AN ISLAND-WIDE STATUS OF SUMATRAN TIGER (PANTHERA TIGRIS SUMATRAE) AND PRINCIPAL PREY IN SUMATRA, INDONESIA

by

Hariyo T. Wibisono

A dissertation submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology and Wildlife Ecology.

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Approved: ______________________________
Jacob L. Bowman, Ph.D.
Chair of the Department of Entomology and Wildlife Ecology

Approved: ______________________________
Calvin Keeler, Ph.D.
Interim Dean of the College of Agriculture and Natural Resources

Approved: ______________________________
Louis F. Rossi, Ph.D.
Vice Provost for Graduate and Professional Education and
Dean of the Graduate College

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: ______________________________

Kyle P. McCarthy, Ph.D.
Professor in charge of dissertation

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: ______________________________

Jacob L. Bowman, Ph.D.
Member of dissertation committee

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: ______________________________

Jeffrey J. Buler, Ph.D.
Member of dissertation committee

I certify that I have read this dissertation and that in my opinion it meets the academic and professional standard required by the University as a dissertation for the degree of Doctor of Philosophy.

Signed: ______________________________

John Goodrich, Ph.D.
Member of dissertation committee

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ABSTRACT

A multilateral effort to establish priorities for global tiger conservation identified 76 Tiger Conservation Landscapes throughout the 13 tiger range countries, 12 are in Sumatra, Indonesia. Despite this designation of conservation landscapes, the status of the Sumatran tiger population is still in question, as existing range-wide density estimates were derived using findings from disparate approaches. Meanwhile, habitat fragmentation and loss continue to threaten the integrity of these landscapes, while demand for tiger body parts, prey depletion, and human–tiger conflict have been documented as causing a rapid decline in tiger numbers. In Chapter 1, we jointly analyzed 29 camera trap datasets from 16 sites collected between 1999 and 2017 in a single multi-session model to allow estimating parameters across sites and sessions and tested a variety of models with different covariates for movement parameter (σ), detection probability (g0), and the density (D). We found that Sumatran tiger densities were significantly higher in lowland habitat and under protected status, that adult male tigers moved significantly further than adult females, and that the Sumatran tiger ranged over larger areas in montane habitats. In Chapter 2, we analyzed an animal sign-based detection/non-detection dataset collected along transects in 389 grid cells,17 by 17 km each, between 2007 and 2009, in 60% of the remaining tiger landscapes in Sumatra, Indonesia. We explored the effect of environmental and anthropogenic factors on the occupancy of Sumatran tiger, their main prey, and poaching and logging, using a multi-species occupancy model. We found that the occupancy of Sumatran tiger, sambar deer, and barking deer were higher in grid cells with higher percent of forest cover. Tiger and wild pig preferred lower elevations while barking deer preferred higher elevations. We found positive correlations

between the predicted occupancy of Sumatran tiger and that of the sambar deer and barking deer. National parks tended to have a positive effect on tiger presence, although poaching and illegal logging were still widespread throughout the surveyed areas, often occurring in conjunction to each other. In Chapter 3, we modelled landscape connectivity in a human–dominated landscape in West Sumatra Province, Sumatra, Indonesia. We first applied maximum entropy modelling using program Maxent v3.4.1 to identify nine core tiger habitat areas in West Sumatra Province and then developed a resistance layer, i.e., landscape friction for the Sumatran tiger to traverse through, based on roads, elevation, slope, and land cover types. We next applied circuit theory and least-cost path analysis to predict structural connectivity between Sumatran tiger core habitat areas based on our landscape resistance layer. We identified a total of 13 linkages (1,978 km^2) connecting nine core areas in West Sumatra Province; mostly skewed to gentler slopes and at higher elevation. The linkages were predominantly secondary forests, shrub, and agriculture, indicating their importance as tiger's structural corridors in a human-dominated landscape. We recommend: a) the application of the multi-session models with environmental covariates on the existing Sumatran tiger density datasets that are not yet incorporated into our study and for future island-wide tiger population assessment, b) to use the occupancy parameters we produced as the first data points against which past conservation interventions should be evaluated, and c) to implement a hands-on training program on habitat connectivity assessment for members of relevant government bodies so that connectivity analysis can be done for the rest of Sumatran tiger landscapes.

Chapter 1

REVISITING THE EXISTING ESTIMATES OF SUMATRAN TIGER POPULATIONS FROM MULTIPLE STUDIES

Introduction

A 2005 multilateral effort to establish priorities for global tiger conservation identified 76 Tiger Conservation Landscapes (TCLs) throughout 13 tiger range countries. Of these landscapes, 12 are within the island of Sumatra, Indonesia, encompassing approximately 88,000 km^2 (Dinerstein et al., 2006). Despite this prioritization, an increasing rate of habitat fragmentation and loss within these TCLs in recent years threatens the integrity of these landscapes. Further, the demand for tiger body parts in traditional medicinal markets and retaliatory killing due to conflict with humans has been driving a rapid decline in tiger numbers (Wibisono et al., 2012).

In the 2010 Global Tiger Recovery Program (GTRP) goals were established to 1) double the global tiger population by 2022, 2) establish unviolated critical tiger habitats and support professionally managed protected areas, 3) reduce demand for tiger parts from illegal hunting, 4) put in place robust tiger population monitoring, and 5) promote sustainable financing for tiger populations throughout their ranges (Global Tiger Initiative, 2010). Specific goals for Indonesia included a 100% increase in tiger populations at 6 priority landscapes and an 80% increase in occupancy levels. However, a concurrent assessment of Sumatran tiger (*Panthera tigris sumatrae*) occurrence across the entire island of Sumatra revealed that subpopulations of tigers persisted in many previously overlooked landscapes. Indeed, 29 of the 38 identified available landscape patches (inclusive of TCLs), each larger than 250 km^2, and covering 140,266 km^2, showed evidence of tiger persistence (Wibisono & Pusparini, 2010). This information brought to light the limitations of past Sumatran tiger population estimates that tended to focus on several core protected areas and, occasionally, peripheral forests, thereby overlooking the more extensive forest estate. To be able to meet the goals of the Global Tiger Recovery program it is essential to have more reliable baseline estimates of tiger population occurrence and density.

The most commonly used estimate for the number of remaining Sumatran tigers is 400-500 individuals; a figure that originated in the 1994 Sumatran Tiger Action Plan (PHPA, 1994). These numbers have been repeatedly quoted in scientific and official documents as representing a definitive estimate of the tiger population in Sumatra (Linkie et al., 2003; Linkie et al., 2008; Soehartono et al., 2007). However, this estimate only considered seven protected areas, including Gunung Leuser National Park (GLNP), Kerinci Seblat NP (KSNP), Bukit Barisan Selatan NP (BBSNP), Berbak NP (BNP), Way Kambas NP (WKNP), Sembilang Game Reserve (SGR), and Rimbang GR (Tilson et al., 1994), or only 16% of the 204,000 km^2 of available forest habitat cover at that time (Laumonier et al., 2010). Furthermore, a large proportion of the national parks included, such as GLNP and KSNP, lie at high elevation and are therefore poorer quality tiger habitat (Scognamillo et al., 2003). Accepting that there were 400 tigers in a combination of optimum and sub-optimum habitats within the 16% of available forest assessed, begs the question; how many more tigers occupy the remaining 84% of suitable habitat, much of it the better-quality lowland-hill forest areas where tigers can maintain higher densities and are still known to exist (Linkie et al., 2006; Wibisono et al., 2009; Wibisono & Pusparini, 2010).

There have been several attempts to update the status of the Sumatran tiger population since that 1994's estimate including an estimate of a minimum of 250 individuals from 8 to 18 landscapes (Soehartono, et al., 2007), 441 – 679 individuals from 10 landscapes (Linkie et al., 2008), 300 individuals with no information on the spatial extent (Seidenstricker et al., 2010), 670 (371 – 1,273) individuals from 13 landscapes (Goodrich et al., 2015), and 604 individuals in 23 landscapes thought to contain the Sumatran tigers to date (Pusparini et al., 2019). However, these estimates share at least two common problems. First, they were obtained by extrapolating site-level densities over the adjacent potential habitats or landscapes. In order to increase sample size, estimates of naturally low-density species such as the tigers are commonly obtained from surveys in optimum habitats where more tigers will be detected. Extrapolating these densities across the remaining suboptimum habitats would therefore overestimate the total abundance. Second, the densities used for the extrapolations were estimated using different methods, namely spatial and the non-spatial capture-recapture models. While spatial capture-recapture models are fairly robust, the non-spatial models tends to overestimate densities (Sunarto et al., 2013; Tobler & Powell, 2013).

