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Patch metrics of roosting site selection by Lyle's flying fox (*Pteropus lylei* Andersen, 1908) in a human-dominated landscape in Thailand

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Abstract

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The association between patch metrics and roosting site (n = 31) suitability of Lyle's flying fox (*Pteropus lylei*) in 26 Central Eastern and Western provinces of Thailand was quantified. Land use classes with 90-m resolution were identified based on various vegetation and land cover types to calculate patch metrics using FRAGSTATS. Then, Maximum Entropy Modeling (MaxEnt) was performed using patch metrics covariates to produce a predictive potential distribution map. The results indicated that patch contiguity (contiguity index, 63.7%), patch area (29.3%), and patch shape complexity (shape index, 5.7%) are the most influential patch metrics, all of which have negative effects on roosting site suitability. In total, 13,222 small patches were considered highly suitable patches, with a mean area of 0.921 ± 0.698 (SD) ha, which accounted for 122,090 ha (2.04%) of the study area. Roosting sites predicted from the model were consistently associated with occurrences of roosting sites observed in temples; such habitats likely provide shelter from external threats for colonies roosting in a human-dominated landscape.

Keywords

Lyle's flying fox, MaxEnt, patch metrics, roosting site selection, species distribution modeling

Introduction

Lyle's flying fox (*Pteropus lylei* Andersen, 1908) inhabits a range from the central, eastern, and western regions of Thailand to Southern Vietnam and Cambodia (Lekagul and McNeely, 1977; Bumrungsri et al., 2008). The largest *P. lylei* colony in the world is found in Thailand, with a population estimated to be about 75,016 ± 1,688.77 (SD)

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individuals, and up to 30 colonies have been identified (Chaiyes et al., 2017). Flying foxes play a significant ecological role as pollinators and seed dispersers by dispersing and replanting native food plants. Due to wide-range foraging across the landscape, Lyle's flying can be considered as a disperser species contributing the renewability of food resources, thus resulting in long-term stabilization of natural vegetation community (Weber et al., 2015). Globally, this species is classified as vulnerable on the International Union for Conservation of Nature (IUCN) Red List and is listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in Thailand. Populations of Lyle's flying fox are threatened by habitat destruction, fragmentation, and scarcity of roosting site resources as existing trees die and are not replaced, as well as hunting (Bumrungsri et al., 2008).

Species distribution models (SDMs) have been used in conservation to address questions related to selection of protected sites, reintroduction, and development of effective species conservation measures (Guisan et al., 2006; Franklin, 2010). SDMs could be used to measure the association between species records and underlying factors, such as environmental conditions or spatial characteristics (Franklin, 2010), to provide valuable information on the preferences, requirements, and suitability of habitats for studied organisms. Maximum entropy modeling (MaxEnt) has been used successfully in SDMs and this approach performs better than other modeling methods (Elith et al., 2006). MaxEnt has been widely used for many purposes, such as in biogeography, conservation biology, and ecology (Elith and Leathwick, 2009). MaxEnt was used in this study because it is one of the best among many different modeling approaches, and estimates the probability distribution of species occurrence even with small sample sizes (Phillips et al., 2006; Elith et al., 2011). An analysis of the distribution and availability of a suitable habitat in landscape context can be integrated with information about patch size, shape, and isolation, which are key components of patch-based approaches for predicting fundamental habitats of spatially subdivided populations (MacArthur and Wilson, 1967). A patch can be defined as a relatively homogenous area that differs from its surroundings and can be classified polygonally as a specific feature (Leitão et al., 2006). Patch metrics have been used to quantify attributes associated with habitat characteristics within patches. The association between patch metrics and habitat utilization can be used to identify and predict distribution patterns of focus species' habitats (McGarigal and Marks, 1995; McGarigal et al., 2012).

Our main objective was to identify the patch metrics covariates most likely to influence the presence of flying fox roosting sites and to assess approaches for conservation of the Lyle's flying fox population. We developed a distribution model by using MaxEnt to derive the association between spatial locations of Lyle's flying fox roosting sites and features of the patch enveloping observed locations. Moreover, these associations were used to interpolate probability of roosting site selection in the entire study area to identify locations of potential key patches. The subsequent predictive map and covariate sensitivity will help to assess conservation approaches for this species.

Materials and methods

Study site

The study comprised 26 provinces in Central Eastern and Western Thailand, covering an approximate area of 104,107 km^2 (Fig. 1) located at 98°06′0.13″–103°04′38.65″E and 10°54′59.49″–15°48′42.54″N.

Field data collection

Field data on Lyle's flying fox across the study area were collected from existing surveys (Duengkae et al., 2015; Thanapongtharm et al., 2015; Chaiyes et al., 2017) with ground truthing for roosting site occurrence. The coordinates of a total of 31 roosting sites were recorded using a Global Positioning System (GPS) receiver. Land use covariates were identified around each roosting site to identify land use changes.

