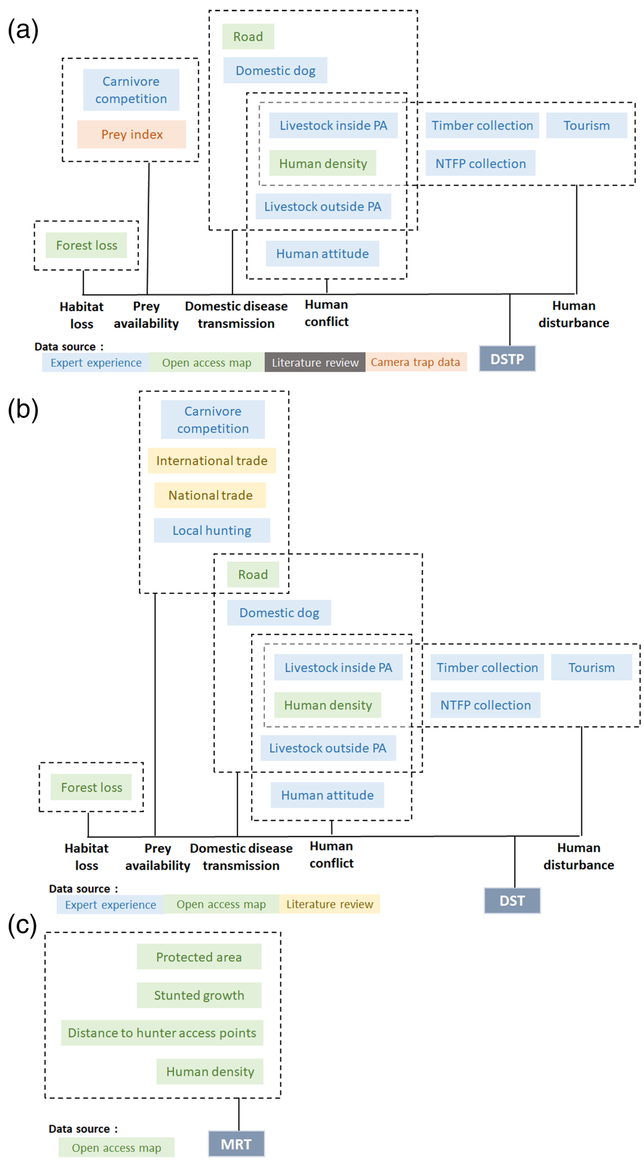

FIGURE 2 Three model structures used to derive dhole threat levels, composed of 19 different factors (8 from expert experience, 7 from open access maps, 3 from the literature, and 1 from camera trap data). (a) The dhole site-specific threat model with the prey index (DSTP) was developed for dhole with the finest details combining four data sources including prey modeling; the model was applied for sites in Cambodia, Malaysia, Myanmar, and Thailand. (b) The dhole site-specific threat model without the prey index (DST) used the same variables as above but used other indicators to represent prey availability; the model was applied to sites in Laos and Vietnam. (c) Mammal hunting regional threat model (MRT) was developed to cover the remaining habitat with no site-specific data, the model was coarse but thoroughly covered the six target countries of Southeast Asia

timber product collection, non-timber forest product collection, tourism; (iii) literature review which incorporated an international trade index (Transparency International, 2020), and a national trade index (Milliken et al., 2013; Milliken et al., 2016; Milliken et al., 2018; Nowell, 2012; TRAFFIC International, 2020; Verheij et al., 2010; Wong & Krishnasamy, 2019); and finally (iv) species occurrence maps of prey. Additional details about data preparation and sources are provided in Table S5. All related components were linked with discriminating probabilities of being in a given state. Model structure and conditional probability tables were examined and adjusted following the opinions of 23 experts investigating dhole or related species in the region for at least 10 years.

Among these nodes, the previously predicted prey index could not be extrapolated to Laos and Vietnam; therefore, another BBN was developed specifically for these two countries. In short, two BBNs were produced at the site-specific level: (1) a dhole site-specific threat model with a prey index incorporated (DSTP; Figure 2a), and (2) a dhole site-specific threat model without a prey index (DST; Figure 2b). In addition, we identified how influential each input node affected the belief of the final threat level for both site-specific threat models using the "sensitivity to finding" tool in Netica. The output of the sensitivity analysis was the percentage of entropy reduction in the posterior probability of the threat level.