A more robust estimate was proposed by Luskin et al. (2017) with an estimated number of 618 (328 – 908) individuals in 15 landscapes. The authors improve previously published Sumatran tiger densities estimated with non-spatial capture-recapture models by re-calculating the effective sampling area for each survey with a standardized buffer. However, using a single corrected buffer for all camera trap studies across Sumatra could also introduce biases, as it does not account for differences in habitat types and prey availability. Interestingly, the three studies which involved site-based densities from all major tiger landscapes suggested a similar mean population size of between 600 and 700 adult Sumatran tigers (Goodrich et al., 2015; Luskin et al., 2017; Pusparini et al., 2019). Although evaluating the largest number of landscapes (23), Pusparini et al. (2019) obtained the lowest estimate because they adjusted the estimated mean abundance obtained from extrapolation with the site-based occupancy rates produced by Wibisono et al. (2011).

In this study, we aim to further refine site-specific tiger density estimates by unifying a disparate array of datasets and analyses from previous studies. These refined density estimates can then be used to make island wide tiger population estimates even more robust. We will achieve this by: i) gathering and collating all available camera trap datasets for tigers from the island of Sumatra, ii) re-calculating site-specific tiger densities based on the collated camera trap datasets using spatial capture-recapture models; and iii) discussing the potential contribution of the revised estimates to a more robust estimate of the island-wide Sumatran tiger population status.

Methods

Study sites

We collated camera trap datasets from a total of 16 study sites consisting of six national parks, two wildlife reserves, one nature reserve, and seven non-protected forest landscapes. These study sites were spread across 8 of the 12 tiger conservation landscapes in Sumatra (Sanderson et al. 2010), namely Leuser – Ulu Masen (2 sites), Batang Gadis (1 site), Kerinci Seblat (8 sites), Rimbang Baling (1 site), Tesso Nilo (1 site), Kampar - Kerumutan (1 site), Berbak – Sembilang (1 site), and Bukit Barisan

Selatan (1 site). Among these landscapes, Bukit Barisan Selatan, Kerinci Seblat, Batang Gadis, and Leuser – Ulu Masen are positioned across the prominent Bukit Barisan Mountain range, along the Southwestern part of the Sumatra Island. These parks represent the coastal lowland habitats of Tanjung Belimbing in Lampung province to mountainous habitats up to the highest peak of Mount Kerinci (3,805 m asl) in Jambi province (O'Brien, et al., 2003). Bukit Barisan Selatan, Kerinci Seblat, and Leuser – Ulu Masen landscapes contain three national parks which have been designated as the Tropical Rainforest Heritage of Sumatra (TRHS), namely Bukit Barisan Selatan National Park (BBSNP), Kerinci Seblat National Park (KSNP), and Gunung Leuser National Park (GLNP), due to their potential as the last strongholds for their unique and diverse wildlife species and evidence of biogeographic evolution of the Island of Sumatra (UNESCO, 2004). Tesso Nilo landscape, where the Tesso Nilo National Park is located, and Rimbang Baling Wildlife Reserve are in Riau Province, Central Sumatra, representing lowland to hill forest habitats (44 – 438 m ASL). In our study, unique peat swamp habitats are represented by Kerumutan and Berbak – Sembilang landscapes where the Berbak National Park and Sembilang National Park are located (Figure 1).

Data collection

We collated 29 camera trap datasets from the Fauna & Flora International – Indonesia Program (16 datasets) (Dinata, 2008; FFI-IP, 2020; Linkie et al., 2006), Wildlife Conservation Society – Indonesia Program (WCS-IP) (4 datasets) (O'Brien et al., 2003; O'Brien & Kinnaird, 2008; Pusparini et al., 2017; Wibisono, 2006), World Wildlife Fund (WWF) (5 datasets) (Sunarto et al., 2013; Widodo et al., 2017), Zoological Society of London – Indonesia Program (2 datasets) (ZSL-IP, 2020), and

Conservation International – Indonesia Program (CI-IP) (1 dataset) (Wibisono et al., 2009). These datasets cover camera trap projects carried out between 1999 and 2017. We then reformatted all original datasets to fit within the spatial capture-recapture (SCR) data format. This included capture histories, trap layouts, and habitat masks. The general sampling procedure of these datasets was as follow:

For the 29 datasets, passive infrared camera traps were set up in pairs with 17-150 (mean: 51±32) stations per survey and a 7 – 5,682 m (mean: 1,706±961 m) distance between two closest camera stations. Camera stations were placed to optimize the probability of obtaining tiger pictures targeting the following features (from the best to the worst) (Pickles et al., 2014): 1) a trail with signs of tiger territoriality (scrape and/or scent marks), 2) a trail with other tiger signs (pugmark and/or scratches), 3) an obvious game trail, particularly along a ridgeline or a river bank, and 4) path or trail with low level of human traffic, ideally at a junction.

We set up the camera traps at approximately 45 cm above and 2 – 4 m from the game trails. Each camera trap was equipped to stamp each photograph with time and date when the photograph was taken. To meet the assumption of demographic closure, cameras were targeted to be active between 30 to 90 days, 24 hours per day, as a sampling session. In reality, however, the average days of camera operations was 154 (±75), mainly due to logistical constrains in several survey sites. Film cameras were used in two studies (O'Brien et al., 2003; Wibisono, 2006) and digital cameras in other studies. For film cameras, the number of trap days for each film was defined as from the activation of the camera until the film was retrieved, if the film had exposures remaining, or until the time and date stamp on the final exposure. For digital cameras, the number of trap days was defined as from the activation of the camera until photograph data was retrieved in each sampling period or the date of the last picture if the camera stopped working.

Data Analysis

We identified individual tigers based on their unique stripe patterns from both left and right sides. We discharged dubious tiger photographs because the capture-recapture procedure requires no misidentification of individuals. We used spatial capture-recapture (SCR) models (Borchers & Efford, 2008) to analyze the data from the 29 camera trap datasets. SCR models use the spatial temporal information from the recaptures to estimate the parameters of a half-normal detection function, the movement parameters (σ), related to the approximate radius of a circular home range, as well as the detection probability at the home range center (g0).

We analyzed all datasets jointly in a single multi-session model. This allowed us to estimate parameters across sites and sessions to improve estimates for sparse datasets. We used habitat masks for each site to exclude areas that were in the ocean. We tested a variety of models with different covariates for σ, g0 and the density D. Spatial covariates included protection status (yes = protected, no = not protected), forest/non-forest, elevation, and habitat type (montane, lowland, peat swamp). For the purpose of this study, we classified the protection status as “yes” if the location was a national park and “no” if the location was a non-national park, as national parks receive more government’s resources compared to other protected areas and thus afforded better protection. Based on habitat types and geographic location on the island of Sumatra, we classified the 29 sessions into four groups, including montane (Central Montane), heavily degraded lowland in Central Sumatra (Central Lowland), lowland in Southern Sumatra (Southern Lowland), and peat swamp (Peat Swamp)

(Table 1). We differentiated the lowlands in Central Sumatra from Southern Sumatra because Central Sumatra, located in the Riau Province, is largely dominated by industrial landscapes, including oil palm and acacia plantations (Sunarto et al., 2012, 2013), whereas Southern Sumatra is a single large protected area namely Bukit Barisan Selatan National Park. We tested this covariate for all parameters.

Several studies have shown that, for large cats, sex is an important covariate (Sollmann et al., 2011; Tobler et al., 2018) as males tend to have larger home ranges than females, and ignoring sex can underestimate densities (Tobler & Powell, 2013). Studies on tigers suggest that adult male tigers had a larger home range than adult females (Goodrich et al., 2010; Tempa et al., 2019). After an initial assessment using model selection based on AICc showed that sex was indeed an important covariate for our dataset, we included sex as a covariate for σ and g0 in all models.

In the first iteration we evaluated five different covariates for the detection model (σ and g0) while estimating a session specific density, including protection status, habitat, percent tree cover, group, and sex. Once we determined the best detection covariates based on AICc, we then modeled density as a function of covariates to determine those that best describe variation in densities across the island. We ran all models in a maximum likelihood framework using the SECR 4.3.1 (Efford, 2020) package in R 4.0.3 (R Development Core Team, 2020). Model selection was done based on AICc (Appendix A).