Data analysis

Preparing spatial data

Land use and land cover data for 2008–2010 were provided by the Land Development Department and updated following a field survey in 2015. Classified map data were grouped into different land use polygons and then reclassified into 20 layers consisting of urban temple and built-up land, perennial, eucalyptus, mango, cashew, banana, tamarind, acacia, guava, papaya, jackfruit, santol, rose apple, manila tamarind, sapodilla, mixed orchard, forest land, mangrove forest, water body, and scrub, according to Weber et al. (2015). This reclassification method was in line with studies of the movement and foraging behavior of Lyle's flying fox using high-resolution GPS loggers over two seasons. Patches were converted into raster format to adjust the size of the study area, with a final resolution of 90 × 90 m. Geospatial data were organized and classified using the QGIS ver. 2.18.7 software (QGIS Development Team, 2009).

Patch metrics for spatial characteristics analysis

We derived 11 patch metrics using the FRAGSTATS ver. 4 software (McGarigal et al., 2012). FRAGSTATS was developed specifically to measure the spatial characteristics of patches, and was used to perform assessments of patch-wise landscape metrics (McGarigal and Marks, 1995; McGarigal et al., 2012): patch area (AREA), patch perimeter (PERIM), radius of gyration (GYRATE), perimeter–area ratio (PARA), shape index (SHAPE),

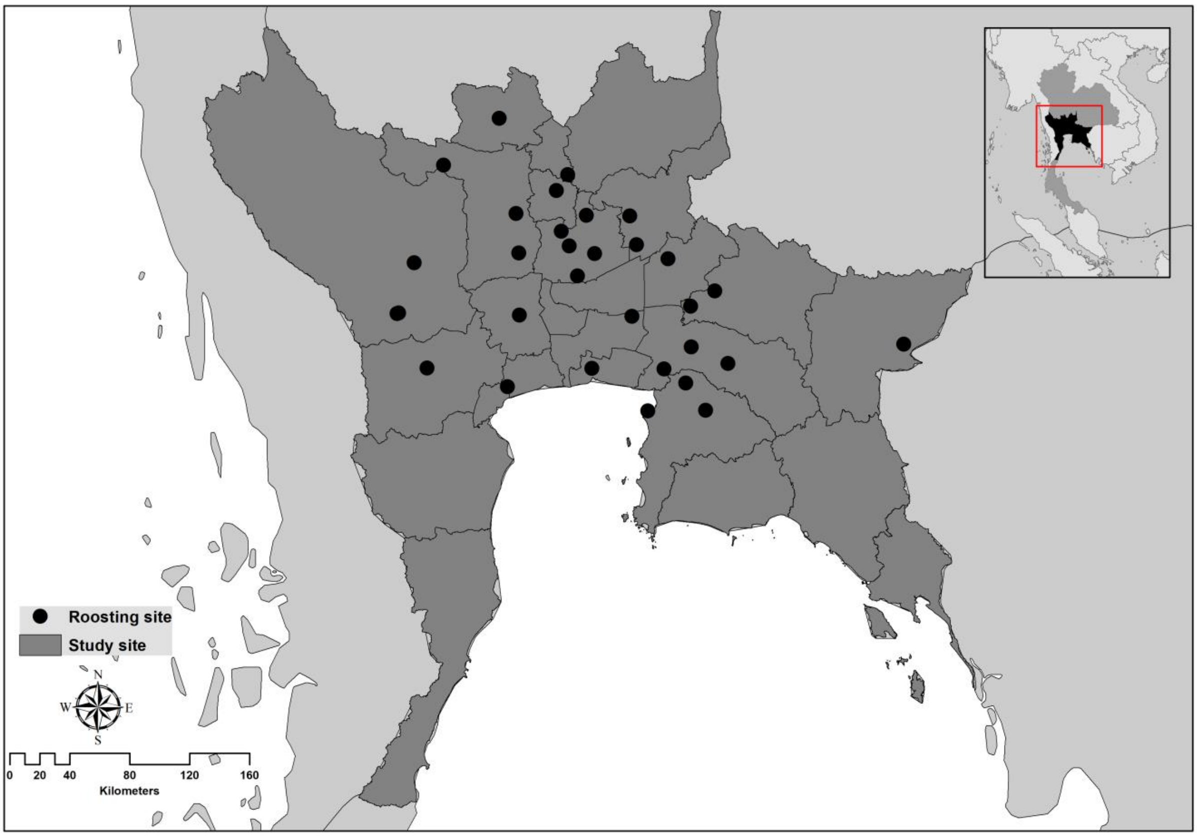

Fig. 1. Study area and location of Lyle's flying fox roosts in Thailand.

