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Habitat connectivity for endangered Indochinese tigers in Thailand

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A R T I C L E   I N F O

A B S T R A C T

Habitat connectivity is crucial for the conservation of species restricted to fragmented populations within human-dominated landscapes. However, identifying habitat connectivity for apex predators is challenging because trophic interactions between primary productivity and prey species influence both the distribution of habitats, and predator movement. Our goal was to assess habitat connectivity for Indochinese tigers (*Panthera tigris*) in Thailand. We quantified suitable habitat and dispersal corridors based an ensemble species distribution model that included prey distributions, primary productivity, and abiotic variables and was based on camera-trap data from 1996 to 2013 in 15 protected areas. We employed graph theory to evaluate the relative importance of habitat patches and dispersal corridors to the overall connectivity network. We found that tiger occurrence models with and without prey distributions performed well (Area Under the Curve: 0.932–0.954). However, inclusion of prey distributions significantly improved model performance (*P < 0.001*). Protected areas with tigers at the time of our surveys were highly isolated with high resistance to movement within the dispersal corridors, and four of them have lost their tiger populations since. Potential habitat patches outside of protected areas were also mostly isolated, but it was encouraging to find that there is ample potential habitat that tigers are not occupying. The Huai Kha Kaeng - ThungYai habitat patch and Kaeng Krachan dispersal corridor were the most important for overall habitat connectivity. Generally, integrating prey distributions into assessments of connectivity is a promising approach that can be widely applied

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to predict species occurrence and delineate dispersal corridors, thereby supporting conservation planning of tigers and other large carnivores.

1. Introduction

The loss and fragmentation of habitat poses an imminent threat to the viability of many species (Breckheimer et al., 2014; Hanski and Triantis, 2015). Survival of species with fragmented habitat depends upon maintaining connectivity between isolated populations (Hanski and Triantis, 2015; Carvajal et al., 2018). Landscape connectivity is defined as the degree to which a landscape facilitates or impedes individual dispersal among habitat patches (Taylor et al., 1993), and connectivity can mitigate effects of climate change by allowing species to track their fundamental niches (Hannah, 2011; Hamilton et al., 2018; Dickson et al., 2019). Therefore, connectivity plays a crucial role in conservation planning where the goal is to preserve resilient habitat networks and design corridors that connect remnant patches or protected areas (Rathore et al., 2012). However, models identifying habitat connectivity networks typically focus on a single species, and do not capture species interactions such as competition and trophic interactions (Beier et al., 2011; Dutta et al., 2018).

Trophic interactions shape the realized niche thereby affecting movement and dispersal success, and hence affect functional habitat connectivity (Hebblewhite et al., 2014; Zarnetske et al., 2017). Carnivores require sufficient densities of prey, and herbivores need plant resources (Bateman et al., 2012; Wisz et al., 2013). Thus, the distributions and abundance of species depends on both prey distributions and abiotic factors, and both affect how species respond to landscape heterogeneity, and where dispersal corridors are located (Araújo and Luoto, 2007; Guisan et al., 2013). However, studies of habitat connectivity for carnivores tend to focus only on abiotic factors due to a paucity of data on prey abundance and occurrence, such as studies for jaguar (*Panthera onca*) (Rabinowitz and Zeller, 2010; Ramirez-Reyes et al., 2016), banded civet (*Hemigalus derbyanus*), Sunda clouded leopard (*Neofelis diardi*), and sun bear (*Helarctos malayanus*) (Brodie et al., 2015). Such models ignore food available, which also affects species distributions. Yet, if food availability is not explicitly included, it is possible that maps of both habitat patches and dispersal corridors lack ecological realism (Bateman et al., 2012; Jenks et al., 2012; Ngoprasert et al., 2012). Indeed, previous studies have demonstrated that the incorporation of prey into occurrence models for large carnivores improve predictions of occurrence and habitat connectivity. For example, in the case of Bengal tigers in the Terai Arc Landscape of India and Nepal, including major prey species such as chital and sambar provided the best-performing occurrence model for assessing connectivity (Kanagaraj et al., 2011, 2013; Harihar and Pandav, 2012). However, while studies of large carnivore connectivity have included food resources into occurrence models, studies of connectivity studies that include interactions between predators, their prey, and ultimately primary productivity, which affects the food availability for ungulate prey, are lacking.

Different methods have been proposed to estimate habitat connectivity, depending on the landscape structure, the scientific questions, and the species of interest (Kindlmann and Burel, 2008; Ziółkowska et al., 2012; Albert et al., 2017). Each method has drawbacks, and none alone can completely guide efforts to maintain or improve connectivity. Thus, it is often necessary to integrate multiple approaches, such as least-cost path analysis, circuit theory, graph theory, and metapopulation modeling (Muratet et al., 2012; Rayfield et al., 2016; Marrotte et al., 2017), different combination of which have been successfully applied to restore or preserve habitat connectivity for species-level conservation (Rabinowitz and Zeller, 2010; Ziółkowska et al., 2012; Brodie et al., 2016). Least-cost path analysis focuses on the permeability of matrix between patches and an individual's movement within a landscape (Adriaensen et al., 2003; Parks et al., 2013). The limitation of least-cost path analysis is that only a single path is identified, even though alternative paths with comparable costs may exist (Pinto and Keitt, 2009; Rayfield et al., 2009). Focusing on optimum routes thus fails to incorporate variation in an organisms' behavior (Lechner et al., 2017). Circuit theory can provide multiple pathways for connectivity and that enhances assessments how individuals move through corridors (Mcrae and Beier, 2007; Boyle et al., 2017; Dickson et al., 2019). Graph theory evaluates the relative importance of individual landscape elements in maintaining an overall habitat connectivity network (Minor and Urban, 2008; Beier et al., 2011; Saura et al., 2011). Graph-based metrics can quantify landscape elements as a source or a stepping stone based on habitat availability and species traits (e.g., dispersal distance), making them well suited for the evaluation of functional connectivity (Rubio and Saura, 2012; Ziółkowska et al., 2014). However, corridor locations derived from least cost modelling and circuit theory are sensitive to the relative cost values assigned (i.e., ecological costs associated with individuals dispersing through a landscape), and to the spatial configuration of habitat patches (Rayfield et al., 2016). A number of studies thus have applied a combined approach to the analysis of landscape connectivity in order to guide conservation and restoration efforts, such as European bison (*Bison bonasus*) (Ziółkowska et al., 2012), jaguar (*Panthera onca*) (Rabinowitz and Zeller, 2010; Ramirez-Reyes et al., 2016), and Bengal tiger (*Panthera tigris*) (Harihar and Pandav, 2012; Roca et al., 2014; Dutta et al., 2015), and we used a combined approach for the same reasons.