Results

From 29 sampling sessions with 1,490 stations and a total of 94,779 trap days, we recorded 209 individual tigers and 751 captures (Table 1). The session-wise densities (D±SE; 95% CI) of Sumatran tiger per 100 km^2 were the lowest in Ulu

Masen (0.16±0.10; 0.05 - 0.51) and the highest in Bukit Barisan Selatan (1.46±0.44; 0.82 - 2.60) (Table 2). When grouped, the densities of Sumatran tiger were the lowest in Rimbang Baling (0.45±0.13; 0.26 - 0.78) and the highest in Bukit Barisan Selatan (1.35±0.28; 0.90 - 2.03) (Table 3). The beta parameters of covariates (β±SE; 95% CI) included in the model shows that densities were significantly higher in the Southern Lowland (0.725±0.239; 0.258 - 1.193) and in protected habitats (0.357±0.164; 0.036 - 0.678). The movement parameter was significantly higher in montane habitats of the Central Montane compared to the lowland habitat in the Southern Lowland (-0.731±0.225; -0.171 - -0.291), but lower to the lowland habitat in the Central Lowland (1.049±0.182; 0.692 - 1.405). The detection probability at activity center was significantly higher in the Central Montane compared to the Central Lowland (-0.198±0.094; -0.382 - -0.013), Southern Lowland (-0.352±0.110; -0.569 - -0.136), and Peat Swamp (-0.363±0.117; -0.592 - -0.135). Male tigers had a movement parameter (0.280±0.139; 0.006 - 0.553) and detection probability at activity center (0.247±0.071; 0.108 - 0.387) higher than female tigers (Table 4).

Discussion

Session-Specific Density

Assessments of Sumatran tiger populations have been carried out in many priority landscapes. However, due to a variety of study designs and analytical methods used, they were not directly comparable. For example, prior to 2010, all site-specific estimates of Sumatran tiger populations were assessed using non-spatial capture-recapture models (Linkie et al., 2006; O'Brien et al., 2003; Wibisono, 2006; Wibisono et al., 2009). Later, several studies implemented the SCR framework to assess the

Sumatran tiger populations in several priority tiger landscapes (Pusparini et al., 2017; Sunarto et al., 2013; Widodo et al., 2017). Additionally, several efforts to assess the status of Sumatran tiger populations failed to produce density estimates due to small sample size issues or resulted in density estimates with very large confidence intervals and of questionable accuracy (Table 5). Even when data were analyzed with SCR models, the final model used varied among studies. For example, Pusparini et al. (2017) developed several models which included a behavioral effect, while Sunarto et al. (2013) and Widodo et al. (2017) did not. This is problematic for large multi-landscape projects, such as the Global Environment Facility/United Nation Development Program's (GEF/UNDP) Sumatran Tiger Project and the International Union for Conservation of Nature/Kreditanstalt Für Wiederaufbau's Integrated Tiger and Habitat Conservation Program (IUCN/KfW ITHCP) in four priority tiger conservation landscapes, where comparable density estimates across the project landscapes were necessary for project evaluation and accountability purposes (FFI-IP, 2020; Priatna, 2020; ZSL-IP, 2020). In addition, none of the existing estimates of Sumatran tiger populations investigated the effect of important covariates, i.e., habitat types and protection status. Our study revisited the density estimates of Sumatran tiger populations across 16 sites with habitat types (represented by altitudinal range) and protected status included in our models, in addition to the commonly used parameters, sex, σ, and $g0$. By combining the 29 sessions from 16 sites into a single, unified model, we were able to improve density estimates by sharing parameters across groups; thus, allowing sparse data from several sites to be analyzed. Our approach, therefore, has the potential to be adopted by large multi-landscape projects as a standard analytical framework where comparable density estimates are required, such as the GEF/UNDP Sumatran Tiger Project and the IUCN/KfW ITHCP. Therefore, evaluation of future recovery programs such as the GTRP and beyond will have a standard and robust analytical framework in place (Global Tiger Initiative, 2010).

Sumatran tiger density in Bukit Barisan Selatan was the highest compared to other landscapes assessed in our study. A large portion of Bukit Barisan Selatan landscape is protected under the Bukit Barisan Selatan National Park (BBSNP; 3,568 km^2) and provides the largest remaining intact lowland rainforest habitat (O'Brien et al., 2003) for the Sumatran tiger. In support of the BBSNP management, several long-term projects have been implemented in the park, including the Rhino Protection Unit (started in 1995) (Pusparini et al., 2015), Wildlife Conservation Society's tiger and rhino monitoring and protection project (started in 1998) (O'Brien et al., 2003), and WWF – Indonesia's tiger, rhino, and elephant conservation projects (started in 1998). Altogether, these projects have provided one of best protection measures for the Sumatran tiger living in Bukit Barisan Selatan landscape compared to other priority tiger conservation landscapes in Sumatra (Pusparini et al., 2017; Wibisono, 2006). Ulu Masen, in contrast, had the lowest tiger density estimates compared to other landscapes. Besides being unprotected, Ulu Masen is the only large landscape with no tiger-dedicated protection measures. Despite being part of the Leuser – Ulu Masen's Tiger Conservation Landscape (Sanderson et al., 2010), the interventions in this landscape have been focused on community-based conservation and development, including the community ranger initiative, through the national program of social forestry's village forest initiative (FFI-IP, *personal observation*) and the Aceh Government's REDD+ Program (Fadilla, 2018). The effectiveness of these conservation interventions in protecting the Sumatran tiger, therefore, needs to be evaluated.

Overall, Sumatran tiger densities tended to be higher in larger landscapes; in our study, including Bukit Barisan Selatan, Kerinci Seblat, and Berbak Sembilang (0.92±0.31; min = 0.61; max = 1.46 adult tigers/100 km^2). Despite large sizes, a large portion of these landscapes are national parks and have received a long-term conservation investment implemented by several international conservation organizations, including the WCS-IP (Bukit Barisan Selatan), FFI-IP (Kerinci Seblat), and ZSL-IP (Berbak and Sembilang). These landscapes have also been designated as three of six priority TLCs by the Government of Indonesia in its National Tiger Recovery Program for tiger population recovery (Global Tiger Initiative, 2010; Ministry of Forestry of Indonesia, 2010); and thus, receive stronger management investment from the central government. Over the past five years, these priority TCLs also received support from the GEF/UNDP Sumatran Tiger Project and the IUCN/KfW ITHCP, focused on six tiger core areas; a smaller area within a larger landscape containing the optimum number of breeding females, in which strongest protection and population monitoring efforts should be taken place (Walston et al., 2010). Key activities in these core areas included regular SMART patrol (Spatial Monitoring and Reporting Tool, https://smartconservationtools.org/), annual camera trap surveys, and human – tiger conflict mitigation.

Together with Kampar, Kerumutan has also been designated as one of the six priority TCLs, namely Kampar – Kerumutan landscape (Global Tiger Initiative, 2010; Ministry of Forestry of Indonesia, 2010). This TCL is an exception to the level of enhanced protection seen in other priority landscapes, with no tiger-dedicated investment in this TCL since its designation. Further, a large portion of this TCL has also been allocated for oil palm and acacia plantations. The low predicted tiger densities from our model suggest that lack of conservation efforts may be resulting in decreased tiger populations. Similarly, Tesso Nilo, one of the 12 TCLs in Sumatra (Sanderson et al., 2010) but not a member of the Government's six priority TCLs, may see a similar decrease if further action is not taken. Although tiger density in this park was relatively high in our model, it is a small, heavily isolated landscape, surrounded by logging concessions, that faces ongoing threats from habitat conversion, illegal hunting, and encroachment (Sunarto et al., 2012, 2013). Between 2002 and 2016, road density within the natural forest of Tesso Nilo landscape doubled, from 0.41 km road/km^2 to 0.88 km road/km^2 (Poor et al., 2019). These illegal activities may eventually suppress the tiger densities relative to other non-protected landscapes seen in our results.

Sumatran tiger densities outside of priority TCLs are worryingly low (0.55±0.23; min = 0.16; max = 0.93). Many of these landscapes either neglected, not well-managed, or underfunded (Pusparini et al., 2019). Bungo, Ipuh, Muara Sako, Sipurak, and Solok are marginal sink habitats of the Kerinci seblat landscape; thus, protection in these forests has been lacking.

Density as a Function of Covariates

When grouped by habitat types and protection status, Sumatran tiger densities were significantly higher in the Southern Lowland and protected habitats compared to other groups and non-protected landscapes. The Southern lowland consisted of a single lowland protected habitat of Bukit Barisan Selatan National Park. In Kerinci Seblat landscape, tiger density was higher in lowland and hilly habitats compared to at higher elevations (Linkie et al., 2006; Linkie & Ridout, 2011; Luskin et al., 2017); possibly related to higher prey productivity in lower elevations. Occupancy of Sumatran tiger, wild pig and sambar deer tended to be higher at lower elevations compared to higher elevations (see Chapter 2). Lowland forest provides warmer temperatures, more abundant water, less rugged terrain for wildlife movement, and a higher plant diversity as food resources for ungulates. All together lowland forests reduce the energy costs for large carnivores and principal prey for their daily activities (Carbone et al., 2007; Scognamillo et al., 2003).