fractal dimension index (FRAC), related circumscribing circle (CIRCLE), contiguity index (CONTIG), core area (CORE), number of core areas (NCORE), and core area index (CAI). Then we used R ver. 3.0.1 to conduct principal component analysis (PCA) to reduce dimensions of variables in the dataset of the 11 parameters (Table 1). Patches and landscape covariates were transformed into principal components, and covariates that contributed to the variation in the data were selected to find the few important variables that were not related and redundant in the biplot (Fig. 2). Eight parameters, namely AREA, GYRATE, PARA, SHAPE, FRAC, CIRCLE, CONTIG, and CORE, were selected for analysis with MaxEnt.

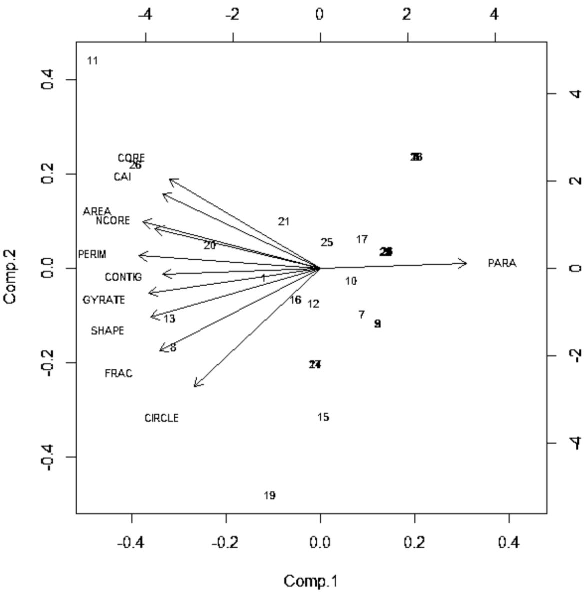

Fig. 2. Principal component analysis (PCA) biplot of the spatial characteristics of 11 parameters. Black arrows indicate original directions of projected landscape metric variables on the PCA plane.

Selection of Lyle's flying fox roosting sites: modeling procedures and analysis

We performed roosting site selection analyses using maximum entropy modeling in MaxEnt version 3.3.3 k. MaxEnt estimates are probability values that represent the suitability or unsuitability of a location for the presence of the species based on the relationship between presence points and patch characteristic parameters calculated from FRAGSTATS (with all spatial characteristic layers represented at a 90-m grid resolution) were used as inputs for the modeling process. The result was used to predict probabilities of Lyle's flying fox roosting sites as a function of patch metrics. In the model evaluation processes, records of roosting sites were randomly partitioned into training and testing subsamples: 80% of the records were used to build up the model, and the remaining records

Table 1. Patch metric parameters

Patch metric	Description
AREA	The area (m^2) of the patch, divided by 10,000 (to convert into hectares).
CAI	Core area index; patch core area (m^2) divided by total patch area (m^2), × 100 (to convert to percentage).
CIRCLE	Related circumscribing circle; 1 – patch area (m^2) divided by the area (m^2) of the smallest circumscribing circle.
CONTIG	Contiguity index; the average contiguity value. The contiguity index assesses the spatial connectedness, or contiguity, of cells within a grid-cell patch to provide an index of patch boundary configuration, and thus patch shape.
CORE	Core area; the area (m^2) within the patch that is further than the specified depth-of-edge distance from the patch perimeter, divided by 10,000 (to convert to hectares). Edge segments along the landscape boundary are treated as background (as specified in the edge depth file) unless a landscape border is present, in which case boundary edge types are made explicit by information in the border.
FRAC	Fractal dimension index; 2 × the logarithm of patch perimeter (m) divided by the logarithm of patch area (m^2), where perimeter is adjusted for raster bias.
GYRATE	Radius of gyration; the mean distance (m) between each cell in the patch and the patch centroid.
NCORE	Number of core areas; the number of disjunct core areas contained within the patch boundary.
PARA	Perimeter–area ratio; the ratio of patch perimeter (m) to its area (m^2).
PERIM	The perimeter (m) of the patch, including any internal holes in the patch.
SHAPE	Shape index; the patch perimeter (m) divided by the square root of patch area (m^2), adjusted for a standard square using a constant.

were used to test the model's accuracy. The model run with random data partitioning with 80% training data and 20% test data had the highest area under the curve (AUC) values for both training and test data. A random partition test was applied to the Lyle's flying fox occurrence data to help minimize substantial errors in the predictions by creating two independent datasets (training and test data) for model validation (Fielding and Bell, 1997). Then we obtained the average final map of roosting site selection from a logistic output format of predictive function and exported the map as an ASCII file.