The input for the site-specific threat map was primarily masked by available protected area boundaries (UNEP-WCMC & IUCN, 2020); however, we also digitized additional forest sites that were not in the protected area databases using information experts provided and/or reports from local organizations.

Fifteen threat components were reclassified into categorical values (Table S5) and were prepared with identical masks and resolutions (250 m × 250 m). All input layers were then stacked and printed into a single case file. Input layers were prepared using ArcGIS Pro 2.4.0, while case files were prepared using R software and compiled with the BBNs using Netica software. We designed three output layers for both DST and DSTP to be probability of threat being low, medium, or high. Final site-specific threat maps were computed using the following formula:

$$\text{Site}-\text{specific threat level} = P(\text{low})^{*}\,0 + P(\text{medium})^{*}\,50 + P(\text{high})^{*}\,100,$$

where P is the probability of the threat being in a particular state. The final level of site-specific threat ranged from no threat (0%) to extremely high threat (100%).

2.3.2 | Regional threat map

Many forests in Southeast Asia have suffered defaunation from overhunting (Benítez-López et al., 2019; Gray et al., 2018; Tilker et al., 2019). For the regional threat map, we adjusted the BBN model of Petersen et al. (2020) that was inspired by Benítez-López et al. (2019). Since the full protocol was specifically developed for clouded leopard (*Neofelis nebulosa*), we used only the general mammal poaching section, which is relevant for dhole. We named this BBN as the mammal hunting regional threat model (MRT; Figure 2c). The model consisted of four components; open access maps, that is, distance to hunter access points (Benítez-López et al., 2019), human population density from the NASA Socioeconomic Data and Applications Center (CIESIN, 2016), stunted growth in the local human population from FAO's GeoNetwork (FAO, 2007), and protected areas from the World Database on Protected Areas (UNEP-WCMC & IUCN, 2020). We repeated the process for the site-specific threat models, but instead used the six country boundaries as analysis masks. The outputs of the regional threat model were five layers based on the protocol using a probability of threat to be very low, low, moderate, high, or very high threat. The final regional threat map was computed using the following formula:

$$\text{Regional treat level} = P(\text{very low})^{*}\,0 + P(\text{low})^{*}\,25 + P(\text{moderate})^{*}\,50 + P(\text{high})^{*}\,75 + P(\text{very high})^{*}\,100,$$

where P is the probability of threat being in a particular state. The final regional threat level ranged from no threat (0%) to extremely high threat (100%), as with the site-specific threat map.

We prioritized the dhole site-specific threat map with the prey index over the site-specific threat map without prey, and the mammal hunting regional threat map respectively, ordered by the detail of input. Three maps were tested for correlation (r_s) before being overlaid to generate the final dhole threat map covering six countries (including Laos and Vietnam).

2.4 | Stronghold prioritization

Only suitable habitat was utilized in the stronghold identification. Based on population viability analysis from Kao et al. (2020), dhole requires at least 100 individuals to have an estimated low risk (1%) of extinction in the next 50 years; however, the population required up to 200 individuals to avoid deleterious inbreeding with near certainty. We calculated the minimum area of a stronghold by multiplying the ideal number of individuals by a rough estimate of density (0.03 individuals/ km^2), according to the only previous density report of dhole from Southeast Asia (Ngoprasert et al., 2019). The minimum size of a stronghold for at least 100 dholes required 3333 and 6667 km^2 for 200 dholes. We also considered smaller patches, 1667 km^2 for 50 dholes (11% extinction risk) if there were possible connections between the patches, thus increasing the capacity of smaller individual patches. Small suitable patches were considered connected if they were less than the median dispersal distance, 36.4 km, away from other suitable patches, and there were natural or artificial dispersal routes between them (e.g., forested areas that were predicted to be unsuitable for dhole). The median dispersal distance of dhole was estimated here as seven times the square root of the dhole home range (following Bowman et al., 2002). The habitat was prioritized based on confirmed dhole presence (from previous reports after 2010), size of suitable habitat, threat level, and legal protection level (percentage of overlap with protected area(s)). We considered a suitable habitat patch to be:

i. Primary stronghold: camera-trap confirmed dhole presence, ≥6667 km^2 of suitable habitat, low threat (below the first tertile in the threat map), and ≥50% legal protection.
ii. Secondary stronghold: camera-trap confirmed dhole presence, 3333–6667 km^2 of suitable habitat, low threat, and ≥50% legal protection.
iii. Tertiary stronghold: camera-trap confirmed dhole presence, 1667–3333 km^2 of suitable habitat, low threat, and ≥50% legal protection.
iv. Potential stronghold: ≥6667, 3333–6667, or 1667–3333 km^2 of suitable habitat but did not meet all other three criteria (dhole presence, threat level, legal protection). The potential strongholds were considered as potential primary, potential secondary or potential tertiary strongholds according to their sizes as described above.