Our study quantified the effect of protection status on Sumatran tiger population, at an island-wide level. We found that the density of Sumatran tiger was ~1.43 times higher within protected areas compared to outside of protected areas. In agreement, Wibisono et al. (2011) found that tiger occupancy was higher within protected areas compared to non-protected areas. In Sumatra, the majority of national parks we studied receive greater support from international conservation organizations and funding agencies, in addition to the state budget. A large portion of conservation investments from conservation organizations have been allocated for law enforcement operations, anti-poaching patrols, and human – tiger conflict mitigations (Linkie et al., 2015; Nugraha & Sugardjito, 2009; Risdianto et al., 2016). A case study in Kerinci Seblat National Park revealed that local informant-based law enforcement patrols increased the detection of snare traps by 40% and sites with greater routine patrols had a lower number of snare trap occurrence (Linkie et al., 2015). Further, studies on the impact of protection status revealed that deforestation was significantly lower inside protected areas; a surrogate measure of a positive impact of protection on wildlife living in protected areas (Gaveau et al., 2007; Gaveau et al., 2009).

Large carnivores, including tiger, are dependent on large ungulates as principal prey (Carbone et al., 2007; Karanth, et al., 2004). As prey become sparser at higher elevation (Scognamillo et al., 2003) large carnivores range over larger areas to forage for prey. This could explain the higher movement parameter in the montane habitat of Central Montane compared to lowland habitat of the Central Lowland and Southern Lowland groups, and peat swamp habitat of the Peat Swamp group. The movement parameter σ is a measure of space used by tigers. In montane and rugged habitat of Leuser National Park, Sumatran tiger home range was larger (250 km^2) (Tilson et al., 1992) than in lowland habitat of Way Kambas National Park (49 km^2 - 114 km^2) (Franklin et al., 1999). Another study involving four GPS collared adult male tigers found that two male tigers that were released back in Bukit Barisan Selatan National Park had smaller home ranges (67 km^2 and 191 km^2) than that of in Kerinci Seblat National Park (400 km^2) and Gunung Leuser National Park (236 km^2) (Priatna et al., 2012). In agreement with our study, Franklin et al. (1999) also found that the home range of an adult male tiger (114 km^2) was significantly larger than that of two adult female tigers (49 km^2 and 70 km^2).

In general, the density estimates from our study are much lower (mean: 0.73±0.11) than the previous comparable studies (mean: 1.04± 0.68). However, our study provides a lower variation (CV = 11%) compared to the previous studies (65%) (Table 5). This raises a question about the existing island-wide tiger population estimates, which may be too optimistic, i.e. between 600 and 700 adult tiger individuals (Goodrich et al., 2015; Luskin et al., 2017; Pusparini et al., 2019). Our study fills a gap in knowledge by adding new data points on Sumatran tiger density estimates in areas previously lack of density estimates. This includes density estimates obtained from camera trapping sessions in Solok, Ipuh, and Muara Labuh. The status of Sumatran tiger population in these sites can now be evaluated by repeating camera trap surveys with an improved sampling design.

An Island-Wide Population Estimate

A robust estimate of global Sumatran tiger population is essential to provide the management authority with the first data point against which conservation intervention will be evaluated. The first attempt to estimate the global Sumatran tiger population was done by Luskin et al. (2017). However, the estimate might be biased as the Sumatran tiger densities they used were estimated using non-spatial CMR models. We combined 29 camera trap datasets and re-calculated the Sumatran tiger densities using more robust SCR models. Therefore, it is possible and necessary to recalculate and produce a more reliable and robust global Sumatran tiger population using results of our study. One option is to improve the approach used by Luskin et al. (2017) by using the session-specific densities reported in our study instead of the non-spatial densities from previous studies. In this case, the potential bias due to the use of single corrected buffer for all previous camera studies can be reduced. Because the SCR model we used takes into account habitat covariates and spatial temporal information from tiger recaptures to estimate density parameters, it reduces biases compared to the use of a single buffer. Another option is combining the island-wide occupancy data (see Chapter 2) with density estimates from our study. By this approach, it is now possible to produce two island-wide estimates of Sumatran tiger populations for a 10-year period (2009 – 2019), i.e., first, by combining the density estimates from our study with the 1st Sumatra-Wide Tiger Occupancy Survey (SWTS) (Wibisono et al., 2011) and second, by combining the most recent density estimates from major projects

(Galindo, 2019; Priatna, 2020) with the ongoing 2nd SWTS (Chandradewi et al., 2019). However, the statistical inference of such options still needs to be discussed.

Recommendation

Our approach offers a robust standardized SCR model which can be applied jointly across all the remaining tiger habitats in Sumatra; thus, comparable tiger density estimates can be obtained and evaluated between both temporal and spatial sessions. We recommend the application of the model on the existing SCR datasets that are not yet incorporated into our study and for future site-specific tiger population assessment. Relative to the ecological requirements of Sumatran tiger, Kerinci Seblat and Leuser – Ulu Masen are the only two that should be considered large enough to maintain viable tiger populations. Given the density estimates presented in our study, it is worth pointing out that the majority of protected areas are far too small to conserve a viable tiger population over long periods, highlighting the critical importance of maintaining connectivity among protected areas, stopping fragmentation and habitat loss within the protected areas, and protected area expansions. Approximately 60 – 70 percent of Sumatran tiger habitats are outside of the national park network (Wibisono & Pusparini, 2010) and lack of conservation investments. Given that, more funds should be re-directed to secure the Sumatran tiger living in these habitats.

TABLES

Table 1 A summary of 29 camera trap sampling sessions dedicated for Sumatran tigers from 16 sites and collected between 1999 and 2017 from across the Sumatra Island. Sessions were classified into four groups based on habitat types, including montane habitats (Central Montane), heavily degraded lowland habitats (Central Lowland), peat swamp forests (Peat Swamp), and lowland habitat (Southern Lowland). For the purpose of this study, the protection status was classified into national park and non-national park as national parks receive more government's resources compared to other types of protected areas.

Session	Year	Group	Pro-tected	# Stations	# Trapdays	# Individuals	# Captures	MMDM (m)	MCP (km^2)
Solok	2009	Central Montane	no	***17***	1,546	5	12	12,570	118
Batang Gadis	2007	Central Montane	yes	37	2,542	6	7	6,910	165
Batanghari	2008	Central Montane	no	20	1,656	3	10	8,190	165
Bungo	2006	Central Montane	no	53	3,719	11	47	6,741	324
Bungo	2013	Central Montane	yes	52	2,874	7	28	9,325	457
Bungo	2017	Central Montane	no	41	2,165	4	13	9,910	321
Ipuh	2006	Central Montane	no	41	3,687	11	35	10,357	701
Kerinci Seblat	2014	Central Montane	yes	71	2,619	12	37	6,473	899
Kerinci Seblat	2015	Central Montane	yes	81	4,202	11	50	7,450	835
Kerinci Seblat	2016	Central Montane	yes	53	2,871	10	33	4,364	876
Kerinci Seblat	2017	Central Montane	yes	84	4,507	**13**	**77**	8,967	906
Langkat	2010	Central Montane	yes	68	3,510	7	32	**20,660**	979
Langkat	2013	Central Montane	no	115	5,801	9	34	10,651	1,343
Muara Labuh	2009	Central Montane	yes	20	***1,322***	4	8	6,892	150
Muara Labuh	2012	Central Montane	yes	37	2,995	4	7	11,713	327
Muara Sako	2004	Central Montane	yes	28	2,278	7	13	5,157	121
Sipurak	2005	Central Montane	yes	22	1,407	6	36	6,410	93
Ulu Masen	2013	Central Montane	no	**150**	6,568	9	14	5,923	**1,846**
Ulu Masen	2017	Central Montane	no	75	3,665	3	15	7,859	619

Session	Year	Group	Pro-tected	# Stations	# Trapdays	# Individuals	# Captures	MMDM (m)	MCP (km^2)
Rimbang Baling	2006	Central Lowland	no	20	1,598	***2***	***5***	9,790	***91***
Tesso Nilo	2005	Central Lowland	yes	22	1,659	5	27	11,371	281
Tesso Nilo	2007	Central Lowland	yes	22	1,553	7	25	8,738	183
Tesso Nilo	2008	Central Lowland	yes	25	1,724	6	45	5,860	205
Berbak Sembilang	2010	Peat Swamp	yes	50	3,953	7	30	5,956	400
Berbak Sembilang	2015	Peat Swamp	yes	46	3,961	6	31	6,874	515
Kerumutan	2006	Peat Swamp	yes	22	1,937	***2***	6	14,360	111
Bukit Barisan Selatan	1999	Southern Lowland	yes	88	2,922	7	9	***1,143***	559
Bukit Barisan Selatan	2015	Southern Lowland	yes	65	**7,769**	12	38	6,116	492
Bukit Barisan Selatan	2015	Southern Lowland	yes	65	**7,769**	**13**	28	7,735	492
Total				1,490.00	94,779.00	209.00	752.00	244,465.00	14,574.00
Mean				51.38	3,268.24	7.21	25.93	8,429.83	502.55
SD				31.70	1,799.97	3.31	16.75	3,583.56	416.13
Minimum				17.00	1,322.00	2.00	5.00	1,143.00	91.00
Maximum				150.00	7,769.00	13.00	77.00	20,660.00	1,846.00

Bolded italic and bolded characters are the minimum and maximum values, respectively.