Model performance

The predictive performance of the roosting site selection model for roosting sites of Lyle's flying fox was evaluated based on AUC values of the receiver operating characteristic (ROC). ROC analysis is recognized as the best measure of model performance, with wide applicability in species distribution modeling (Fielding and Bell, 1997; Phillips et al., 2006, Elith et al., 2011). An ROC plot was built by plotting sensitivity (1 − omission rate) against 1 − specificity (fractional predicted area) for all available probability thresholds (Manel et al., 2001). AUC values range from 0 to 1, such that 1 represents perfect accuracy for a given optimal cutoff, 0.5 corresponds to no improvement from model prediction compared to making a prediction by chance, and 0 represents a model with predictive ability lower than prediction by random chance. For the discrimination of suitable and unsuitable areas, the threshold was applied by selecting the point on the ROC curve that was closest to the upper-left corner (0, 1), which represents a perfect test with 100% sensitivity and specificity (Cantor et al., 1999). The areas with probability values below the threshold were excluded from predictions. Useful models produce AUC values around 0.7 to 0.9, and models with good discriminating ability produce AUC values above 0.9 (Swets, 1988; Fielding and Bell, 1997; Boyce et al., 2002; Elith et al., 2006). In addition, the contribution of these variables in the model was evaluated. To represent the suitability of roosting site, MaxEnt-estimated selection probability was categorized into three classes: unsuitable (0.00–0.40), moderately suitable (0.40–0.70), and highly suitable (0.70–1.00).

Identification of relevant conservation area for Lyle's flying fox near a temple

Temples in Thailand may provide shelter and protection for flying fox populations. After obtaining MaxEnt data, we categorized the predicted selection of roosting sites in highly suitable patches with the location of a temple and distance to water. In this study we categorized the roosting area with cutoff at maximum distance to water of 1,500 m due to previous study (Chaiyes et al., 2017). The overlap with fitted points was assessed and confirmed using Google Earth. The locations of roosting sites were then validated with the prediction of probability from MaxEnt results.

Results

Model performance

The AUC values of the receiver operating characteristic (ROC) plots was high for both training data (AUC = 0.885) and testing data (AUC = 0.872), indicating the ability of MaxEnt to discriminate between suitable and unsuitable areas for roosting site occurrence (Fig. 3). These results suggest that the model predictions were accurate for representing roosting sites for the distribution of Lyle's flying fox. The predicted probabilities ranged from 0.002 to 0.842. The logistic threshold value of 0.306 represented a perfect test with 100% sensitivity and specificity based on the point closest to the upper-left corner (0, 1) of the ROC curve, with a fractional predicted area of 0.168, training omission rate of 0.240, and test omission rate of 0.167.

Variable importance and response curves

Analyses of the relative importance of MaxEnt variables showed that CONTIG was the most important spatial characteristic predictor, accounting for 63.7% of the contribution to model variation. The next most important predictors were AREA (29.3%), SHAPE (5.7%), and PARA (1.3%), followed by GYRATE, FRAC, CORE, and CIRCLE (0%), respectively. The response curves associated with the most influential factor showed that roosting site selection was highest at low values of CONTIG, AREA, and SHAPE, but declined at higher values (Fig. 4a–c). By contrast, the response curve for PARA showed a positive relationship with roosting site selection (Fig. 4d).

The model with the highest AUC value was considered the best performer and can be used to predict roosting site selection for Lyle's flying fox. With the advent of the landscape paradigm in ecology, great attention has been paid to the composition and configuration of the landscape, determined by quantifying type of use, size, shape, arrangement, and distribution of landscape