3 | RESULTS

3.1 | Suitable habitat for dhole

Based on averaged beta coefficients from our models (delta AIC <6; Table 1), dhole presence was well explained by the prey index (0.33 ± SE 0.09), forest cover (0.30 ± SE 0.16), annual precipitation (−0.23 ± SE 0.09) and mammal poaching threat (−0.22 ± SE 0.08). The suitable habitat map covered 146,155 km^2 across the four countries. Of this total remaining habitat, 46.3% was in Myanmar, 27.4% in Thailand, 16.3% in Cambodia, and 10.0% in Malaysia (Figure 3).

3.2 | Dhole threat map

We had 92 responses from experts covering 74 sites in six countries; however, in the model we only used 68 sites

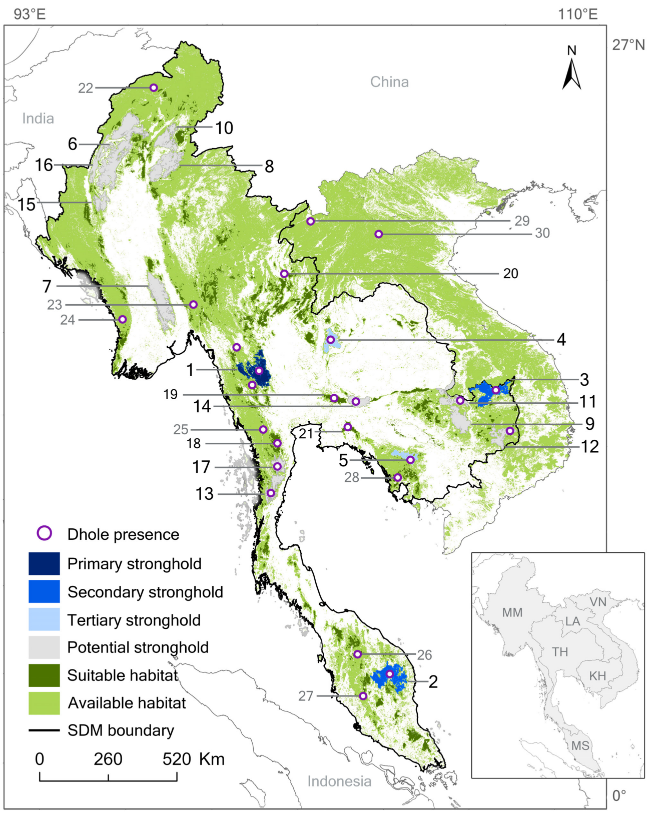

FIGURE 3 The suitable habitat was designated by those areas above the threshold MaxSSS = 0.5 from the dhole species distribution model. The patch number ranking from their priority (Table 3); (1) Western Forest complex (TH), and Kweekoh Wildlife Sanctuary landscape (MM), (2) Taman Negara (MS), (3) Northeastern landscape (KH), (4) Phukieo-Namnao Forest Complex (TH), (5) Cardamom rainforest landscape (KH), (6) Htamanthi Wildlife Sanctuary (MM), and Taungthonlon Mountains (MM), (7) Bago Yoma (MM), (8) Momeik-Mabein township (MM), (9) Prey Lang Wildlife Sanctuary (KH), (10) Kawan Reserve Forest-Loiyang range (MM), (11) Chhaeb Wildlife Sanctuary (KH), (12) Eastern plains landscape (KH), (13) Lenya and Nga Wun Reserve Forests (MM), and Chumporn Forest complex (TH), (14) Dong Phayayen Forest Complex (TH), (15) Alaungdaw Kathapa National Park (MM), (16) Thaungdut township (MM), (17) Kui Buri National Park (TH), and Tagyet reserve Forest (MM), (18) Kaeng Krachan National Park (TH), (19) Khao Yai National Park (TH), (20) Wiang Lo Wildlife Sanctuary and northern forest (TH), (21) Eastern Forest complex (TH). The other important areas (22) Hukaung Valley Wildlife Sanctuary and northern forest (MM), (23) Salween Peace Park (MM), (24) Rakhine Yoma Elephant Range (MM), (25) Tanintharyi Nature Reserve (MM), (26) Temengor Forest Reserve (MS), (27) Sungkai Wildlife Reserve (MS), (28) Southern Cardamom National Park (KH), (29) Nam Ha-Nam Kan Protected Area (LA), (30) Nam Et-Phou Louey National Park (LA)