#Trapdays is the total hours of camera trap operation within a session.

#Individuals is the number of unique tiger individuals identified within a session.

#Captures is the total number of tiger photographed within a session.

MMDM is a mean maximum distance moved between two camera stations of all tiger individuals.

MCP is a minimum convex polygon of the outermost camera trap stations.

Table 2 A summary of density estimates of 29 individual camera trap sessions dedicated for Sumatran tigers from 16 sites and collected between 1999 and 2017 from across the Sumatra Island. The effects of sex and group covariates were evaluated against the movement parameter (σ) and detection probability at activity center (g0) while estimating a session specific density. Sessions were classified into four groups based on habitat types, including montane habitats (Central Montane), heavily degraded lowland habitats (Central Lowland), peat swamp forests (Peat Swamp), and lowland habitat (Southern Lowland). Sex was classified into adult female (Female) and adult male (Male). For the purpose of this study, the protection status was classified into national park and non-national park as national parks receive more government's resources compared to other types of protected areas.

Session	Year	Group	*D* (adult tigers/100 km^2)				Sex	*σ* (m)				*g*0			
			Mean	*SE*	LCL	UCL		Mean	*SE*	ICL	UCL	Mean	*SE*	LCL	UCL
Batang Gadis	2006	Central	0.70	0.30	0.31	1.56	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Batanghari	2008	Central	0.45	0.28	0.15	1.40	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Bungo	2006	Central	0.93	0.29	0.51	1.70	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Bungo	2013	Central	0.61	0.24	0.29	1.28	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Bungo	2017	Central	0.42	0.22	0.15	1.12	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Ipuh	2006	Central	0.64	0.20	0.35	1.16	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Kerinci Seblat	2014	Central	0.80	0.24	0.45	1.42	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Kerinci Seblat	2015	Central	0.75	0.23	0.41	1.36	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Kerinci Seblat	2016	Central	0.63	0.21	0.34	1.18	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Kerinci Seblat	2017	Central	0.75	0.21	0.43	1.30	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Langkat	2010	Central	0.43	0.17	0.20	0.91	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Langkat	2013	Central	0.41	0.14	0.21	0.80	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116

Session	Year	Group	D (adult tigers/100 km^2)				Sex	σ (m)				$g0$			
			Mean	*SE*	LCL	UCL		Mean	*SE*	ICL	UCL	Mean	*SE*	LCL	UCL
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Muara Labuh	2009	Central	0.53	0.29	0.20	1.43	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Muara Labuh	2012	Central	0.34	0.19	0.13	0.92	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Muara Sako	2004	Central	0.84	0.33	0.40	1.77	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Sipurak	2005	Central	0.87	0.38	0.39	1.96	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Solok	2009	Central	0.69	0.33	0.29	1.69	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Ulu Masen	2013	Central	0.31	0.11	0.16	0.61	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Ulu Masen	2017	Central	0.16	0.10	0.05	0.51	Female	4,218	252	3,752	4,742	0.0092	0.0011	0.0073	0.0116
		Montane					Male	5,469	280	4,947	6,045	0.0121	0.0011	0.0101	0.0145
Rimbang-	2006	Central	0.27	0.22	0.07	1.10	Female	3,470	354	2,843	4,236	0.0261	0.0052	0.0177	0.0383
Baling		Lowland					Male	4,500	377	3,819	5,302	0.0343	0.0057	0.0248	0.0474
Tesso Nilo	2005	Central	0.49	0.23	0.20	1.19	Female	3,470	354	2,843	4,236	0.0261	0.0052	0.0177	0.0383
		Lowland					Male	4,500	377	3,819	5,302	0.0343	0.0057	0.0248	0.0474
Tesso Nilo	2007	Central	0.93	0.38	0.43	2.01	Female	3,470	354	2,843	4,236	0.0261	0.0052	0.0177	0.0383
		Lowland					Male	4,500	377	3,819	5,302	0.0343	0.0057	0.0248	0.0474
Tesso Nilo	2008	Central	0.73	0.32	0.32	1.65	Female	3,470	354	2,843	4,236	0.0261	0.0052	0.0177	0.0383
		Lowland					Male	4,500	377	3,819	5,302	0.0343	0.0057	0.0248	0.0474
Berbak-	2010	Peat	0.82	0.33	0.38	1.77	Female	2,966	324	2,396	3,671	0.0095	0.002	0.0062	0.0144
Sembilang		Swamp					Male	3,845	466	3,036	4,871	0.0125	0.0026	0.0083	0.0188
Berbak-	2015	Peat	0.69	0.30	0.31	1.57	Female	*2,966*	324	2,396	3,671	0.0095	0.002	0.0062	0.0144
Sembilang		Swamp					Male	3,845	466	3,036	4,871	0.0125	0.0026	0.0083	0.0188
Kerumutan	2006	Peat	0.47	0.38	0.11	1.90	Female	2,966	324	2,396	3,671	0.0095	0.002	0.0062	0.0144
		Swamp					Male	3,845	466	3,036	4,871	0.0125	0.0026	0.0083	0.0188
Bukit Barisan-	1999	Southern	1.29	0.54	0.59	2.83	Female	2,982	329	2,403	3,700	0.0044	0.001	0.0028	0.0069
Selatan		Lowland					Male	3,866	412	3,139	4,762	0.0058	0.0013	0.0038	0.0088
Bukit Barisan-	2015	Southern	1.30	0.41	0.71	2.36	Female	2,982	329	2,403	3,700	0.0044	0.001	0.0028	0.0069
Selatan		Lowland					Male	3,866	412	3,139	4,762	0.0058	0.0013	0.0038	0.0088

Session	Year	Group	*D* (adult tigers/100 km^2)				Sex	σ (m)				*g*0			
			Mean	*SE*	LCL	UCL		Mean	*SE*	ICL	UCL	Mean	*SE*	LCL	UCL
Bukit Barisan-Selatan	2015	Southern Lowland	1.46	0.44	0.82	2.60	Female	2,982	329	2,403	3,700	0.0044	0.001	0.0028	0.0069
							Male	3,866	412	3,139	4,762	0.0058	0.0013	0.0038	0.0088
Minimum			0.16	0.10	0.05	0.51	Female	2,966	252	2,396	3,671	0.0044	0.001	0.0028	0.0069
							Male	3,845	280	3,036	4,762	0.0058	0.0011	0.0038	0.0088
Maximum			1.46	0.54	0.82	2.83	Female	4,218	354	3,752	4,742	0.0261	0.0052	0.0177	0.0383
							Male	5,469	466	4,947	6,045	0.0343	0.0057	0.0248	0.0474

Table 3 A summary of density estimates of 29 camera trap sessions from 16 sites dedicated for Sumatran tigers and collected between 1999 and 2017 from across the Sumatra Island, Indonesia. The effects of sex and group covariates were evaluated against the movement parameter (σ) and detection probability at activity center (g0) while estimating the densities as a function of group and protection status. Sessions were classified into four groups based on habitat types, including montane habitats (Central Montane), heavily degraded lowland habitats (Central Lowland), peat swamp forests (Peat Swamp), and lowland habitat (Southern Lowland). Sex was classified into adult female (Female) and adult male (Male). For the purpose of this study, the protection status was classified into national park and non-national park as national parks receive more government's resources compared to other types of protected areas.

Session	Year	Group	Pro-tected	*D* (adult tigers/100 km^2)					*σ* (m)				*g*0			
				Mean	*SE*	LCL	UCL	Sex	Mean	*SE*	LCL	UCL	Mean	*SE*	LCL	UCL
Batang Gadis	2006	Central Montane	yes	0.46	0.06	0.35	0.60	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Batanghari	2008	Central Montane	no	0.46	0.06	0.35	0.60	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Bungo	2006	Central Montane	no	0.46	0.06	0.35	0.60	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Bungo	2013	Central Montane	yes	0.65	0.08	0.52	0.83	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Bungo	2017	Central Montane	no	0.46	0.06	0.35	0.60	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Ipuh	2006	Central Montane	no	0.46	0.06	0.35	0.60	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Kerinci Seblat	2014	Central Montane	yes	0.65	0.08	0.52	0.83	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Kerinci Seblat	2015	Central Montane	yes	0.65	0.08	0.52	0.83	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Kerinci Seblat	2016	Central Montane	yes	0.65	0.08	0.52	0.83	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Kerinci Seblat	2017	Central Montane	yes	0.65	0.08	0.52	0.83	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Langkat	2010	Central Montane	yes	0.65	0.08	0.52	0.83	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
								Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144