Tigers (*Panthera tigris*) now occupy only 7% of their historical range, and have declined precipitously over the last century due to habitat loss, degradation and fragmentation, poaching, and decreased prey availability (Linkie et al., 2006; Seidensticker, 2010; Duangchantrasiri et al., 2016). Long-term persistence of tigers depends on large, well-connected habitat patches. Thus, it is imperative to assess connectivity of suitable habitat for tigers to inform conservation planning and projects such as habitat restoration, translocations, and reintroductions (Kanagaraj et al., 2013). Tigers in Thailand are at risk of extirpation, even though Thailand occupies the historical center of the tiger's range, with recent estimate showing only 190–250 tigers remaining in Thailand. Tiger subpopulations are vulnerable to extirpation due to deforestation, illegal trade, and insufficient prey due to poaching (Steinmetz et al., 2006; Lynam, 2010; Rayan and Linkie, 2015). In 2010, the Global Tiger Initiative identified priority areas for tiger conservation. However,
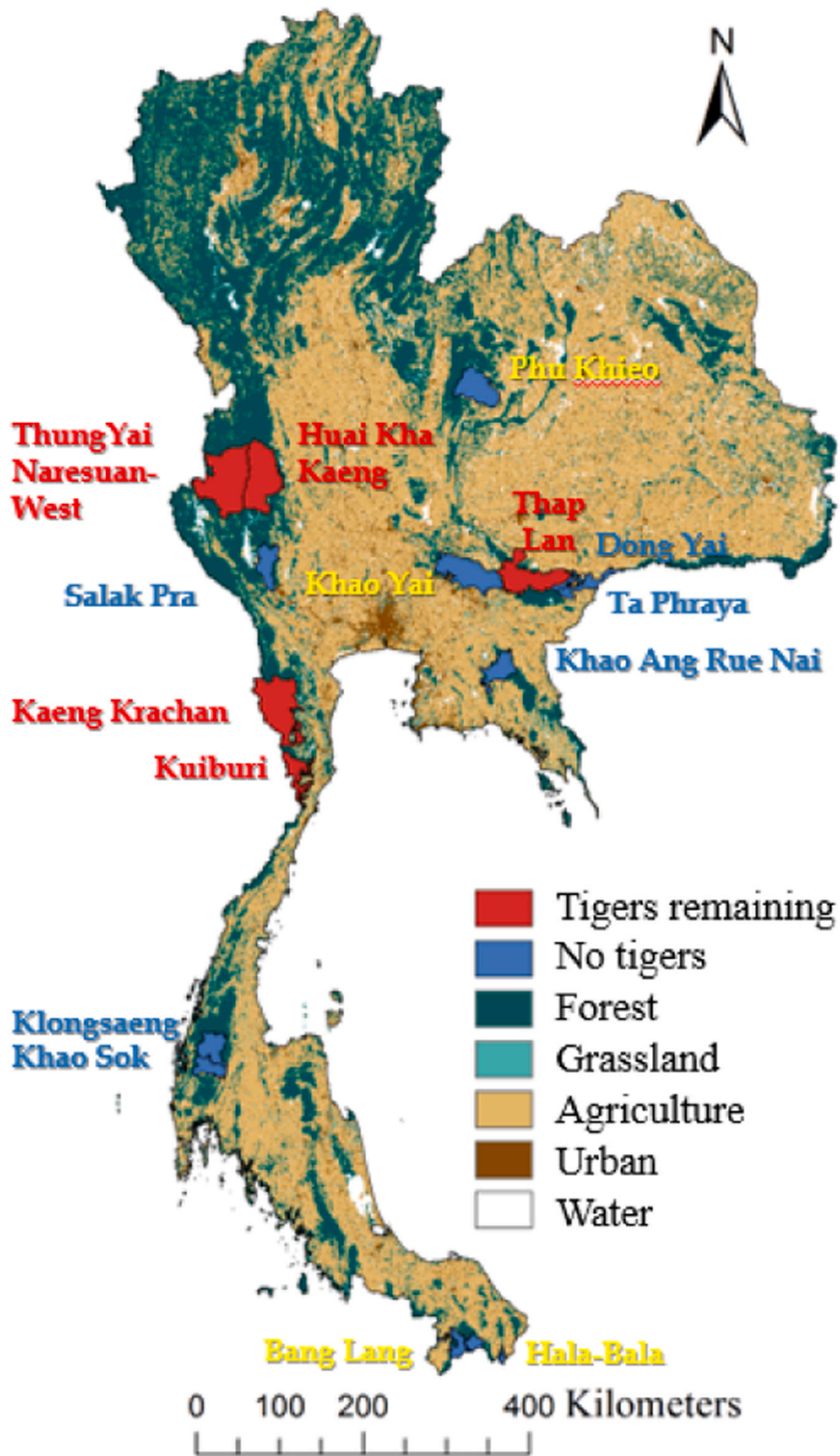
Fig. 1. Land cover across Thailand, and the 15 protected areas across Thailand where we conducted our surveys. Protected areas where tiger remain are shaded in red. Protected areas where they no longer occur are shaded in blue and include areas where they were lost since our survey (yellow label), and those without tiger at the time of our survey (blue label). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

incomplete assessments of tiger distribution and habitat connectivity in many regions hamper conservation efforts. Thailand is one of the regions that still needs better understanding of the patterns of tiger distributions and habitat connectivity (Duangchantrasiri et al., 2019).

To assess habitat connectivity for tigers, landscape elements (i.e., patches, and corridors) must allow the species to survive and reproduce, and provide shelter, prey, absence of human disturbances which cause mortality, and connectivity to other occupied patches for dispersal and maintenance of genetic diversity (Harihar and Pandav, 2012; Rathore et al., 2012; Joshi et al., 2013). Tigers prefer a mosaic of forest and grassland habitats that maximize prey density, and offer cover to hunt, breed, and raise cubs. In Thailand, such habitat is largely restricted to protected areas (Lynam, 2010; Ngoprasert et al., 2012). In terms of species interactions, tiger distribution is primarily driven by prey availability, rather than competition with potential competitors (i.e., by leopard, cloud leopard, and dhole) (Jenks et al., 2012; Steinmetz et al., 2013). The major prey species of tiger are wild pig, red muntjac, sambar deer, gaur, and banteng (Ngoprasert et al., 2012; Simcharoen et al., 2018; Duangchantrasiri et al., 2019). Although tiger's natural history is well known, it remains unclear how prey distributions and abiotic factors together affect habitat connectivity patterns.

Our goal was to assess habitat with tiger occurrences and potential habitat plus its connectivity for the tigers in Thailand. Our specific objectives were to:

(i) test our prediction that including information on primary productivity and prey results improves predictions of tiger occurrence;
(ii) identify patches with tiger occurrences and potential habitat patches and dispersal corridors;
(iii) evaluate the relative importance of habitat patches and dispersal corridors in maintaining an overall habitat connectivity network in order to identify priority sites for tiger and prey reintroduction.

2. Methods

We modeled the distribution of both tigers and their prey and combined this with connectivity analyses to understand the mechanism underlying patterns of habitat connectivity for tigers in Thailand. We employed least-cost modelling, circuit theory, and graph theory to assess and predict habitat connectivity across Thailand. The cost-path analyses (i.e., least-cost modeling and circuit theory) based on predicted occurrence, together with spatial data on dispersal barriers, yielded potential dispersal corridors, and graph theory allowed us to evaluate the relative importance of habitat patches and dispersal corridors for overall connectivity.

2.1. Study area

Thailand covers 513,000 km^2 of land area between latitudes 5°45′ and 20° 27′N and longitudes 97° 22′ and 105° 37′E (Fig. 1). Elevation ranges from 0 to 2565 m. The climate is influenced by seasonal monsoons and varies by region. Only 31.6% of natural forest

Table 1

Summary of the photo camera survey data that we analyzed. Protected areas are grouped into those that had already no tigers at the time that we conducted our surveys, those that lost tigers since our surveys, and those that had tigers when this manuscript was submitted in 2021.

	Protected area	Years	Trap nights (no.)	Camera locations (no.)	Number of photos				
					Tiger	Wild boar	Muntjac	Sambar	Gaur
Areas where tigers remain	Huai Kha Kaeng Wildlife Sanctuary	1999–2011	4155	230	89	367	397	564	116
	Kaeng Krachan National Park	2003–2004	6893	72	9	94	423	133	210
	Kuiburi National Park	2007–2011	5007	80	25	109	58	8	77
	Thap Lan National Park	2009–2013	2456	23	90	2496	196	12	148
	ThungYai Naresuan Wildlife Sanctuary-West	2007–2012	11,518	196	34	108	334	160	86
Areas that lost tigers since our surveys	Bang Lang National Park	1998	803	25	17	19	35	32	15
	Hala-Bala Wildlife Sanctuary	2004–2007	11,384	53	3	481	399	0	0
	Khao Yai National Park	1999–2011	12,623	273	10	529	652	234	397
	Phu Khieo Wildlife Sanctuary	1998	1486	43	3	50	99	0	34
Areas without tigers in our surveys	Dong Yai Wildlife Sanctuary	2012	629	21	0	41	10	27	8
	Khao Ang Rue Nai Wildlife Sanctuary	2008–2009	6399	246	0	41	165	254	55
	Khao Sok National Park	1996	246	10	0	3	0	2	0
	Klongsaeng Wildlife Snactuary	1996	35	1	0	3	0	0	0
	Salak Pra Wildlife Sanctuary	2012	2688	70	0	36	28	27	4
	Ta Phraya National Park	1998–2012	3723	136	0	43	94	0	23
		Totals:	70,045	1479	280	4420	2890	1453	1173

remains, mostly within protected areas at higher elevations (RFD 2017). Thailand is a global biodiversity hotspot, and home to more than 300 mammal species, including endangered tigers (Goodrich et al., 2015).