that experts had at least 2 years of working experience to increase the reliability of the expert opinion data. The site-specific threat map consisted of 10 sites in Cambodia, 10 sites in Laos, 4 sites in Malaysia, 14 sites in Myanmar, 29 sites in Thailand, and 1 site in Vietnam. The most frequently reported threats from 68 sites were local hunting (85.3%), non-timber forest product collection (82.4%), and domestic dog incursion in the forest (80.9%). For the conditional probability tables, experts considered prey availability to have on average a 24.4% influence on the dhole threat level, followed by habitat loss (23.6%), human disturbance (20.3%), disease transmission (18.3%), and human conflict (13.5%) respectively. Comparing 12 input nodes of the site-specific threat map with the prey index, the sensitivity analysis indicated that forest loss (Figure S2 and Table S5) was the most sensitive, followed by prey, carnivore competition, and livestock inside the protected area with equivalent sensitivities (Table 2). In the same direction, for the site-specific threat map without the prey index, forest loss also had the highest sensitivity compared to the other 13 input nodes, followed by the distribution of livestock inside the protected area, distance to roads, and tourism (Table 2). Unexpectedly, the sensitivity analysis of both site-specific threat models indicated that human attitudes did not significantly influence dhole threat level. This could imply that local people do not directly persecute dhole regardless of their attitudes. We found that both final site-specific threat maps were highly correlated ($r_s = 0.9$, Figure 4a,b), while they were moderately correlated with the regional threat map ($r_s = 0.5$, Figure 4).

3.3 | Stronghold prioritization

Based on the above criteria, we identified one primary stronghold in the Western Forest Complex (WEFCOM) of Thailand and the Kweekoh Wildlife Sanctuary landscape of Kawthoolei (defined by the Kawthoolei Forestry Department near the Thailand-Myanmar border, hereafter Kweekoh Wildlife Sanctuary) covering 6693 km^2 (patch 1; Figure 3 and Table 3). There were two patches of secondary strongholds in greater Taman Negara landscape, Peninsular Malaysia (patch 2; 6474 km^2), and the Northern Plains landscape of Cambodia (patch 3; 4816 km^2). Two patches of tertiary strongholds included the Phukieo-Namnao Forest Complex in northern Thailand (patch 4; 2617 km^2) and Cardamom rainforest landscape in western Cambodia (patch 5; 1705 km^2).

We identified three potential primary strongholds (Figure 3 and Table 3) in Myanmar including Hukaung and Taungthonlon mountain (patch 6; 16,451 km^2), Bago Yoma (patch 7; 9223 km^2), and Momeik-Mabein township (patch 8; 7034 km^2). Three patches were identified as potential secondary strongholds. These included Prey Lang Wildlife Sanctuary in central Cambodia (patch 9;

TABLE 2 Sensitivity analysis comparing all nodes of the dhole site-specific threat map with the prey index (DSTP) and without the prey index (DST)

DSTP	Mutual information	Variance of belief	DST	Mutual information	Variance of belief
Forest loss	0.1229	0.0063	Forest loss	0.2392	0.0204
Prey index	0.0560	0.0015	Livestock inside PA	0.0377	0.0014
Carnivore competition	0.0445	0.0012	Road	0.0238	0.0008
Livestock inside PA	0.0413	0.0013	Tourism	0.0228	0.0007
Tourism	0.0239	0.0007	TFP collection	0.0137	0.0005
TFP collection	0.0144	0.0004	NTFP collection	0.0134	0.0004
NTFP collection	0.0141	0.0004	Carnivore competition	0.0130	0.0008
Human density	0.0092	0.0003	Human density	0.0079	0.0003
Road	0.0088	0.0002	Domestic dog	0.0044	0.0001
Domestic dog	0.0052	0.0001	Livestock outside PA	0.0038	0.0001
Livestock outside PA	0.0044	0.0001	Local consumption	0.0032	0.0001
Human attitude	0.0000	0.0000	National trade	0.0030	0.0001
			International trade	0.0008	0.0000
			Human attitude	0.0000	0.0000

Note: The higher mutual information, the more entropy reduction percentage indicating greater sensitivity of a particular node in its effect on the belief of the final dhole threat level.