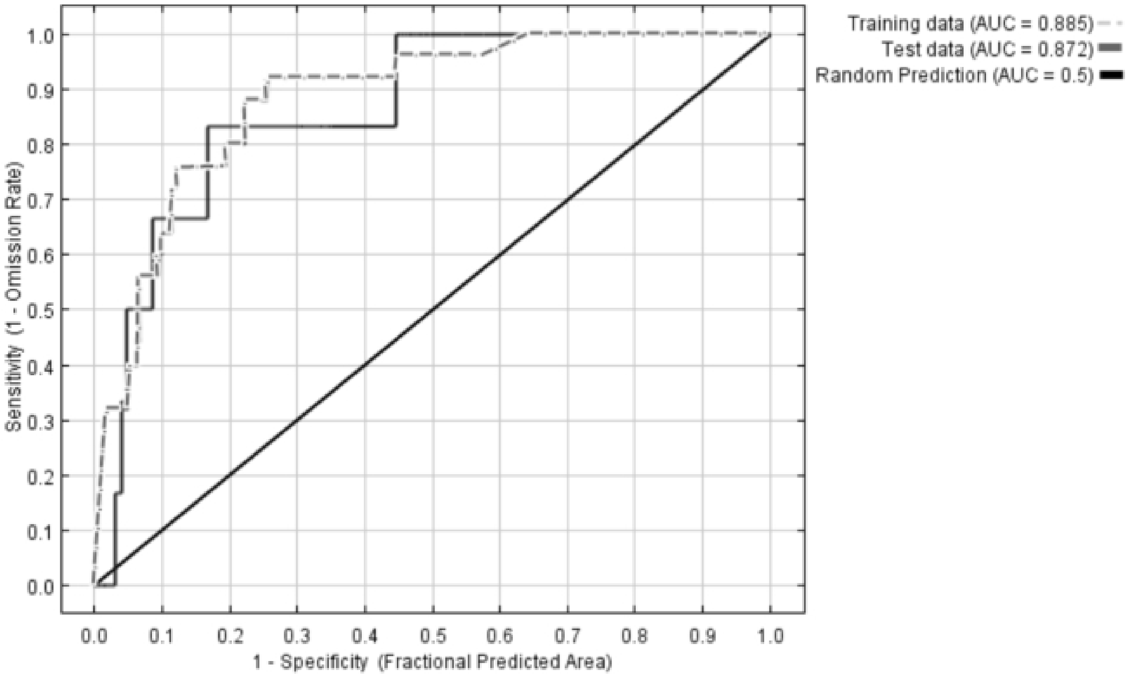

Fig. 3. Receiver operating characteristic curves for sensitivity versus 1 − specificity for the studied species based on the area under the curve (AUC) determined by the Lyle's flying fox roosting site model. Black diagonal line corresponds to an AUC value of 0.5, indicating random prediction. Dash (training) line shows the fit of the model to the training data. Gray (testing) line indicates the fit of the model to the test data and is the real test of the model's predictive power.