2.2. Camera trap survey data

We collected camera trap data from 1996 to 2013 in 15 protected areas (Table 1, Fig. 1), and used the presence data of tiger and ungulate s pecies to predict tiger occurrence and assess habitat connectivity. Cameras were located to maximize chances of capturing animals, particularly where animal signs were found (i.e., prints and scats), on wildlife trails, stream beds, and ridges, Camera locations spanned gradients in elevation (ranging from 0 to 1351 m), and habitat conditions (hill evergreen forests, mixed deciduous forest, dry dipterocarp forest, and grassland). We attached the cameras to the base of trees about 50 cm aboveground with a minimum distance of 0.5 km between cameras. We operated cameras 24 h per day, and cameras recorded time and date for each exposure. We did not use baits or lures. Based on photo records, we determined for each camera location the presence or absence of tiger and their four major ungulate prey species: Eurasian wild boar (*Sus scrofa*), Gaur (*Bos gaurus*), Red muntjac (*Muntiacus muntjac*), Fea's muntjac (*M. feae*), and Sambar deer (*Rusa unicolor*). Muntjac species were lumped for analysis. In total, we analyzed data from 70,045 trap nights obtained from 1479 camera locations, that contained 10,216 photos of our species of interest, 280 of which were for tiger (Table 1).

2.3. Habitat variables

We modeled tiger occurrence based on prey distributions and abiotic variables that are critical to tiger reproduction and survival. We included (1) the probability of occurrence of the four ungulate prey species; (2) primary productivity; (3) proportion of different habitat types; (4) mean elevation; (5) slope; (6) terrain ruggedness; (7) distance to nearest rivers and streams; (8) mean annual precipitation; (9) distance to nearest forest edge; (10) distance to nearest human settlement and roads. We calculated values of habitat variables at 1-km resolution (e.g., we calculated the proportion of habitat types in 1-km grid cells) and assigned them to each camera location. This grain scale has been previously applied in the calculation of habitat variables in studies of mammalian carnivores and ungulate prey species in Thailand (Jenks et al., 2012; Duangchantrasiri et al., 2019).

Variables associated with food availability included the probability of occurrence of four prey ungulate species, and primary productivity. To capture primary productivity, we included cumulative annual productivity and seasonal variation in productivity, which are two of the three Dynamic Habitat Indices (DHIs), and we used the DHIs derived from the MODIS fPAR (fraction Photosynthetically Active Radiation) product (Hobi et al., 2017; Radeloff et al., 2019), and which we obtained from https://silvis.forest. wisc.edu. We calculated the probability of occurrence of four prey ungulate species as a proxy for prey availability and abundance (Ngoprasert et al., 2012; Hebblewhite et al., 2014; Simcharoen et al., 2018).

Abiotic variables included habitat types, elevation, slope, terrain ruggedness, distance to nearest rivers or streams, mean annual precipitation, and human disturbance variables. We computed the proportion of eight habitat types: grassland, secondary forest, bamboo forest, mixed deciduous forest, dry dipterocarp forest, hill evergreen forest, moist evergreen forest, and dry evergreen forest according to the Thailand land cover map of 2000 provided by the Thailand Department of National Parks, Wildlife, and Plant Conservation, which was derived from Landsat TM and ETM+ using supervised classification at a scale of 1:50,000. We calculated mean elevation, slope (in degrees, 0–90), and terrain ruggedness from the Shuttle Radar Topography Mission (SRTM, http://srtm.csi. cgiar.org, (Jarvis et al., 2008)). We extracted mean annual precipitation derived from averages for 1961–1990 from the WorldClim data (https://www.worldclim.org/, (Hijmans et al., 2005)). We also calculated distance to nearest rivers or streams, forest edge, and human settlement or road using the Thailand land cover map of 2000. We chose distance to the nearest forest edge and human settlement or road as a surrogate for human hunting pressure assuming that hunting intensity is inversely related to the distance that poachers have to travel to access to wildlife habitat (Jenks et al., 2012; Lynam et al., 2012; Ngoprasert et al., 2012).

2.4. Tiger occurrence

To estimate tiger occurrence, we parameterized an ensemble model based on the camera trap data and environmental variables. An ensemble model combines multiple Species Distribution Models (SDMs) to reach a consensus outcome for probability of species occurrence to account for variability among SDM algorithms (Thuiller et al., 2009; Martinez-Freiria et al., 2013; Puddu and Maiorano, 2016). Initially, we included ten different species distribution modelling algorithms implemented within the BIOMOD2 package version 3.1–64 in R (R Development Core Team 2015): three regression methods (generalized linear model, GLM; generalized additive model, GAM; and Multiple Adaptive Regression Splines, MARS), two classification methods (flexible discriminant analysis, FDA and classification tree analysis, CTA), and four machine-learning methods (artificial neural networks, ANN; generalized boosted model, GBM; random forests, RF; and maximum entropy MAXENT), and a climate envelope method (surface range envelope, SRE) (Thuiller et al., 2009; Thuiller, 2013, 2014). We applied model algorithms with default parameters. The SDM algorithms require background data, we therefore combined true absences and generated pseudo-absences from within 70 km^2 of each presence location based on average home range size for female Indochinese tigers (Simcharoen et al., 2014). We generated 10,000 pseudo-absence location (Elith et al., 2011).

In order to evaluate the predictive performance of the SDMs for prey species and tigers, we calculated Area Under the Curve scores (AUC), with 10-fold cross-validation (Elith et al., 2011; Bateman et al., 2016). To provide an unbiased measure of model performance and obtain standard deviations for evaluation metrics, we replicated data splitting 10 times (90:10 split) with the two pseudo-absence

replicates (a total of 20 replicates for each model algorithm). To ensure that all replicates were comparable, we rescaled each replicate within BIOMOD2 using a binomial GLM. We considered AUC values above 0.7 to be indicative of useful models (Thuiller et al., 2009; Thuiller, 2014), and conducted bias-corrected null model tests. To obtain the consensus distribution for ungulate prey and tigers, we selected the top five performing models and calculated their weighted mean distributions. In order to transform the probabilistic consensus distribution from the ensemble model to a binary suitable/non-suitable habitat for each prey species and tigers, we considered suitability values above the sensitivity-specificity sum maximization threshold (Phillips and Dudík, 2008; Guisan et al., 2013).

To compare occurrence models for tigers with and without prey availability, we modeled tiger distribution with three different sets of variables: abiotic variables alone, prey alone, or abiotic plus prey. For the tiger model with prey, we first computed species distributions for the four prey ungulate species as a function of primary productivity (i.e., cumulative productivity, and seasonality in productivity as proxies for forage availability) plus the other abiotic variables described above. To obtain the importance of the variable for each model and each species, BIOMOD2 applies a randomization approach as one minus the correlation between the standard predictions and predictions with randomized variables (Thuiller et al., 2009; Thuiller, 2014).

To test if prey availability significantly improved the prediction of the occurrences of the Indochinese tiger in Thailand, we examined: (a) if the best fit model included abiotic, prey, and primary productivity variables; (b) and if model performance (i.e., AUC values) differed significantly between the models based on abiotic model, prey model, and abiotic and prey model. We tested for significant differences in model outputs with Wilcoxon signed-rank tests for related samples (Bateman et al., 2012).

2.5. Identifying habitat patches and dispersal corridors

We combined three methods to assess habitat connectivity for tigers: least cost modelling, circuit theory, and graph theory (Fig. 2). We applied these methods to three sets of habitat patches. The first set included the 9 protected areas that had tigers during the time span of our surveys (1996–2013). We included all of these protected areas, even though four have lost tigers by 2019 (Fig. 1) because we were interested to see if the ones that lost tigers were more isolated. The second set included all 15 protected areas that we surveyed to identify which of the ones that lacked tigers already at the time of our survey might be good candidates for reintroductions based on their connectivity. The third set included all potential habitat patches throughout Thailand that were greater than 70 km^2 based on average home range size for female tigers in Thailand (Simcharoen et al., 2014). Similar to the second set, the third set identified potential habitat patches that may be good candidates for reintroductions based on their connectivity.