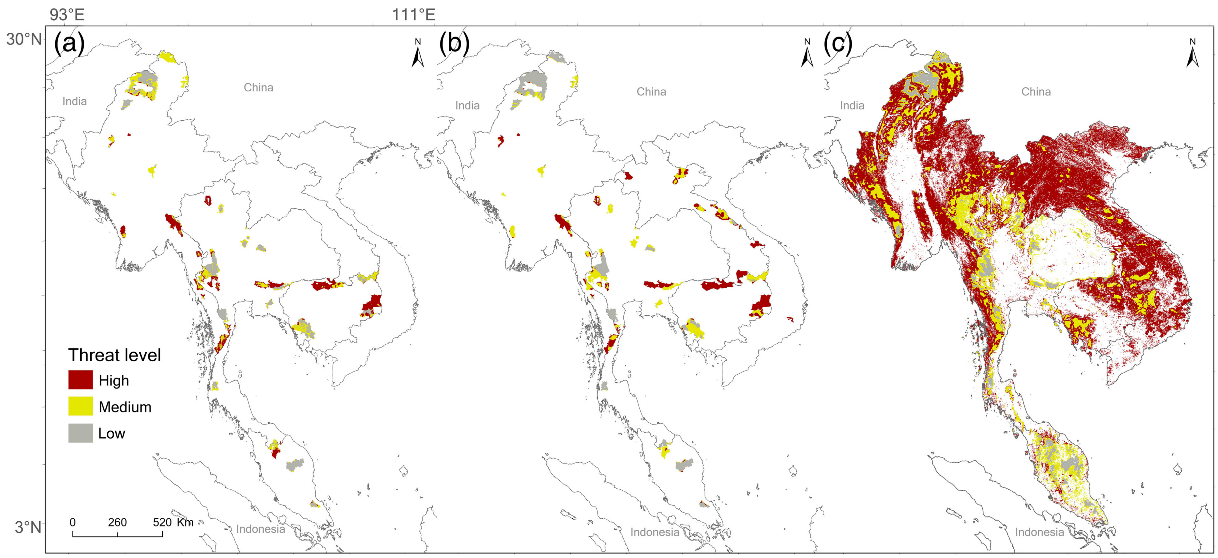

FIGURE 4 Threat level maps for (a) dhole site-specific threat map with prey (DSTP), (b) dhole site-specific threat map without prey (DST), and (c) mammal hunting regional threat map (MRT). All three threat maps were highly to moderately correlated ($r_s \geq 0.5$). The maps were reclassified into low, medium, and high threat level based on tertile values. Red indicated high threat, yellow indicated medium threat, while gray indicated a low threat level

4335 km^2), Kawan Reserve Forest-Loiyang range in Myanmar (patch 10; 4363 km^2), and Chhaeb Wildlife Sanctuary in northern Cambodia (patch 11; 3679 km^2). Lastly, we identified five potential tertiary strongholds including the Eastern Plains landscape of Cambodia (patch 12; 3103 km^2), Lenya and Nga Wun Reserve Forests area and Chumporn Forest Complex along the southern border of Myanmar and Thailand (patch 13; 2991 km^2), Dong Phayayen Forest Complex in northeastern Thailand (patch 14; 2506 km^2), Alaungdaw Kathapa National Park in northeastern Myanmar (patch 15; 2366 km^2), and Kui Buri National Park and Tagyet Reserve Forest in southern Thailand and Myanmar (patch 17; 2033 km^2).

TABLE 3 The quality and stronghold prioritization of 17 of the most suitable habitat patches capable of maintaining dhole populations for the long-term (≥50 individuals, 1667 km^2) focusing on Cambodia (KH), Malaysia (MS), Myanmar (MM), and Thailand (TH)