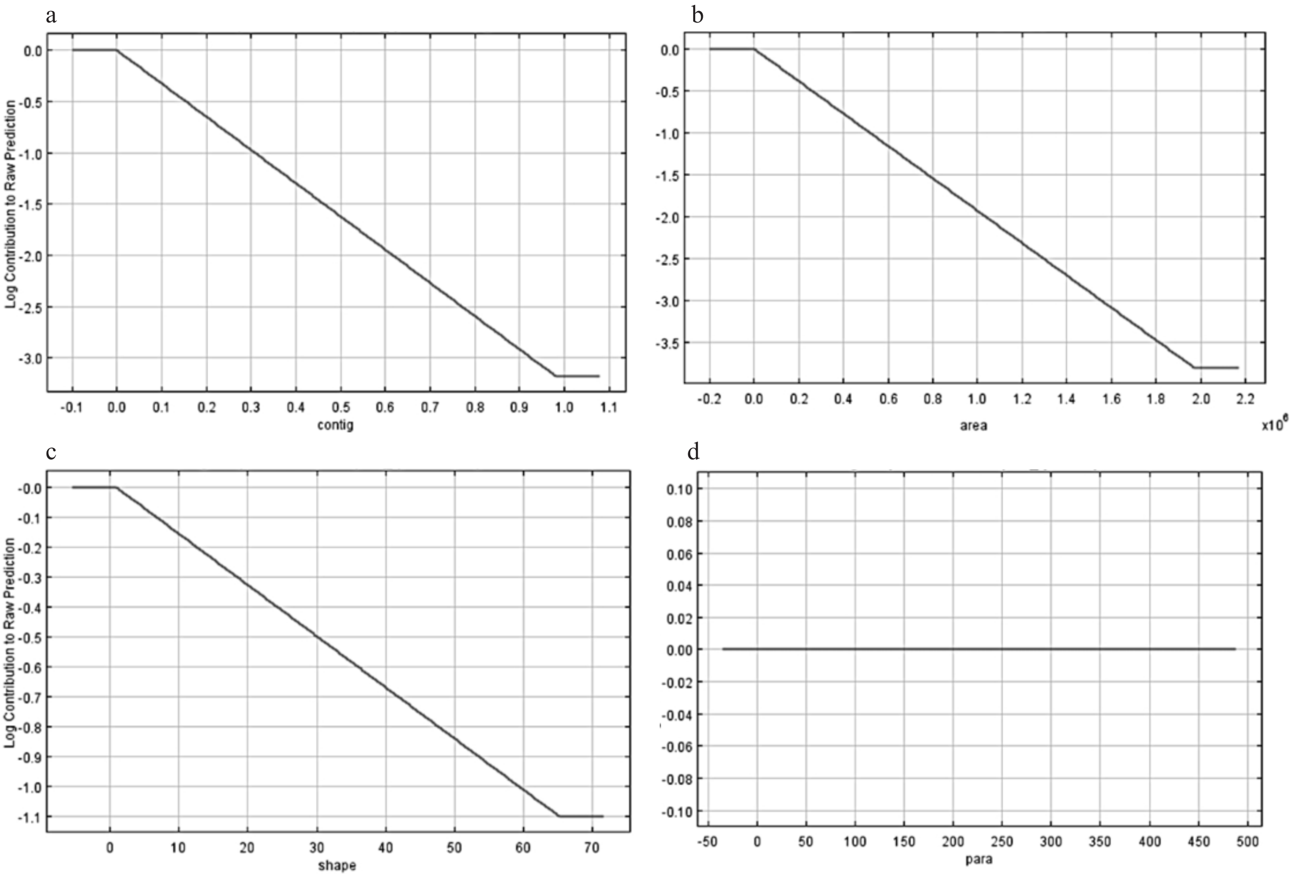

Fig. 4. Response curves for Lyle's flying fox roosting site selection variables determined by MaxEnt modeling: (a) CONTIG, contiguity index, (b) AREA, patch area, (c) SHAPE, shape index, (d) PARA, perimeter–area ratio.

elements; such qualities affect species distribution and population dynamics deals fundamentally with how, when, and why patterns of environmental factors influence the distribution of organisms and ecological processes, and reciprocally, how the actions of organisms and ecological processes influence ecological patterns (Turner et al., 2001).

From the models, we found a high contribution of CONTIG. A large contiguous patch body resulted in larger CONTIG values, indicating a high degree of connection between roosting site patches and other patches of the same type in proximate areas. The negative association of roosting site selection with AREA indicated a strong preference for small, fragmented patches as roosting sites. Given the high degree of disturbance in human-dominated landscapes, escaping from such a threat likely involves selecting less-suitable but more secure roosting areas, particularly temples, according to Weber et al. (2015). Movement between temples and temporary roosting sites was observed, with Lyle's flying fox usually returning to the temples if disturbed at a temporary roosting site. The selection of patches with a low degree of continuity and small area may be related to specific patterns of utilization of available roosting resources, e.g., trees, in the remaining vegetation patches on cleared land and urbanized areas (Eby, 1991). Despite making a relatively low contribution to the model, SHAPE could be used to indicate that the presence of roosting sites is related to regular and compact habitat patches.

The contiguity of natural areas is increasingly at risk from conversion to agriculture as the increased global human population causes rising demand for food. The impacts of landscape fragmentation on population can be reduced through the development of buffer zones around fragmented habitats to protect those natural habitats from disturbances from neighboring land. The structure of the habitat at a site influences its suitability for a species and determines presence or abundance; however, this is not always the case. Characteristics of the surrounding landscape context and hidden ecological factors can have an impact on the suitability of habitat.

Small woodlots within an agricultural landscape have the potential to support a community of wildlife that is different from that found in woodlots surrounded by commercial or industrial areas. Because of land ownership issues, it may be impossible to control or manage the landscape surrounding a habitat patch (Delong and Brittingham, 2015). The minimum roosting site area was 5,472 m^2, and the maximum was 435,700 m^2; the average was 44,290.67 m^2. In addition, 31 roosting sites were at least 436,000 m^2, indicating that Lyle's flying fox does not need a large area for roosting. This information is in agreement with reports of no sightings of Lyle's flying fox in large forest patches such as in protected areas.

Roosting site selection maps

This study examined the application of species distribution modeling to estimate roosting site selection by Lyle's flying fox using appropriate patch characteristic predictors. Roosting site selection values were classified into three levels based on probability scores (Table 2). Highly suitable patches comprised 13,222 small patches with mean area of 9,212.93 ± 6980.58 (SD) m^2 and total area of 1,220,900,000 m^2 (2.04%) within the study area; these were characterized as noncontiguous, small, and sometimes regularly shaped patches matched to patches underlying roosting sites by ground truthing. Areas with the highest suitability were mainly distributed in the central region (Fig. 5).

Identification of relevant conservation areas for Lyle's flying fox in temples

Sites in temples were validated and selected for their association with the estimated probability, canopy tree cover, and the maximum distance to the main stream of a river of 1,500 m from the temple (Chaiyes et al., 2017). Roosts located in temples contained 58% of the total Lyle's flying fox population. These results indicate that highly suitable patches contained urban temples and built-up land (more than 22%). Based on 31 roosting sites, temples appeared to provide key roosting sites for 15 Lyle's flying fox colonies. We identified 5, 4, 3, 2, and 2 roosting sites in mixed orchard, scrub, mangrove forest, perennial trees, and built-up land, respectively. There were 8,883 temples