To identify locations of dispersal corridors, we employed least-cost path modeling. We used a probabilistic occurrence map for tigers derived from the model including prey distributions to generate least-cost path corridors for tigers. A cost surface is derived by quantifying the resistance of different land cover classes and summing the travel cost over the route of least resistance when individuals move between two patches (Adriaensen et al., 2003; Parks et al., 2013; Kaim et al., 2019). We inverted the occurrence map for tigers with a linear function as a measure of resistance surfaces, rescaled from 1 (lowest resistance) to 100 (highest) (Ziółkowska et al., 2012). Dispersing tigers avoid agricultural areas and human disturbance, but may travel through a mosaic of forest and grassland with disturbed and undisturbed tracts of forest offering cover for movement (Dutta et al., 2015; Duangchantrasiri et al., 2019). We therefore included potential dispersal barriers for tigers: agriculture area, settlement, highways, major roads, and large rivers into the resistance surface map. To determine the position of least-cost path locations, we used the cost distance tool in ArcGIS 10.1 (ESRI 2011) with scripts written in Python 2.7 (Python Software Foundation 2013).
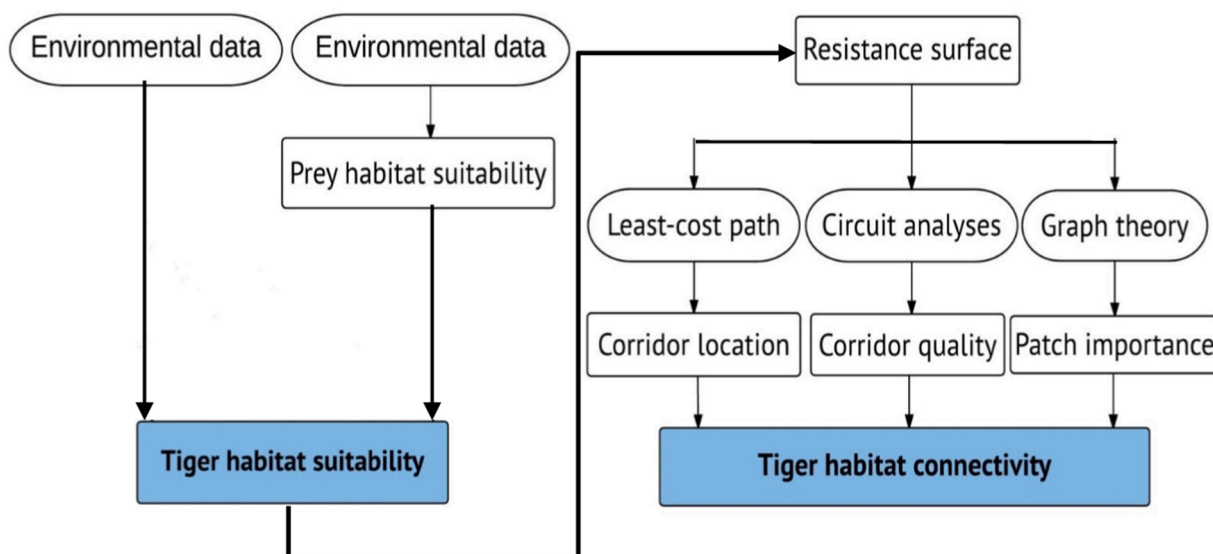

Fig. 2. Flowchart describing our approach to assess habitat connectivity for the Indochinese tigers in Thailand.

To complement the least-cost path analyses, we conducted a connectivity analysis based on circuit theory. Least-cost path can identify a corridor location, but least-cost path algorithms do not calculate optimum width for corridors, nor rank corridors in terms of their ability to facilitate movements (Boyle et al., 2017; Dickson et al., 2019). Therefore, we applied circuit theory using Circuitscape software (v. 4; McRae et al., 2013) to identify other potential movement routes near the least-cost path corridor and quantify how individual tigers (i.e., electrical current) would move across the landscape within a corridor width. We buffered the least-cost paths by 10 km on each side to define dispersal corridors that are wide enough to support the tiger movement, and assessed the current between each pairwise combination of suitable habitat patches (Brodie et al., 2015; Dutta et al., 2015).

2.6. Assessing the importance of habitat patches and dispersal corridors

To evaluate the relative importance of individual patches and dispersal corridors for the overall connectivity network, we used the Probability of Connectivity index (PC) based on graph theory (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007; Saura and Torné, 2009). PC is a graph-based metric that indicates the probability that two tigers randomly placed in the study area fall into habitat patches that are connected. The probability of individual tigers moving between habitat patches depends on both the amount of suitable habitat (nodes of the graph), and the distance and resistance to movement (resistance surface) across landscape matrix (links of the graph). A graph component composed of a set of nodes corresponding to the suitable habitat patches with an area of > 70 km^2. Each pair of nodes was connected through links (least-cost paths), which indicated the potential movement paths of tigers.

To assess the probability of connectivity, we used effective distances, that is, we replaced Euclidean distances by the cost-distance, to calculate inter-patch-cost-dispersal probabilities (p_{ij}) as a decreasing exponential function of the effective distance between nodes (d_{ij}) and dispersal abilities of tigers (k) (Saura and Pascual-Hortal, 2007), as follows:

$$p_{ij} = e^{-kd}ij \qquad (1)$$

We set k = 0. 028, 0.012, and 0.011, which corresponds to dispersal distance of three individual tigers of 25, 58, and 64 km, and a dispersal probability of 0.5 for each distance. These three distances correspond to three observed tiger dispersal event from Huai Kha Kaeng Wildlife Sanctuary to Mae Wong and Klong Lan National Parks (WWF Thailand, unpublished data). These are minimum observed distances traveled by dispersing tigers and are likely less than the actual maximal dispersal distance for tiger. Therefore, we set the dispersal probability to 0.5 for those three distances, and conducted our analysis three times to assess how uncertainty about actual maximum dispersal distances may have affected our results. We then computed the PC index for each landscape element (i.e., habitat patches, and dispersal corridors), and for each dispersal distance (Saura and Pascual-Hortal, 2007). PC index summarizes the
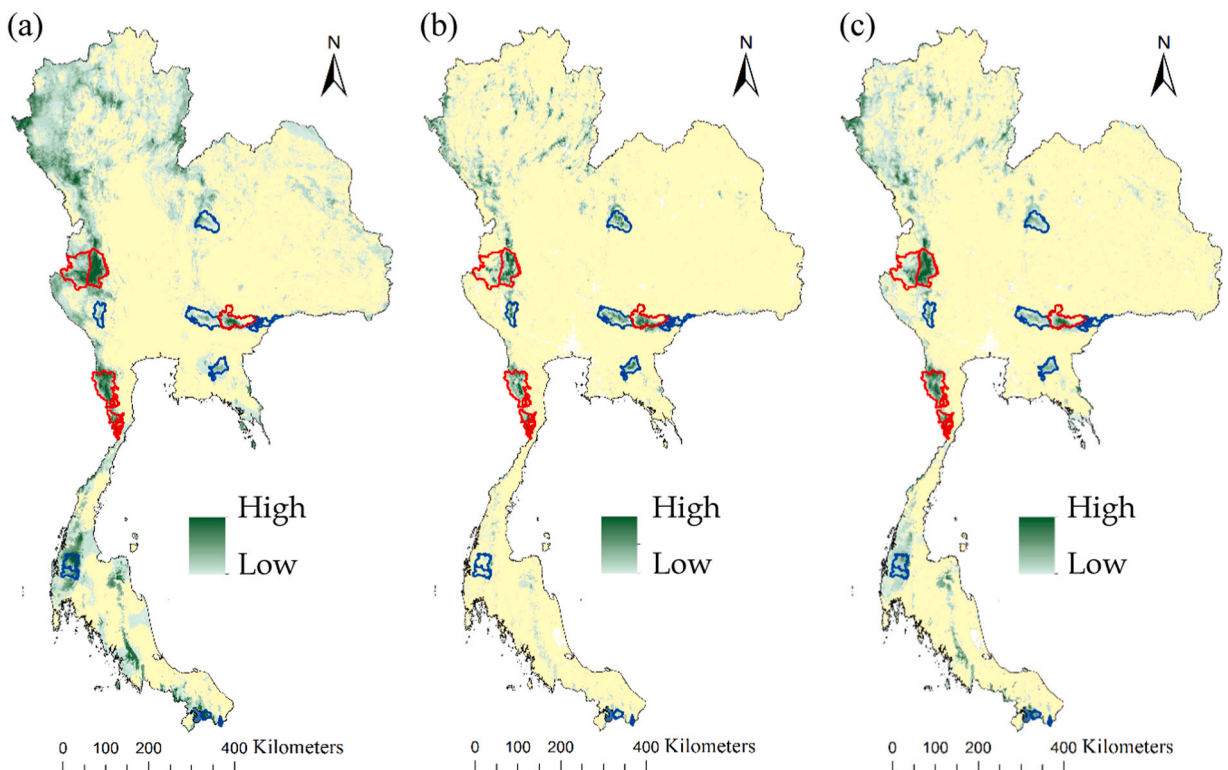

Fig. 3. Occurrence models for Indochinese tigers in Thailand derived from an ensemble of species distribution models showing the probability of occurrence, (a) occurrence models based on tiger ~ abiotic variables, (b) tiger ~ prey, (c) tiger ~ prey + abiotic variables.

contribution of all habitat patches to tiger movements across the whole study area, as follows

$$PC = \frac{\sum_{i-1}^{n}\sum_{j-1}^{n}a_i \quad a_j \quad p_{ij}^{max}}{A_L^2} \tag{2}$$

where a_i and a_j are the areas of habitat patches i and j, p_{ij}^{max} is the maximum product probability of all the possible paths between habitat patches i and j (including the direct route between the two patches), and A_L is the study area.