Session	Year	Group	Pro-tected	*D* (adult tigers/100 km^2)					σ (m)				*g*0			
				Mean	*SE*	LCL	UCL	Sex	Mean	*SE*	LCL	UCL	Mean	*SE*	LCL	UCL
Langkat	2013	Central	no	0.46	0.06	0.35	0.60	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
		Montane						Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Muara Labuh	2009	Central	yes	0.65	0.08	0.52	0.83	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
		Montane						Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Muara Labuh	2012	Central	yes	0.65	0.08	0.52	0.83	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
		Montane						Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Muara Sako	2004	Central	yes	0.65	0.08	0.52	0.83	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
		Montane						Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Sipurak	2005	Central	yes	0.65	0.08	0.52	0.83	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
		Montane						Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Solok	2009	Central	no	0.46	0.06	0.35	0.60	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
		Montane						Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Ulu Masen	2013	Central	no	0.46	0.06	0.35	0.60	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
		Montane						Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Ulu Masen	2017	Central	no	0.46	0.06	0.35	0.60	Female	4,272	257	3,796	4,807	0.0091	0.0011	0.0072	0.0115
		Montane						Male	5,470	277	4,954	6,041	0.0120	0.0011	0.0100	0.0144
Rimbang-	2006	Central	no	0.45	0.13	0.26	0.78	Female	3,506	358	2,871	4,281	0.0260	0.0052	0.0176	0.0382
Baling		Lowland						Male	4,489	376	3,811	5,289	0.0343	0.0057	0.0248	0.0475
Tesso Nilo	2005	Central	yes	0.64	0.16	0.40	1.04	Female	3,506	358	2,871	4,281	0.0260	0.0052	0.0176	0.0382
		Lowland						Male	4,489	376	3,811	5,289	0.0343	0.0057	0.0248	0.0475
Tesso Nilo	2007	Central	yes	0.64	0.16	0.40	1.04	Female	3,506	358	2,871	4,281	0.0260	0.0052	0.0176	0.0382
		Lowland						Male	4,489	376	3,811	5,289	0.0343	0.0057	0.0248	0.0475
Tesso Nilo	2008	Central	yes	0.64	0.16	0.40	1.04	Female	3,506	358	2,871	4,281	0.0260	0.0052	0.0176	0.0382
		Lowland						Male	4,489	376	3,811	5,289	0.0343	0.0057	0.0248	0.0475
Berbak-	2010	Peat	yes	0.70	0.20	0.41	1.20	Female	2,971	321	2,405	3,669	0.0095	0.0021	0.0062	0.0144
Sembilang		Swamp						Male	3,804	452	3,016	4,798	0.0125	0.0027	0.0083	0.0189
Berbak-	2015	Peat	yes	0.70	0.20	0.41	1.20	Female	2,971	321	2,405	3,669	0.0095	0.0021	0.0062	0.0144
Sembilang		Swamp						Male	3,804	452	3,016	4,798	0.0125	0.0027	0.0083	0.0189
Kerumutan	2006	Peat	yes	0.70	0.20	0.41	1.20	Female	2,971	321	2,405	3,669	0.0095	0.0021	0.0062	0.0144
		Swamp						Male	3,804	452	3,016	4,798	0.0125	0.0027	0.0083	0.0189
Bukit Barisan-	1999	Southern	yes	1.35	0.28	0.90	2.03	Female	3,003	332	2,420	3,726	0.0044	0.0010	0.0028	0.0068
Selatan		Lowland						Male	3,845	409	3,124	4,734	0.0058	0.0013	0.0038	0.0089
Bukit Barisan-	2015	Southern	yes	1.35	0.28	0.90	2.03	Female	3,003	332	2,420	3,726	0.0044	0.0010	0.0028	0.0068

Session	Year	Group	Pro-tected	D (adult tigers/100 km^2)				Sex	σ (m)				$g0$			
				Mean	*SE*	LCL	UCL		Mean	*SE*	LCL	UCL	Mean	*SE*	LCL	UCL
Selatan		Lowland						Male	3,845	409	3,124	4,734	0.0058	0.0013	0.0038	0.0089
Bukit Barisan-	2015	Southern	yes	1.35	0.28	0.90	2.03	Female	3,003	332	2,420	3,726	0.0044	0.0010	0.0028	0.0068
Selatan		Lowland						Male	3,845	409	3,124	4,734	0.0058	0.0013	0.0038	0.0089
Minimum				0.45	0.06	0.26	0.60	Female	2,971	257	2,405	3,669	0.0044	0.0010	0.0028	0.0068
								Male	3,804	277	3,016	4,734	0.0058	0.0011	0.0038	0.0089
Maximum				1.35	0.28	0.90	2.03	Female	4,272	358	3,796	4,807	0.0260	0.0052	0.0176	0.0382
								Male	5,470	452	4,954	6,041	0.0343	0.0057	0.0248	0.0475

Table 4 A summary of beta parameters of densities of 29 camera trap sessions dedicated for Sumatran tigers from 16 sites and collected between 1999 and 2017 from across the Sumatra Island, Indonesia. The effects of sex and group covariates were evaluated against the movement parameter (σ) and detection probability at activity center (g0) while estimating the densities as a function of group and protection status. Sessions were classified into four groups based on habitat types, including montane habitats (Central Montane), heavily degraded lowland habitats (Central Lowland), peat swamp forests (Peat Swamp), and lowland habitat (Southern Lowland). Sex was classified into adult female (Female) and adult male (Male). For the purpose of this study, the protection status was classified into national park and non-national park as national parks receive more government's resources compared to other types of protected areas.

Model	*β*	*SE*	*LCL*	*UCL*
D(.)	**-9.992**	**0.135**	**-10.256**	**-9.729**
D(Central Lowland)	-0.021	0.265	-0.541	0.500
D(Peat Swamp)	0.067	0.302	-0.524	0.568
D(Southern Lowland)	**0.725**	**0.239**	**0.258**	**1.193**
D(ProtectedYes)	**0.357**	**0.164**	**0.036**	**0.678**
σ(.)	**-4.700**	**0.120**	**-4.936**	**-4.464**
σ(SexMale)	**0.280**	**0.139**	**0.006**	**0.553**
σ(Central Lowland)	**1.049**	**0.182**	**0.692**	**1.405**
σ(Peat Swamp)	0.042	0.216	-0.382	0.466
σ(Southern Lowland)	**-0.731**	**0.225**	**-0.171**	**-0.291**
*g*0(.)	**8.360**	**0.060**	**8.242**	**8.478**
*g*0(SexMale)	**0.247**	**0.071**	**0.108**	**0.387**
*g*0(Central Lowland)	**-0.198**	**0.094**	**-0.382**	**-0.013**
*g*0(Peat Swamp)	**-0.363**	**0.117**	**-0.592**	**-0.135**
*g*0(Southern Lowland)	**-0.352**	**0.110**	**-0.569**	**-0.136**
pmix.SexMale	0.136	0.148	-0.153	0.425

Bolded values are significant.

Table 5 Comparison of site-specific density estimates of Sumatran tiger populations of this study and previous studies in several tiger conservation landscapes in Sumatra, Indonesia, reported between 1999 and 2017. Parameter estimates in the same rows used the same capture-recapture datasets, except for Berbak – Sembilang. Tiger density estimates from Bukit Barisan Selatan, Kerinci Seblat, and Berbak Sembilang were obtained from well-established tiger monitoring sites designated by the Ministry of Environment and Forestry of Indonesia to double the tiger populations in the landscapes by 2022 in its National Tiger Recovery Program.