Patch no.	Associated protected area/forest complex	Dhole report	Size (km^2)	Threat level	% legal protection	Stronghold priority
1	Western Forest Complex (TH) and Kweekoh Wildlife Sanctuary landscape (MM)	**Yes**	**6693**	**Low**	**87**	1st
2	Taman Negara (MS)	**Yes**	**6474**	**Low**	**60**	2nd
3	Northeastern landscape (KH)	**Yes**	**4816**	**Low**	**99**	2nd
4	Phukieo-Namnao Forest Complex (TH)	**Yes**	**2617**	**Low**	**95**	3rd
5	Cardamom rainforest landscape (KH)	**Yes**	**1705**	**Low**	**97**	3rd
6	Taungthonlon Mountains (MM), Greater Mahamyaing (MM) and Htamanthi Wildlife Sanctuary (MM)	**Yes**	**16,451**	**Low**	13	Potential 1st
7	Bago Yoma (MM)	**Yes**	**9223**	High	11	Potential 1st
8	Momeik-Mabein township (MM)	NA	**7034**	High	00	Potential 1st
9	Prey Lang Wildlife Sanctuary (KH)	No	**4335**	High	**96**	Potential 2nd
10	Kawan Reserve Forest-Loiyang range (MM)	NA	**4363**	Medium	00	Potential 2nd
11	Chhaeb Wildlife Sanctuary (KH)	**Yes**	**3679**	High	**94**	Potential 2nd
12	Eastern plains landscape (KH)	**Yes**	**3103**	Medium	**99**	Potential 3rd
13	Lenya and Nga Wun Reserve Forests (MM) and Chumporn Forest Complex (TH)	**Yes**	**2991**	High	05	Potential 3rd
14	Dong Phayayen-Khao Yai Forest Complex (TH)	**Yes**	**2506**	Medium	**97**	Potential 3rd
15	Alaungdaw Kathapa National Park (MM)	NA	**2366**	Medium	**56**	Potential 3rd
16	Thaungdut township (MM)	NA	**2146**	Medium	00	Potential 3rd
17	Kui Buri National Park (TH) and Tagyet Reserve Forest (MM)	**Yes**	**2033**	Medium	29	Potential 3rd

Note: The qualified minimum criteria values were presented in bold. NA, no camera trap confirmation of dhole; 1st, 2nd, 3rd referred to primary, secondary, and tertiary strongholds respectively.

4 | DISCUSSION

This is the first regional-scale study of dhole status and distribution in Southeast Asia. We delineated suitable habitats and prioritized areas based on recent occurrence records, patch size, legal protection, and threat level. Consistent with expert opinion, our dhole distribution results suggest prey availability and forest cover were the most influential predictors of recent dhole occurrence. Based on our suitability model, we found that <20% of the remaining forest in Cambodia, Malaysia, Myanmar, and Thailand was predicted to be suitable. We identified 17 suitable patches that were potentially large enough to support populations of dhole over the long term. Although all 17 patches met the minimum size criteria, patches smaller than 3333 km^2 may require site management either by increasing the ecological carrying capacity (i.e., prey abundance) or maintaining forest extent and improving habitat connectivity. Accomplishing these objectives will require proactive management and strong legal protection. Examples include Kui Buri National Park, Kaeng Krachan National Park, and Lenya and Nga Wun Reserve Forests (patch 17, 18, 13 respectively; Figure 3), all of which predicted suitable habitats for dhole were disconnected despite belonging to the same forest complex. Although our analysis did not specifically measure the effect of habitat connectivity, it is important to at least qualitatively assess the significance of connectivity for dhole movements and survival. Restoring vegetation between Kui Buri and Kaeng Krachan National Parks could promote the movement of dhole and their prey, in contrast to Lenya and Nga Wun Reserve Forests which are separated by the Maw daung-Singkhon highway. A physical habitat corridor would need to be developed to promote wildlife movement, which itself would require serious political commitment as the management of habitat across this transboundary forest complex will be challenging (Greenspan et al., 2021). Other suitable patches that are isolated and would require connectivity to be restored in the landscape for them to function as habitats for dhole include patches in northern Myanmar (patch 6, 8, 10, 15, 16; Figure 3), northern Thailand (area 20; Figure 3), and the Dong Phayayen—Khao Yai Forest Complex of central Thailand (patch 14, 19; Figure 3).