To assess the relative importance of habitat patches and dispersal corridors to overall connectivity, we calculated d(PC)$_k$ where 'd' is the percentage of the importance of a given node for the connectivity according to a given index (Saura and Pascual-Hortal, 2007). We partitioned d(PC)$_k$ into three fractions that quantify the role of each habitat patch and dispersal corridor in maintaining or enhancing the movements of tigers with respect to habitat availability, connectivity, and stepping stone, as follows.

$$dPC_k = dPC\text{intra}_k + dPC\text{flux}_k + dPC\text{connector}_k \tag{3}$$

The intra term (dPCintra $_k$) is the contribution of habitat patch k given by the suitable habitat that it contains. The flux term (dPCflux $_k$) measures the degree of connection of a habitat patch k with the other habitat patches. The connector term (dPCconnector $_k$) corresponds to the contribution of a habitat patch and dispersal corridor k to the connectivity between other habitat patches as a stepping-stone or connectivity facilitating dispersal between them. All three measures are reported as percentages, and larger values indicate that a given patch or connector is more important for overall connectivity. We used Conefor 2.6 software for the graph-theory-based analyses (Saura and Torné, 2009).

3. Results

3.1. Tiger occurrence

Our three occurrence models for the Indochinese tiger in Thailand, i.e., the abiotic model, prey model, and abiotic and prey model, all performed well based on model accuracy for protected areas (Fig. 3). However, the incorporation of food availability significantly improved model performance (Table 1). Of all three tiger habitat models, model accuracy was highest for abiotic and prey model (AUC = 0.954, SD = 0.06) followed by abiotic-only model (AUC = 0.939, SD = 0.06) and prey-only model (AUC = 0.932, SD = 0.05). Model performance was significantly different (Wilcoxon signed-rank test, $P < 0.001$) for all model comparisons. These results supported our expectation that including variables that capture both primary productivity and prey distributions provides better predictions of tiger occurrence (Table 1).

Prey occurrence was more important than abiotic factors for predicting tiger occurrences. Occurrence of tigers increased with the probability of occurrence of wild boar (variable importance score = 0.38) and gaur (score = 0.15), the proportion of mixed deciduous forest (score = 0.15), distance to human settlement (score = 0.17), and distance to forest edge (score = 0.12). For the abiotic model, tiger occurrence was greater at higher proportion of mixed deciduous forest (score = 0.26), and further distance to human settlement (score = 0.37), and forest edge (score = 0.26). The occurrence of wild boar was the best predictor of tiger occurrence in both the prey-only and the prey plus primary productivity model.

The effect of variables on predictions of occurrence for ungulate prey varied among species. Occurrences of wild boar, gaur, muntjac, and sambar were highly correlated with cumulative productivity, seasonality in productivity, annual precipitation, and distance to forest edge. Occurrences of all four species increased with higher cumulative productivity. Occurrences of wild boar and gaur were highest at a moderate level of seasonality in productivity, while seasonality in productivity had less effect on muntjac and sambar. Occurrences of all four species were highest where annual precipitation was 1000–1500 mm, and decreased as annual pre-cipitation increased. All prey species had higher probabilities of occurrence within 1000–1500 m from forest edge.

3.2. Habitat patches

Tiger occurred in nine habitat patches during the time span of our surveys, but those patches were highly isolated (Fig. 5a). Indeed, by 2019, four of the protected areas that had tigers at the time of our survey, and where we captured them with our cameras, no longer

Table 2
Mean model performance and ensemble measures (AUC scores) of top performing occurrence models for Tiger based on a) abiotic variables only, b) prey variables only), and c) prey & abiotic variables, and for wild boar, gaur, muntjac, and sambar. The significance values (*** $P < 0.001$) are based on Wilcoxon signed-rank test for the abiotic versus prey model, and the abiotic versus the prey & abiotic model.

Model	Generalized Linear	Generalized Additive	Generalized Boosted	Random Forest	MAXENT	Ensemble
Tiger: Abiotic only	0.763 ± 0.055	0.693 ± 0.068	0.784 ± 0.054	0.707 ± 0.070	0.774 ± 0.060	0.939 ± 0.06* **
Tiger: Prey only	0.735 ± 0.061	0.757 ± 0.061	0.761 ± 0.058	0.726 ± 0.071	0.772 ± 0.067	0.932 ± 0.052* **
Tiger: Prey & Abiotic	0.784 ± 0.055	0.692 ± 0.059	0.805 ± 0.043	0.734 ± 0.053	0.782 ± 0.058	0.954 ± 0.060* **
Wild boar	0.855 ± 0.017	0.858 ± 0.015	0.880 ± 0.016	0.854 ± 0.020	0.876 ± 0.016	0.962 ± 0.028
Gaur	0.790 ± 0.027	0.806 ± 0.038	0.844 ± 0.025	0.812 ± 0.030	0.825 ± 0.029	0.962 ± 0.047
Muntjac	0.896 ± 0.010	0.917 ± 0.011	0.932 ± 0.010	0.936 ± 0.011	0.930 ± 0.010	0.976 ± 0.018
Sambar	0.913 ± 0.013	0.929 ± 0.018	0.941 ± 0.009	0.904 ± 0.029	0.934 ± 0.013	0.981 ± 0.019

harbored any (Fig. 1, unpublished data). During the time span of our surveys though, habitat patches with tiger occurrences covered a total area of 8675 km^2 ranging from 85 to 3665 km^2 with a mean patch size of 528 km^2, with 94.8% of the patches with tiger occurrences inside protected areas. The largest patch was located in the Western Forest Complex (Huai Kha Kaeng, Thung Yai Naresuan, and Mae Wong).

In terms of potential tiger habitat, i.e., areas outside of protected areas with suitable habitat, none of which had tiger occurrences though, we identified 26 patches ranging from 74 to 1513 km^2 with a mean area of 305 km^2. Total area was 7929 km^2, out of which 88.8% were located in protected areas. The largest patch was located in Salawin Wildlife Sanctuary (Fig. 5b).(Table 2).

3.3. Habitat connectivity and dispersal corridors

We identified seven potential corridors between the patches that with tiger occurrences at the time of our surveys (Fig. 5a). There were only two dispersal corridors when we assumed that the probability of dispersal reaches 0.5 at 25 km in length (between Kaeng Krachan and Kuiburi, and Banglang and Hala-Bala), and three when assuming that threshold occurs at 58 km, or ≤ 64 km length (between Kaeng Krachan and Kuiburi, between Bang Lang and Hala-Bala, and Khao Yai and Thap Lan). Other potential corridors among habitat patches with tiger occurrences were blocked by dispersal barriers (e.g., highways, agriculture, and urban) or were long (> 64 km), making it difficult for tigers to disperse (Table 3). Among the potential habitat patches outside of protected areas, we located 13 connections among suitable habitat patches of the probability of dispersal is 0.5 at 25 km, 20 connections if that occurs at 58 km, and 22 for 64 km. The circuit analyses quantified the resistance of movement for tigers within each corridor, and resistance to movement for tigers varied considerably among the least-cost path corridors for both habitat patches with tiger occurrences and potential habitat patches. Among the patches with tiger occurrences at the time of our surveys, the least-cost path corridor between the Kaeng Krachan and Kuiburi habitat patches had the lowest resistance for tiger movement, meaning that there is little barrier separating them. Conversely, the resistance for the Haui Kha Kaeng and Kaeng Krachan corridor, and the Khao Yai and Thap Lan corridor were medium-high, thus likely inhibiting tiger dispersal (Fig. 5c, Table 3). For the resistance of movement in the dispersal corridors among potential habitat patches, there was low resistance of movement among the least-cost path corridors in northern Thailand, which could potentially serve as dispersal corridors connecting patches with tiger occurrences at the time of our survey to potential habitat patches (Fig. 5d).