Session	Year	habitat	Pro-tected	This Study (adult tigers/100 km^2)				Previous Study (adult tigers/100 km^2)				Method	Reference
				Mean	SE	LCL	UCL	Mean	SE	LCL	UCL		
Bukit Barisan Selatan	1999	lowland	yes	1.29	0.54	0.59	2.83	1.20	0.32	0.57	1.87	CMR	Wibisono (2015)
Bukit Barisan Selatan	2015	lowland	yes	1.30	0.41	0.71	2.36	**2.80**	NA	1.70	4.40	SCR	Pusparini et al. (2018)
Bukit Barisan Selatan	2015	lowland	yes	**1.45**	0.41	0.71	2.36	**2.80**	NA	1.70	4.40	SCR	Pusparini et al. (2018)
Rimbang Baling[1]	2006	lowland	no	0.27	0.22	0.07	1.10	0.34	0.22	NA	NA	SCR	Sunarto et al. (2013)
Northeastern block[2]	2012	lowland	no					***0.19***	0.16	NA	NA	SCR	Widodo et al. (2017)
Northwestern block[2]	2013	lowland	no					0.23	0.14	NA	NA	SCR	Widodo et al. (2017)
Southern block[2]	2014	lowland	no					0.51	0.22	NA	NA	SCR	Widodo et al. (2017)
Tesso Nilo[3]	2005	lowland	yes	0.49	0.23	0.20	1.19	0.59	0.26	NA	NA	SCR	Sunarto et al. (2013)
Tesso Nilo[3]	2007	lowland	yes	0.93	0.38	0.43	2.01	0.87	0.33	NA	NA	SCR	Sunarto et al. (2013)
Tesso Nilo[3]	2008	lowland	yes	0.73	0.32	0.32	1.65	0.77	0.32	NA	NA	SCR	Sunarto et al. (2013)
Batang Gadis	2006	montane	yes	0.70	0.30	0.31	1.56	1.80	0.73	1.80	6.40	SCR	Wibisono et al. (2009)
Batang hari	2008	montane	no	0.45	0.28	0.15	1.40	1.13	0.36	1.13	2.87	CMR	Dinata (2008)
Kerinci Seblat	2014	montane	yes	0.80	0.24	0.45	1.42	1.04		0.58	1.86	SCR	FFI - IP (2020)
Kerinci Seblat	2015	montane	yes	0.75	0.23	0.41	1.36	1.11		0.53	2.33	SCR	FFI - IP (2020)
Kerinci Seblat	2016	montane	yes	0.63	0.21	0.34	1.18	0.82		0.38	1.76	SCR	FFI - IP (2020)
Kerinci Seblat	2017	montane	yes	0.75	0.21	0.43	1.30	0.94		0.54	1.62	SCR	FFI - IP (2020)
Muara Sako[2]	2004	montane	yes	0.84	0.33	0.40	1.77	1.83		NA	NA	CMR	Linkie et al. (2006)
Sipurak[2]	2005	montane	yes	0.87	0.38	0.39	1.96	1.40		NA	NA	CMR	Linkie et al. (2006)
Ulu Masen	2013	montane	no	0.32	0.11	0.16	0.61	0.89		NA	NA	SCR	FFI-IP (unpublished)
Ulu Masen	2017	montane	no	***0.16***	0.10	0.05	0.51	0.29		NA	NA	SCR	FFI-IP (unpublished)

Session	Year	habitat	Pro-tected	This Study (adult tigers/100 km²)				Previous Study (adult tigers/100 km²)				Method	Reference
				Mean	SE	LCL	UCL	Mean	SE	LCL	UCL		
Berbak Sembilang[4]	2010	peatswamp	yes	0.82	0.33	0.38	1.77	1,02		0.50	1.51	SCR	Priatna (2020)
Berbak Sembilang[4]	2015	peatswamp	yes	0.69	0.30	0.31	1.57	1.54		0.89	2.35	SCR	Priatna (2020)
Berbak[5]	2015	peatswamp	yes					1.20		0.56	2.16	SCR	ZSL - IP (2020)
Berbak[5]	2018	peatswamp	yes					1.46		0.79	2.70	SCR	ZSL - IP (2020)
Berbak[5]	2020	peatswamp	yes					0.72		0.33	1.58	SCR	ZSL - IP (2020)
Sembilang[5]	2019	peatswamp	yes					0.74		0.00	1.45	SCR	ZSL - IP (2020)
Sembilang[5]	2018	peatswamp	yes					0.56		0.45	0.89	SCR	ZSL - IP (2020)
Kerumutan[3]	2006	peatswamp	yes	0.47	0.38	0.11	1.90	0.25	0.18	NA	NA	SCR	Sunarto et al. (2013)
Mean				0.73	0.30	0.35	1.59	1.04	0.29	0.78	2.51		
SE				0.34	0.11	0.19	0.57	0.68	0.16	0.53	1.42		
Minimum				0.16	0.10	0.05	0.51	0.19	0.16	NA	NA		
Maximum				1.45	0.41	0.71	2.36	2.80	NA	1.80	6.40		

[1] No confidence interval reported in Sunarto et al. (2013).

[2] Different datasets were used by Widodo et al. (2017).

[3] For comparison purpose, only model with halfnormal detection function was cited from Sunarto et al. (2013).

[4] Different datasets used for the estimates; thus, the closest years of estimates were used.

[5] Different datasets were used for the estimates.

Bolded italic and bolded characters are the minimum and maximum values, respectively.

Minimum and maximum *SE* and 95% CI follow the estimated means.

CMR is the non-spatial capture-recapture.

SCR is the spatial capture-recapture.

FIGURE

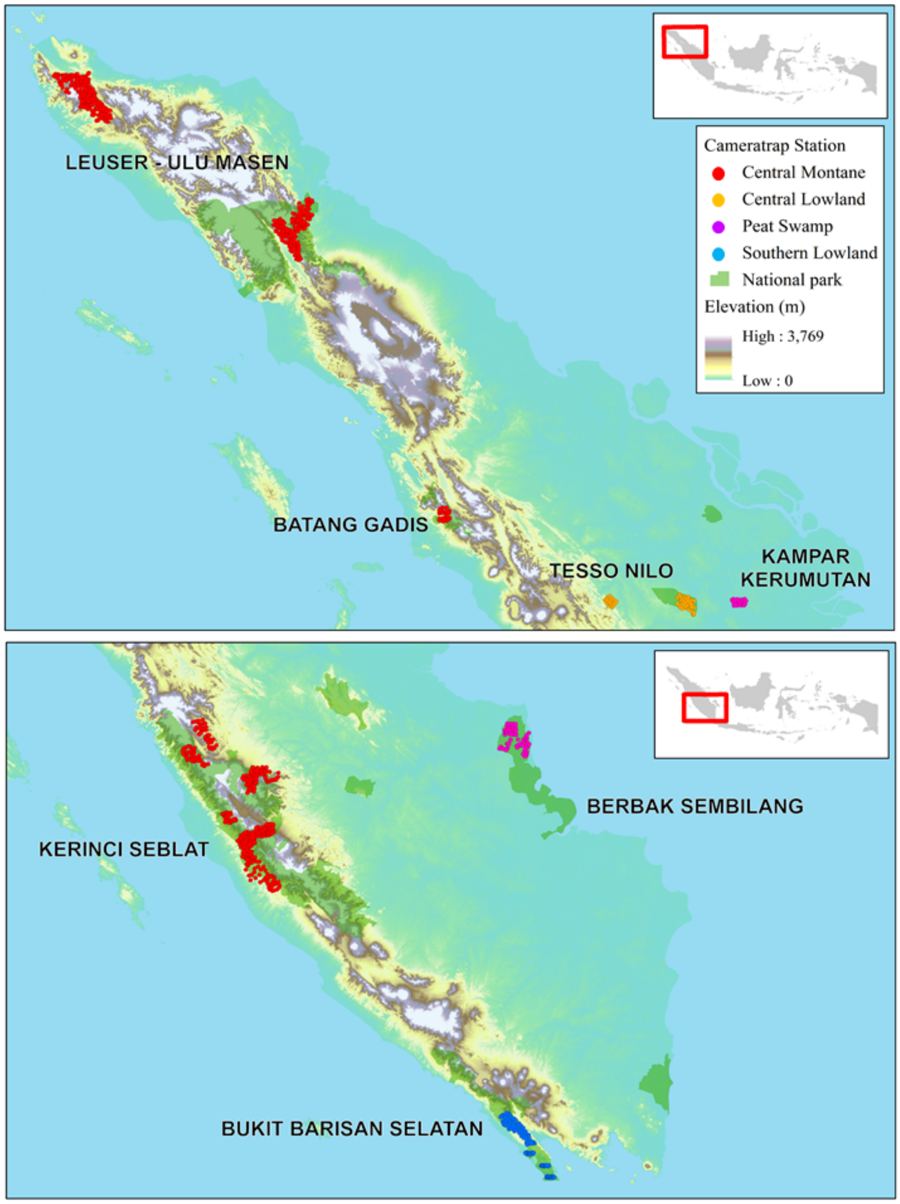

Figure 1 Locations of 29 camera trap sampling sessions from 16 sites collected between 1999 and 2017. All sampling sessions were dedicated for the Sumatran tigers and used for a broad re-analysis of previously collected datasets. Colors of camera trap locations represent four different groups of sampling sessions in montane habitats (Central Montane), heavily degraded lowland habitats (Central Lowland), peat swamp forests (Peat Swamp), and lowland habitat (Southern Lowland).