Although earlier studies suggested that dhole may have higher tolerance to degraded landscapes than other large carnivores in Southeast Asia (e.g., tiger and leopard; Rayan & Linkie, 2016), the species is still facing a range of threats. Reduced prey availability is a primary threat to all obligate large carnivores (Wolf & Ripple, 2016), especially in Southeast Asia, where many forest areas have experienced intensive snaring and hunting for decades (Gray et al., 2018). Only 13.8% of all sites were classified as having a high prey index (>60) based on our prey model, while most of the sites possessed moderate prey levels. At a regional scale, local hunting was the most frequently reported threat in our survey, especially affecting ungulates (85.3% of all sites) including key prey species of dhole (Hayward et al., 2014; Kamler et al., 2020). Non-timber forest product collection was also reported in over half of the forest area (82.4% of all sites), as local people's subsistence often depended on natural resources for either consumption within households or selling in local markets. It is not clear what effect humans have on dhole, but presence of humans may alter carnivore activity patterns and indirectly limit their dispersal (Ngoprasert et al., 2017), and serve as an indicator of other direct disturbance (e.g., domestic dogs). Disease transmission from domestic dogs poses another potential threat to remaining dhole populations, especially when those populations are small and isolated. Domestic dogs can serve as a reservoir for multiple diseases that can negatively affect dhole populations (e.g., rabies, Mani et al., 2021), additionally our interview survey found that domestic dogs were reported inside the forest in 80.9% of study sites. Although most sites reported no direct interactions between dhole and domestic dogs, there is an inherent risk of disease transfer (Doherty et al., 2017) in areas where the species overlap (Jenks et al., 2012). Annual vaccination of domestic dogs for relevant diseases and improved surveillance in potential contact areas may reduce the risk of transmission to dhole and other wildlife populations (Lushasi et al., 2021).

We have identified five strongholds (patch 1–5; Figure 3 and Table 3) for dhole in mainland Southeast Asia. The transboundary Western Forest Complex of Thailand (WEFCOM)/ Kweekoh landscape of Kawthoolei (primary stronghold patch 1) and greater Taman Negara landscape of Malaysia (secondary stronghold patch 2) were better-studied and had stronger law enforcement levels (e.g., anti-poaching, control of habitat disturbance) compared to other areas. In contrast, the other three strongholds in the northeastern landscape of Cambodia (secondary stronghold patch 3), Phu Khieo-Nam Nao Forest Complex of Thailand (tertiary stronghold patch 4), and Cardamom rainforest landscape of Cambodia (tertiary stronghold patch 5) have received less attention to date. As with most sites assessed in this study, researchers in these five strongholds also reported local hunting and domestic dog incursions. Other issues of these strongholds include anthropogenic development, especially the construction of roads which negatively impact endangered species in Southeast Asia (Carter et al., 2020).

Smaller patches like the tertiary strongholds, would require additional interventions (e.g., prey enhancement) to encourage dhole population growth since it is unlikely that the forest extent can be meaningfully expanded, especially those sites surrounded by urban and agricultural landscapes such as the Phukieo-Namnao Forest Complex in central Thailand. For the patches with nearby forests, the development of physical connections and maintenance of corridors would also be useful to facilitate dispersal (Rodrigues et al., 2021). Social predators like dhole, where reproductive opportunities are unevenly distributed among pack members, would likely experience a greater decline in genetic diversity when subpopulations are small and isolated (Modi et al., 2021). As such, we consider connectivity modeling that incorporates locations with recent occurrence data as source sites to be a priority for the species. Based on our model, several large areas with confirmed dhole records were predicted to have low-quality habitat and low prey availability for example, Hukaung Valley, Salween Peace Park, Rakhine Yoma, Tanintharyi Nature Reserve, and Temengor Forest Reserve (area 22–26, respectively; Figure 3). Indeed, even a study by Jornburom et al. (2020) on ungulates in WEFCOM, the only primary stronghold identified and home to the region's largest breeding population of Indochinese tigers, found that large ungulate availability was probably less than half of its habitat capacity.

The other suitable patches that we identified as potential strongholds (patches 6–17; Figure 3 and Table 3) were either facing extensive threats or poor legal protection. These potential strongholds will need urgent changes to current management to ensure the survival of dhole. Based on our suitability model, Myanmar had the largest contiguous suitable habitat (patch 6) and several large patches that could potentially support dhole populations in the long-term. However, most forests in Myanmar have no or minimal legal protection, and some forests were legally allowed timber harvesting (Tantipisanuh et al., 2016). Although there were attempts to establish protection in several biodiversity hotspot areas, it is challenging because of conflicts between the central government, ethnic authorities, and indigenous groups (Shwe et al., 2019), especially now given the current civil war. Apart from commonly reported threats mentioned above, other threats found in potential strongholds in Myanmar were timber product collection, livestock distributed inside the forest, and short average distances to roads (patches 6, 7, 13). These results suggest much of Myanmar's forests are under high anthropogenic pressure, this finding is consistent with previous studies (Evans et al., 2020). Furthermore, four of the predicted potential strongholds in northern Myanmar (patches 8, 10, 15, 16) had no confirmed dhole records as camera trap studies were extremely limited due in part to remoteness, inaccessibility for survey, and civil conflict. A similar threat pattern was found in Cambodia (patches 9, 11, 12). Although Cambodia appeared to have better governance than Myanmar based on our survey, the emerging forest loss analysis revealed that there were higher probabilities of deforestation (see the analysis and forest loss map in Figure S2 and Table S5). The potential strongholds in Thailand (patches 14, 17) appeared to have higher average human density in the surrounding landscape compared to other patches. Despite the higher human densities, experts reported lower direct human impacts, which might be related to differences in market demand, social and economic conditions, aor enforcement efforts.