3.4. Importance of patches and dispersal corridors

Our graph theory analysis of the networks of the patches with tiger occurrences at the time of our survey, and of the potential habitat patches showed that most patches were locally connected, but not regionally and much less nationally (Fig. 6). The relative importance of habitat patches with tiger occurrences and the dispersal corridors in maintaining the overall connectivity for Indochinese tigers in Thailand were similar for all dispersal distances (Table 3). Among the patches with tiger occurrences at the time of our survey, the habitat patch located in the Western Forest Complex was the most important for habitat connectivity (as quantified by the percentage of contribution to overall connectivity; dPC = 61–63%, Table 4). This habitat patch is highly valuable because it covers a large area of quality habitat (highest dPCintra). However, the Keng Kracha habitat patch was also well connected to other habitat patches to which tiger populations could potentially disperse (highest dPCflux). The Kaeng Krachan habitat patch could serve as a stepping-stone because it has a topological position that can sustain connectivity among other habitat patches (highest dPCconnector). In terms of the relative importance of dispersal corridors between patches with tiger occurrences, the Kaeng Krachan to Kuiburi dispersal corridor had the highest contribution to the connectivity network (dPCconnector = 9–11%) (Table 5), and the highest dispersal probability and lowest resistance cost of movement.

Among the potential habitat patches and dispersal corridors, the Western Forest Complex habitat patch had the highest contribution to overall connectivity (dPC = 47–52%). The Kaeng Krachan to Kuiburi dispersal corridor was the most important linkage

Table 3

Cost dispersal probabilities (p_{ij}) and sum of cost of resistance movement (Resistance) calculated for each dispersal distance delineated dispersal corridors between habitat patches that were occupied by Indochinese tigers at the time of our surveys. Higher values of cost dispersal probability indicate a higher chance of movement between suitable patches. Higher values of cost of resistance movement indicate a lower chance of movement between suitable patches.

[a] Corridor	Distance (km)	p_{ij} 25 km[b]	p_{ij} 58 km	p_{ij} 64 km	Resistance
KK-KB	13	0.69	0.85	0.86	59.98
BL-HB	20	0.58	0.79	0.81	disconnected
KY-THP	36	0.37	0.65	0.68	223.14
HKK-KK	195	0.00	0.10	0.12	1551.59
PK-KY	258	0.00	0.05	0.06	disconnected
PK-HKK	605	0.00	0.00	0.00	disconnected
KB-BL	950	0.00	0.00	0.00	disconnected

[a] KK-KB = Kaeng Krachan and Kuiburi, BL-HB = Bang Lang and Hala-Bala, KY-THP = Khao Yai and Thap Lan, Huai Kha Kaeng and Kaeng Krachan, PK-KY = Phu Khieo and Khao Yai, Phu Khieo and Huai Kha Khaeng, and Kuiburi and Bang Lang.

[b] When p_{ij} = 25 km, then the probability of dispersal at 25 km is 0.5, which means that tigers can potentially disperse further, but at a low likelihood. When p_{ij} is 58 or 64 km, it means that the probability of dispersal drops to 0.5 at those distances, i.e,. that tigers can disperse further.

Table 4

Contribution of each habitat patch with tiger occurrences to overall landscape connectivity as measured by the relative importance of the probability of connectivity index *dPC* (%) and its fractions for tigers' movement assuming that the probability of dispersal drops to 0.5 at 64 km distance.

Node	*dPC*	*dPC*intra	*dPC*flux	*dPC*connector
PK	0.77	0.61	0.16	0.00
WFC	62.85	53.15	9.69	0.00
KY	1.06	0.16	0.88	0.03
TL	3.30	2.36	0.94	0.00
KK	38.02	19.10	17.56	1.36
KB	13.57	1.71	11.86	0.00
BL	2.34	1.96	0.38	0.00
HB	0.41	0.03	0.38	0.00

Table 5

Contribution of each dispersal corridor to the maintenance of the overall landscape connectivity as measured by *dPC*connector (%) for all tiger dispersal distances.

	*dPC*connector25	*dPC*connector58	*dPC*connector64
KK-KB	9.0	11.1	11.2
BL-HB	0.3	0.4	0.4
KY-TL	0.5	0.8	0.9
HKK-KK	0.4	6.2	7.2
PK-KY	0.0	0.0	0.1
PK-HKK	0.0	0.0	0.0
KB-BL	0.0	0.0	0.0

(*dPC*connector = 6%). Several potential habitat patches and dispersal corridors located in the Western Forest Complex and northern Thailand were important in maintaining the overall potential connectivity network, but they did not have tiger occurrences in our surveys (Fig. 6).

4. Discussion

Our goal was to assess habitat connectivity for the endangered tiger in Thailand for areas with tiger occurrences at the time of our surveys (1996 – 2013), and for habitat that could be potentially re-occupied by tigers. We found that incorporating primary productivity and prey distributions significantly improved predictions of occurrence for the tiger in Thailand. Tiger populations in Thailand at the time of our survey were already confined to small, unconnected patches, and several of those areas have lost tigers since (Fig. 1). Potential dispersal corridors between existing tiger populations were long and most had high resistance to movement. Indeed, four of the nine protected areas where we found tigers have lost them since, and three of the four were high isolated according to our network analyses. The connectivity networks within the Western Forest Complex and the Kaeng Krachan forest complex were the most important for the overall functional connectivity for tigers in Thailand. Furthermore, we identified potential habitat patches that do not contain tiger currently, but could serve as priority sites for reintroduction and dispersal corridors. However, these potential habitat patches were highly fragmented, and regaining a connectivity network across Thailand may prove difficult.

4.1. Tiger occurrence

We found that incorporating prey distributions plus primary productivity significantly improved the predictive power of our occurrence models, thereby providing more realistic occurrence maps for connectivity assessments. Our finding was consistent with previous studies that tiger presence is highly dependent on prey availability, and that including prey occurrence enhances the predictive performance of occurrence models (Ngoprasert et al., 2012; Hebblewhite et al., 2014; Duangchantrasiri et al., 2019). When interpreting our maps of both tiger occurrences (Fig. 3) and occurrences of their prey (Fig. 4), it is important to note that the areas outside of the protected areas contain no tigers at this point, and little of their prey, and represent potential habitat only. However, it is encouraging that there are substantial areas where the environmental template is suitable for tigers and their prey, and where stronger enforcement and reduction in poaching may permit recolonization.