Table 2. Lyle's flying fox roosting site selection scores

Score	Probability	Number of patches	Mean patch size (m^2)	Total area (m^2)/(%)
Unsuitable	0.1–0.4	13,222	4,085,661 ± 286,683,188.7	54,020,610,000 (90.20)
Moderately suitable	0.4–0.7	69,998	6,648.2 ± 19,545.5	4,651,240,000 (7.77)
Highly suitable	0.7–1.0	13,520	9,212.93 ± 6,980.58	1,220,900,000 (2.04)

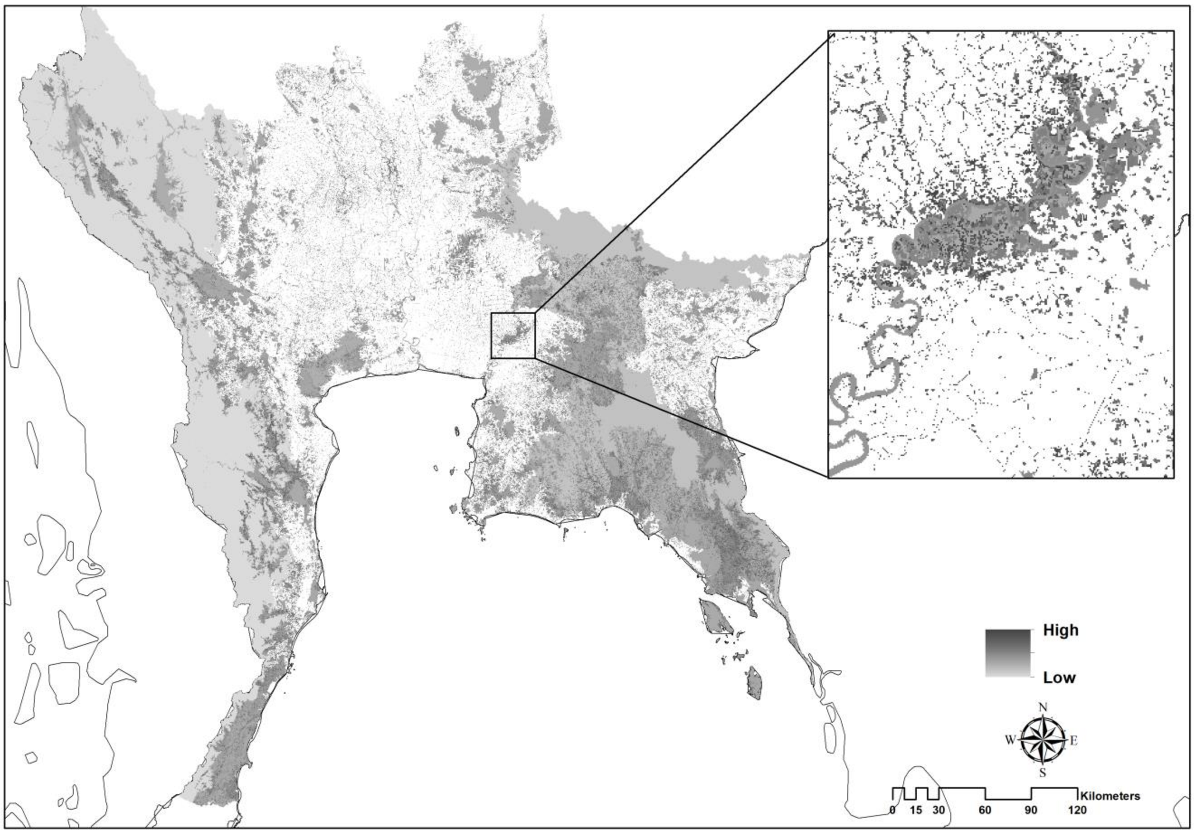

Fig. 5. Predicted roosting site selection maps for Lyle's flying fox from MaxEnt results, where 0 = low suitability and 1 = high suitability.

in the study area, of which 53 were found to overlie highly suitable areas. The location of each temple was verified using Google Earth. We ultimately identified 34 temples (Fig. 6) as potentially suitable roosting sites.

Discussion

Relevant conservation areas for Lyle's flying fox at temple roosting sites were found to be associated with canopy tree cover near the temples and the distance to the nearest reservoir or river, which was usually no farther than 1,500 m from the temples, based on our data and the findings of a previous study (Chaiyes et al., 2017). By considering the proximity of water bodies, the location of each temple was checked using Google Earth. We identified 34 temples as potentially suitable roosting sites, most of which were small areas in temple patches. The availability of roosting trees and the absence of human threat made temples safe places for the Lyle's flying fox (Louis et al., 2008; Weber et al., 2015). Globally, the main threats to tree-roosting colonies of *Pteropus* species are hunting and habitat loss due to agriculture (Kunz and Pierson, 1994). Within Thailand, bat hunting has been reported around 57% of the roost sites, and 62% of the total bat population located near these sites (Chaiyes et al., 2017). However, as human populations expand and more land is developed, the benefits to flying foxes due to niche alteration are likely to be exceeded by deleterious consequences of human activities and competition for space.