These strongholds will need to prioritize management to prevent the extinction of subpopulations while they still exist. For example, in Vietnam, dholes are probably extirpated throughout the country, as intensive camera trap studies have not detected the species in the past 9 years (Kamler et al., 2015; M. Nguyen, personal communication, September 18th, 2020). At best, the Vietnam population is likely functionally extinct. In recent decades, Vietnam's forest suffered from wildlife overexploitation due to the poaching and illegal trade, resulting in reduction and loss of ungulate populations, while in Laos, unsustainable hunting and land concession practices have also led to “empty forests” (Belecky & Gray, 2020).

Due to limitations in data availability and a lack of representation (Figure S1), we did not extrapolate our habitat suitability model's predictions to Laos. We recognize, however, that there are recent dhole records in some parts of the country and there may be direct connections between potential habitat in Laos and known habitat in northern Thailand and northeastern Cambodia (secondary stronghold patch 3; Figure 3). Available information indicates that dhole occurs in some protected areas in northern Laos that is, Nam Ha-Nam Kan protected area, and Nam Et-Phou Louey National Park (area 29, 30; Figure 3; Kamler et al., 2015). However, they have likely been extirpated from their historical habitat in central and southern Laos as there have not been any recent detections despite many years of camera-trap survey efforts (C. Phommachanh, personal communication, September 4th, 2020). According to our analysis, the overall threat level in Laos was considered high. Protected forests in Laos have short average distances to roads and have a high chance of deforestation based on our forest loss analysis (Figure S2 and Table S5), along with other widespread threats such as poor enforcement of forest and wildlife protection regulations. Because of our current limited information, the dhole population status in Laos should be assessed to enhance understanding of the species and increase regional conservation efficiency. We suggest more international collaboration for sharing data to improve the species habitat prioritization, especially for transboundary landscapes. For instance, detection rates of dhole and prey in Phnom Prich Wildlife Sanctuary were higher than Sre Pok Wildlife Sanctuary in Cambodia. However, we were unable to access available data from Phnom Prich and this may understate the likelihood that the Eastern Plains landscape was potentially a tertiary stronghold (patch 12; Figure 3).

Nonetheless, most camera trap studies were not designed for dhole and survey locations may not be representative of the species' current distribution. For example, available studies often target charismatic species such as bears, galliformes, or tigers; landscapes without such species may lack camera-trap surveys (e.g., montane forest in northern Thailand). As a result, our model's predictions may underestimate actual suitable habitat for dhole. In addition, there is a need to increase camera trap survey effort across the remaining dhole habitats to gain greater understanding of the distribution and aid in delineating priority areas to conserve remaining populations. We propose surveys of previously unsurveyed but otherwise suitable patches such as those in northwestern Myanmar (patches 8, 10, 15, 16; Figure 3), as well as areas with few incidental reports but little research effort that is, northern Thailand (area 20; Figure 3), and western Peninsular Malaysia (area 27; Figure 3). Another research priority is to quantify the impact of lost connectivity on dhole population persistence and identify areas inside strongholds where habitat restoration can sustain intra-patch connectivity. We also recommend further research on dhole population density since our stronghold criteria were based on the only available density estimate in Southeast Asia. Finally, our threat models were limited because detailed information on local threats was unavailable. Our results therefore provide a general assessment of the species in this region and highlight areas where conservation strategies to strengthen the population viability of dhole should be focused. Ultimately, determining strongholds and priority areas will be beneficial not only for dhole but can strengthen the conservation of other co-occurring species as well (Roberge & Angelstam, 2004).

AUTHOR CONTRIBUTIONS

Jiratchaya Tananantayot gathered all data, analyzed the data and wrote the initial manuscript. Dusit Ngoprasert, George A. Gale, Naruemon Tantipisanuh, and Antony J. Lynam provided overall guidance for the study, particularly regarding research design and analysis. Other co-authors contributed camera trap data and provided feedback on the draft.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data cannot be distributed to third parties without contributors' permission.

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