Our findings also agree with those for other carnivores, where suitable habitat for connectivity networks is both a function of food resources (e.g., prey availability, primary productivity, land cover types) and the absence of human disturbances (Jenks et al., 2012; Ramirez-Reyes et al., 2016). For example, occurrence of grizzly bears in North America is correlated with forage-related variables (i.e., greenness, soil wetness, and nearest rivers), whereas cougar distributions are affected by terrain ruggedness, greenness, and avoidance of roads (Chetkiewicz and Boyce, 2009). European brown bears occurrence is associated with forest cover, higher elevations, and avoidance of roads and human activity in both the east-central Alps (Güthlin et al., 2011), and the Italian Alps (Peters et al., 2015). In Borneo, abundance of sun bears (*Helarctos malayanus*), Sunda clouded leopards (*Neofelis diardi*), and banded civet (*Hemigalus derbyanus*) is related to elevation, logging, and road density (Brodie et al., 2015). Similarly, habitat connectivity for Jaguars depends on
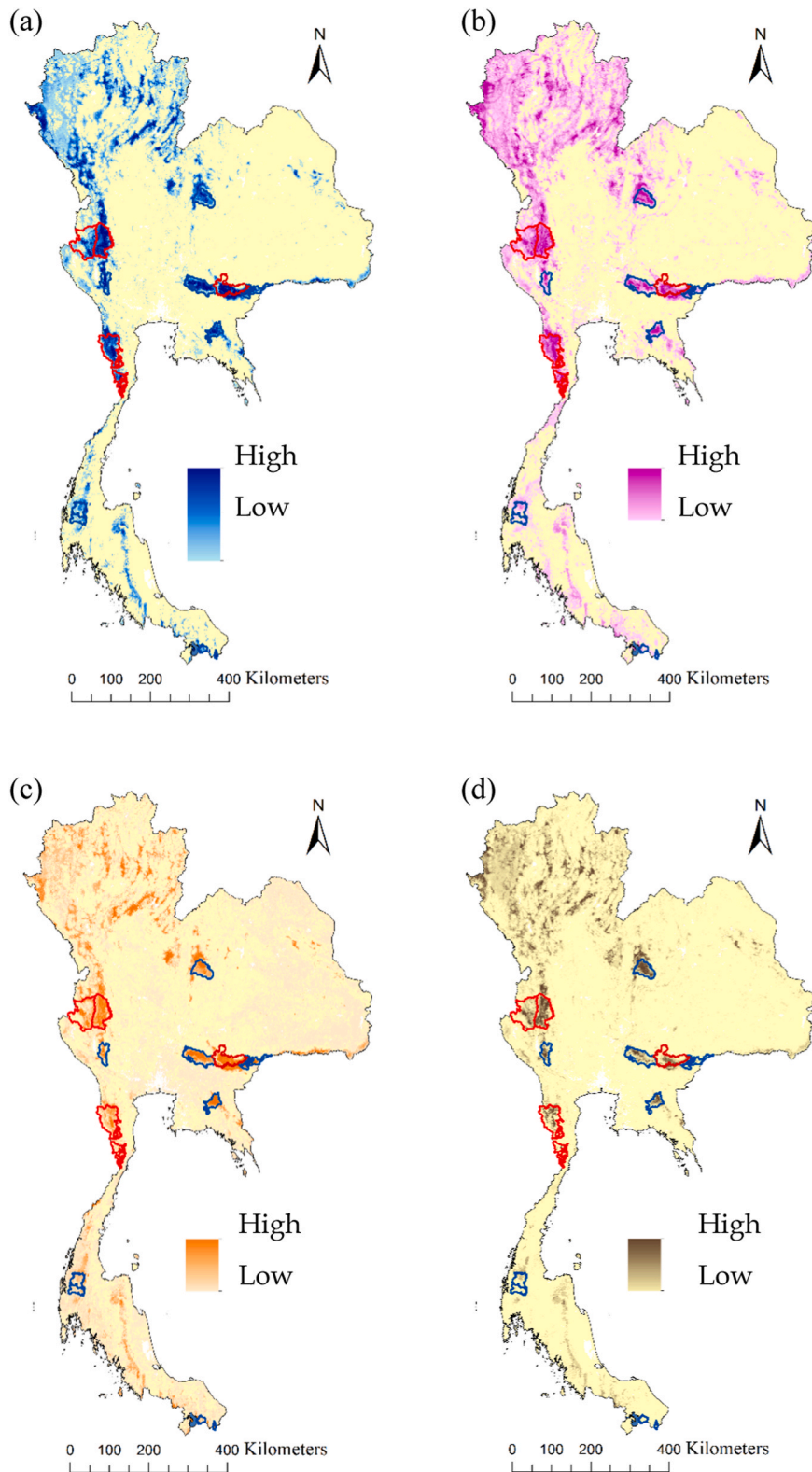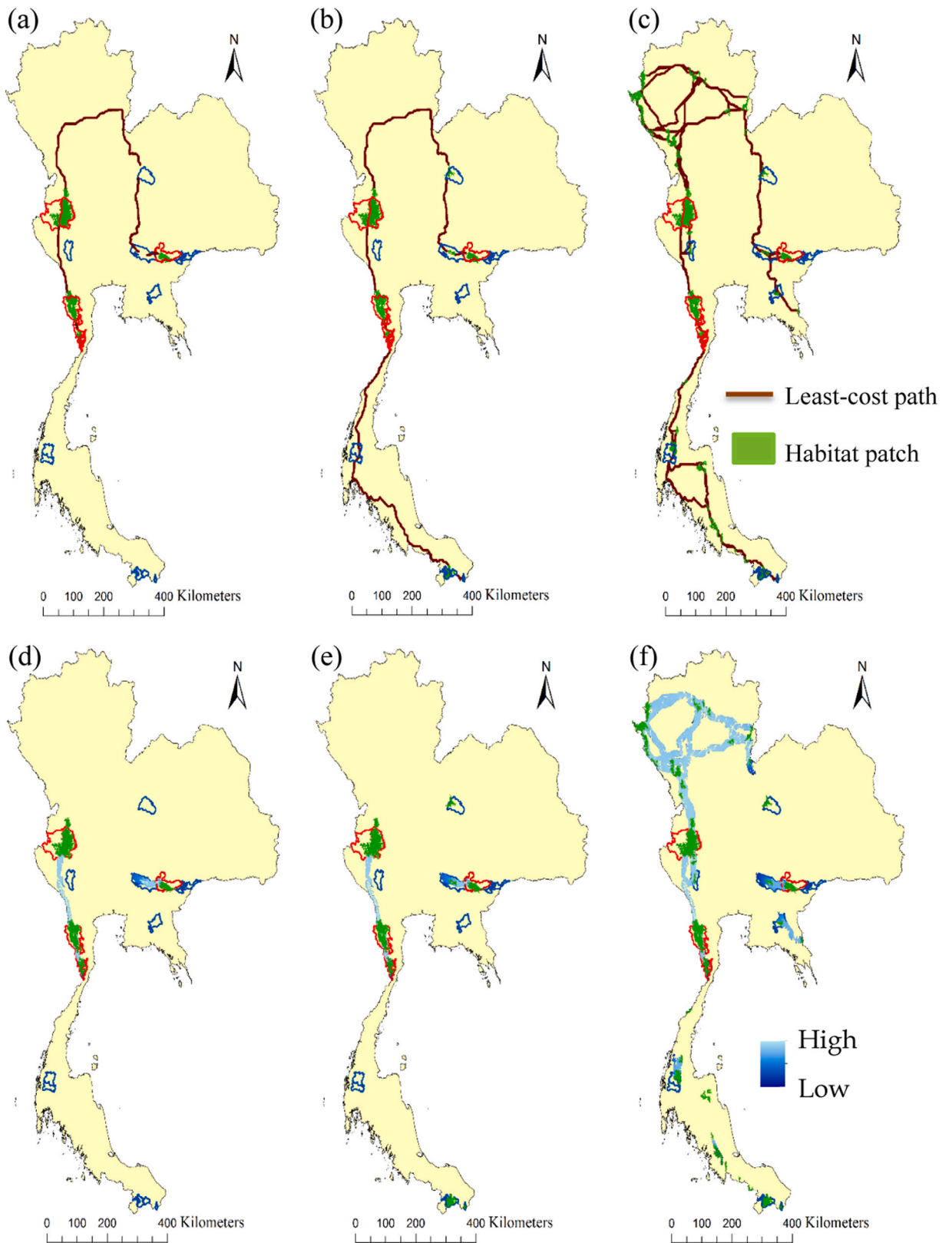
Fig. 4. Occurrence models for ungulate prey: (a) wild boar in blue, (b) gaur in purple, (c) muntjac in orange, (d) sambar deer in brown derived from an ensemble species distribution model showing the probability of occurrence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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Fig. 5. Connectivity across Thailand, (a) habitat patches with tiger occurrences at the time of our survey (green) and their least-cost path corridors (brown line), (b) habitat patches in the fifteen protected areas that we surveyed and their least-cost path corridors (c) potential habitat patches and their least-cost path corridors; and the same three sets of habitat patches with circuit theory corridors with 10 km (e-f), showing high probability of tigers' movements (light blue) and low probability of tigers' movements (dark blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

land cover type, percent tree and shrub cover, elevation, and human disturbances (Rabinowitz and Zeller, 2010; Ramirez-Reyes et al., 2016; Diniz et al., 2018). In addition to including prey availability, we integrated the cumulative annual productivity and seasonal variation in productivity derived from the Dynamic Habitat Indices (DHIs), which have been successfully used for predictions of species richness (Hobi et al., 2017; Radeloff et al., 2019; Suttidate et al., 2019), and the occurrence of moose in Canada (Michaud et al., 2014), but not used to model large mammal occurrence patterns in the tropics. We found that primary productivity variables were important factors in predicting the occurrence of both ungulate prey species, and therefore tigers in Thailand.

4.2. Connectivity assessment

We found that the remaining large, intact habitat patches for Indochinese tigers in Thailand were mostly located within protected areas, and they were highly fragmented, with high resistance across dispersal corridors. The Western Forest Complex was the largest contiguous area of suitable habitat, but, between it and other habitat patches, it had low dispersal probability and high resistance to movement due to its isolation. Based on available information for Indochinese tigers in Thailand, individual tigers may not be able to travel to the nearest patches with tiger occurrences because of urban and agricultural areas that are in-between (Simcharoen et al., 2014; Duangchantrasiri et al., 2019). Moreover, the East-West economic corridor, a highway connecting Myanmar to Vietnam through Thailand, which is currently being upgraded, may become increasingly a barrier that blocking tiger movement between the Western Forest Complex and Kaeng Krachan Forest Complex. On the other hand, our results indicate that tiger populations in the Keng Krachan-Kuiburi complex, though smaller, occur in well-connected patches and that potential dispersal corridors for tigers exist, or can be restored.