Consequently, temples may provide shelter and protection for Lyle's flying fox, and temple sites likely contain more suitable trees for roosting. These flying fox populations are at risk due to highly specialized roosting requirements (Ali, 2010; Dey et al., 2013). Roosting sites nearly always occur in small patches (Delong and Brittingham, 2015). It is necessary to conserve habitat within temples to support Lyle's flying fox populations by providing roosting sites safe from disturbance (Boonkird et al., 2006; Jeyapraba, 2016).

Conclusion

The results of this study suggest that the most suitable habitat areas for Lyle's flying fox were associated with low patch contiguity, which was the most important spatial parameter affecting roosting site location. The model results and observed locations show that this species prefers such areas, particularly within temple habitats. We have provided new and valuable information on potentially suitable habitats and on the possible distribution range of the species.

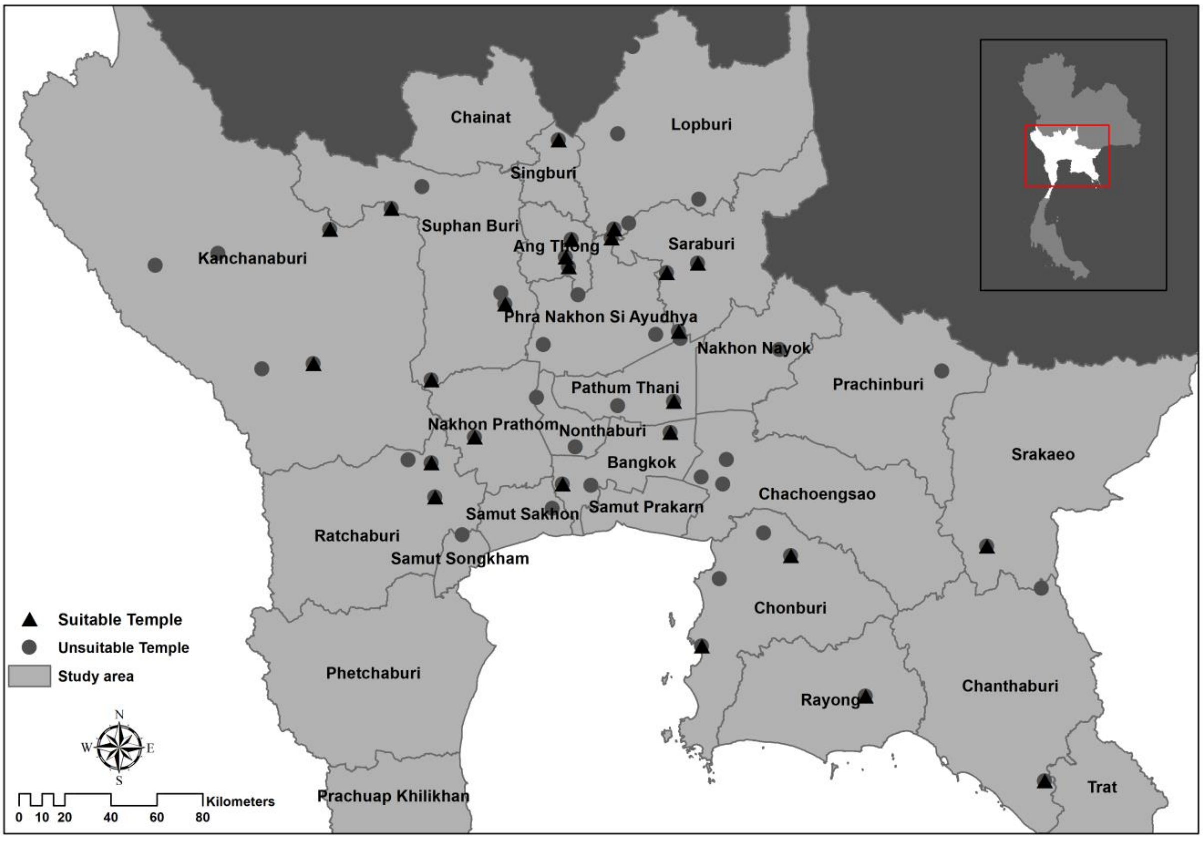

Fig. 6. Lyle's flying fox colonies residing in temples, classified by suitability. Temple locations were verified using Google Earth. Triangle dots indicate suitable sites; circle dots indicate unsuitable sites.

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