Regaining connectivity across Thailand may prove to be difficult. Habitat connectivity remains intact only in protected areas within the Western Forest Complex and Kaeng Krachan Forest Complex. By ranking the relative importance of each habitat patch and dispersal corridor in maintaining the connectivity among existing tiger populations and potential suitable habitat for tigers' dispersal, we identified where future reintroduction could be considered if prey availability is sufficient and hunting pressure can be minimized. We found that the habitat patch located in the Western Forest Complex was the most important refuge for tigers because it covers a large area of suitable habitat with abundant prey (Steinmetz et al., 2008; Simcharoen et al., 2018; Duangchantrasiri et al., 2019). However, this habitat patch is fairly isolated, which could eventually lead to inbreeding depression, as is the case for isolated tiger populations in India and Nepal (Smith, 1993; Wikramanayake et al., 2004). The Kaeng Krachan patch has a smaller habitat area, but is well connected to the Kuiburi habitat patch. Therefore, Keng Karchan is an important stepping-stone and dispersal corridor between the Western Forest Complex and Kuiburi, and is the most important in maintaining the overall connectivity network in the country. Other patches with tiger occurrences had low contribution to the overall connectivity network. A special case is the dispersal corridor between Thap Lan and Khao Yai, which could connect relatively large suitable habitat areas. In our models, the resistance of movement was medium-high partly because of highly 304, which runs right between the two areas. However, recently a wildlife overpass has been constructed, and fences are being built to guide wildlife to this overpass, which may substantially reduce dispersal cost, and provide important new connectivity.

4.3. Management implications

The remaining suitable habitat patches are located within protected areas because forested areas outside are increasingly degraded by human activity. However, we found that these suitable habitat patches are fragmented and isolated, which is worrisome because of the effects of habitat fragmentation on population survival, which can occur over decades (Gibson et al., 2013). It is therefore imperative to act now to ensure long-term survival of the species. Our analyses identified several priority patches and dispersal corridors for connectivity, where future introductions could contribute to existing tiger populations as long as prey availability is sufficiently high, poaching can be controlled, and local communities are supportive. The north of Thailand seems particularly promising for recolonization or reintroduction efforts. However, such efforts will require to first identify why tigers are no longer found there, and to assess if the causes for their extirpation can be mitigated. While it is encouraging that there is ample potential habitat according to our models, that information alone does not suffice to initiate reintroductions.

In terms of improving the connectivity of tiger populations in Thailand, we suggest several conservation strategies. First, it is important enhance the quality of the areas where tigers remain, and where they were lost since our surveys, by decreasing land use pressure in the potential habitat patches outside of protected areas, and controlling poaching. Second, we recommend protecting potential habitat patches and dispersal corridors identified by our study. Third, it is necessary to maintain high-value habitat patches and dispersal corridors to ensure persistence of a connectivity network. Fourth, it will be valuable to restore degraded habitat through strategic land-use planning so that prey species population can increase. These four steps, in addition to improving the connectivity of tiger population in Thailand would also improve habitat quality and connectivity for their prey species, thereby providing both additional conservation benefits (gaur and sambar deer are both ranked as 'vulnerable' by IUCN), and higher prey availability for tigers.
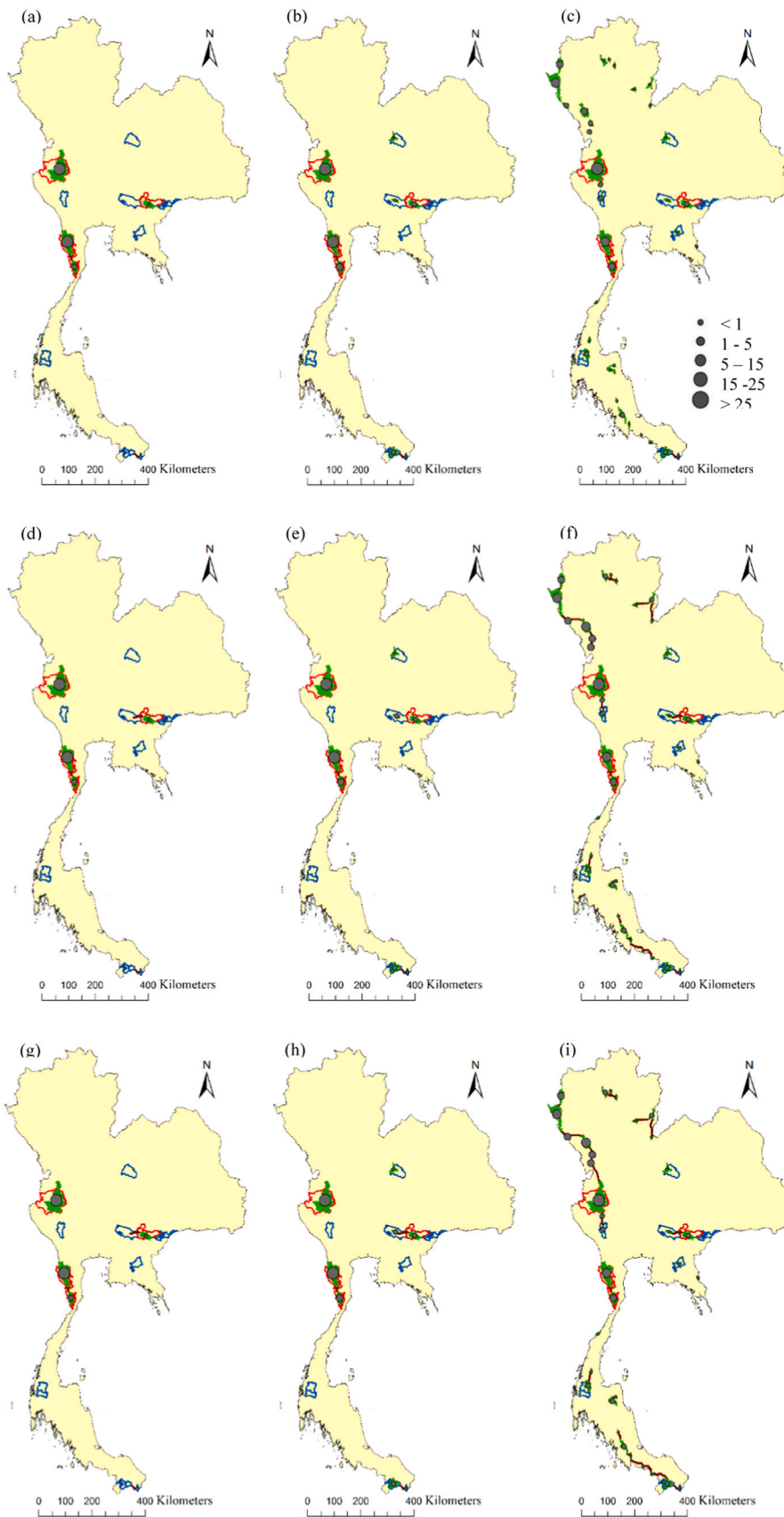
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Fig. 6. The relative importance of habitat patches and dispersal corridors for the Indochinese tigers in Thailand. The importance of each habitat patch is shown in term of its contribution to maintain the overall landscape connectivity as measured by the probability of connectivity index for occupied at the time of our surveys, all fifteen protected areas, and potential habitat patches: (a), (b), and (c) probability of dispersal is 0.5 at 25 km distance, (d), (e), and (f) at 58 km, (g), (h), and (i) at 64 km.

In summary, the goal for tiger conservation is to create large and well-connected populations that can persist long-term. We found that the habitat connectivity network for the Indochinese tigers in Thailand consists of highly isolated patches. However, we highlight priority areas for conserving existing tiger populations, and potential candidate sites for future reintroductions and potential dispersal corridors. It is crucial to protect both remaining and potential habitat patches and corridors. Enhancing the quality of the area where tigers remain, and reintroducing tiger populations and their prey in other areas could substantially increase the overall connectivity among the Indochinese tiger populations in Thailand. Our connectivity analyses also highlight the importance of incorporating prey distributions plus primary productivity interactions to quantify occurrence, and demonstrate how combining least-cost modeling, circuit analysis, and graph theory approaches with species' dispersal ability can improve assessments of habitat quality and connectivity. This information is important for understanding patterns of habitat connectivity and for developing management strategies to ensure long-term survival of tigers and other carnivores in Thailand.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01718.

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