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Chapter 2

AN ISLAND-WIDE ASSESSMENT OF THE DISTRIBUTION OF THE SUMATRAN TIGER IN RELATION TO ITS MAIN PREY SPECIES AND MAYOR THREATS IN SUMATRA, INDONESIA

Introduction

As indicated by their large distribution, tigers are capable of living in a wide range of environments, from tropical rainforests in Southeast Asia to boreal forests in Siberia (Schaller, 1967; Seidenstricker et al., 1999; M. E. Sunquist, 1981). Tigers have large home ranges and need vast, contiguous, intact, habitats with a sufficiently large prey base. In Sumatran, the majority of wild tigers persist in 12 tiger conservation landscapes (TCL) covering approximately 88,000 km² (Dinerstein et al., 2006). Despite their large size, continued habitat loss and fragmentation threatens the long-term integrity of these tiger landscapes (Kinnaird et al., 2003; Linkie et al., 2006; Nowell & Jackson, 1996; Walston et al., 2010; Weber & Rabinowitz, 1996; Wibisono & Pusparini, 2010; Wikramanayake et al., 1998). This has led to a steady decline of tiger populations throughout Sumatra (Linkie et al., 2008), accelerated by direct poaching, retaliatory killing due to tiger's reputation as human-killers (Weber & Rabinowitz, 1996), authorized removal of "problems tigers" following tiger-human conflicts (Sunquist et al., 1999; Tilson et al., 1994), and depletion of prey species by poachers (Karanth & Stith, 1999; Seidensticker, 1986).

As a large carnivore, tigers depend on medium to large-bodied ungulates as their primary prey (Karanth & Stith, 1999) and prey availability is one of the limiting factors affecting tiger persistence and recovery across their range (Karanth et al., 2004; Karanth & Sunquist, 1995). Monitoring of the primary tiger prey species should therefore be an integral part of a global strategy to protect the remaining tiger populations (Global Tiger Initiative, 2010). In Sumatra, however, past studies have centered only on the small-scale spatio-temporal relationship between the Sumatran tigers and their prey (Linkie & Ridout, 2011; O'Brien et al., 2003; Wibisono, 2006), and there is a paucity of information regarding underlying prey distribution. For Sumatran tigers, these primary prey species are Sambar deer (*Cervus unicolor*), wild pigs (*Sus scrofa*), and barking deer (*Muntiacus muntjac*) (Linkie & Ridout, 2011; O'Brien et al., 2003; Wibisono, 2006).

Estimating the abundance and the spatial distribution of not just tigers but also their prey is critical for at least four reasons: 1) to evaluate the viability and carrying capacity of different tiger populations and landscapes, 2) to design and implement conservation interventions, 3) to monitor and evaluate the effectiveness of conservation interventions, and 4) to develop adaptive management for future conservation planning and interventions (Karanth et al., 2017). While several organizations have carried out studies on the distribution and density of the Sumatran tiger (Sunarto et al., 2012, 2013; Walston et al., 2010; Wibisono et al., 2009, 2011; Widodo et al., 2017), no such assessments have been made for Sambar deer, wild pigs, or barking deer; the key determinant of tiger occurrence, and thus persistence. This is not surprising, as, in contrast to several endangered wildlife species, these animals are fairly common and are not a conservation priority of the Government of Indonesia (KLHK, 2015). They are classified as Vulnerable (Sambar deer) and Least Concerned (wild pig, barking deer) by the World Conservation Union (IUCN, 2017) and species in these categories are commonly neglected by the international scientific communities. However, the tiger is a great example of how knowledge of the ecology of associated species is critical for designing successful conservation strategies given the close predator-prey relationship (Karanth et al., 2017). To be meaningful in a management context, research needs to identify factors influencing the distribution patterns of the prey species, including both anthropogenic and ecological factors. This will provide guidance for management authorities to develop conservation strategies and priority actions for Sumatran large mammal conservation.

Elucidating the distribution of tiger prey species in Sumatra is challenging. Estimating densities of large ungulates in rainforest environments through direct sighting surveys is often difficult because of low visibility and limited access given the dense ground vegetation and rugged terrain, especially at higher elevations (Hines et al., 2010; Karanth & Chundawat, 2002). In addition, methods like line transects require a substantial number of sightings of animals for reliable data (Vongkhamheng et al., 2013), which again, can be difficult in a rainforest environment. Further, ungulates with no unique body marks, such as Sambar deer, wild pigs, and barking deer, are not individually identifiable, thus the implementation of capture-recapture studies using camera traps is not possible (O'Brien, 2011). While traditional mark-recapture studies or the use of genetic markers in feces is theoretically possible, the expense and logistics of such work across the entire island of Sumatra are not feasible. Given the challenge of estimating absolute densities, assessing the spatial distribution or occupancy of wildlife species may be a much more plausible and cost-effective objective for large areas, such as the island of Sumatra, and occupancy can serve as a robust surrogate for abundance in a population monitoring framework at large spatial scales (Mackenzie & Nichols, 2004; Nichols et al., 2017). This method is cost-effective because it requires only a detection history of the target species which can be obtained from a basic detection/non-detection survey of animal signs. Furthermore, this method allows for unequal sampling size and can incorporate both site and sampling covariates to estimate the proportion of area occupied by the target species as a function of environmental and anthropogenic covariates while explicitly accounting for imperfect detection (Mackenzie et al., 2002).

Here, we performed occupancy modelling to estimate the spatial distribution of the three tiger prey species as well as the presence of logging and poaching activities, which can influence continued prey presence. This is the first rigorous island-wide assessment of the distribution patterns of three main tiger prey, i.e. Sambar deer, wild pigs, and barking deer in Sumatra. Based on our results we provide management authorities with: 1) a robust map of the spatial distribution patterns of the primary tiger prey species, 2) information on environmental and anthropogenic factors that explain the distribution of the species and threats, and 3) practical recommendations on the management of the target species in relation to the conservation of the critically endangered Sumatran tiger throughout their geographic range in Sumatra.

Methods

Study Area

From 2007–2009, we carried out detection/non-detection surveys in nine priority tiger conservation landscapes (TCL) as well as non-protected forests across the island of Sumatra, Indonesia, encompassing various management regimes, including national parks, protection forests, game reserves, and adjacent forest concessions. This included the Leuser Ecosystem, Kerinci Seblat, Bukit Rimbang Baling, Bukit Tigapuluh, Tesso Nilo, Kuala Kampar – Kerumutan, Berbak, Bukit Barisan Selatan South, Bukit Balai Rejang – Selatan, Bukit Dua Belas, Dangku, Way Kambas, and the Northern Riau forest complex. The field teams surveyed all habitat types likely to support Sumatran tigers, ranging from the lowland peat swamp habitat of the Kampar – Kerumutan to pristine forests around the peak of Mount Kerinci in Kerinci Seblat landscape (3,764 m asl), the highest point on Sumatra (Figure 2). A large portion of the surveyed areas were dominated by primary (19%) and secondary forest (29%), followed by agriculture (18%), bare land (14%), and shrub land (12%).

Field Surveys

Led by the Ministry of Environment and Forestry, the Sumatra-wide tiger survey was conducted between 2007 and 2009, involving eight non-governmental organizations, i.e. the Wildlife Conservation Society, Fauna & Flora International, Durrell Institute of Conservation and Ecology, World Wildlife Fund, Zoological Society of London, Sumatran Tiger Conservation and Protection, Leuser International Foundation, Rhino Foundation of Indonesia and the Sumatran Tiger Protection and Conservation Foundation.

We implemented a detection/non-detection survey protocol that collected signs along continuous transects following (Hines et al., 2010) and (Karanth & Nichols, 2010). We surveyed a total of 394 grid cells of 289 km^2 (17 x 17 km), each containing at least 10% potential tiger habitat. Our cell size was based on the putative home range size of an adult male Sumatran tiger. Within each 289 km^2 cell we randomly selected two smaller cells 18 km^2 through which the field teams had to walk at some point during the greater survey, to introduce an element of randomness while still maintaining spatial coverage of the overall grid. Within each 289 km^2 cell, 1–2 teams of 4–5 field technicians walked across the area following animal trails likely to contain signs of tiger and primary prey, including sambar deer, barking deer, and wild pig. These animal trails were irregular by nature and typically found along ridgelines, riparian corridors, valleys, and human trails. The detection /non-detection history for tiger and prey based on their signs was established based on 1-km segments used as spatial replicates. Therefore, the field teams recorded only the first sign of each species they found on the trail in every 1-km segment walked. Due to extensive survey areas, each recorded sign was georeferenced using a GPS unit. We limited tiger signs to pugmarks only and prey signs to footprints, feces, and rooting (wild pig), to avoid false positive due to misidentification of other types of non-typical signs (i.e., scrape marks, claw marks, scent marks for tigers and feces, tree twists, rubbing, wallows, beds for prey). Signs of poaching were any snares which targeted principal prey, found on the survey trail. After recording, the team dismantled the snares to eliminate the potential of trapping animals. We recorded any evidence of logging activities, which were typically tree stumps, logged over trees, logged over spots, and processed woods left in the forest awaiting to be dragged of along streams to the nearest villages or floated rivers to the closest illegal logging docks. Only forest habitat was surveyed, and the survey effort was proportionate to the extent of forest habitat in the cell, with a minimum of 4 km surveyed via transect when 10% of the 289 km^2 cell was forested to a maximum of 40 km of transect surveyed when 100% of the 289 km^2 cell was forested.

Data Analysis

We explored the effect of environmental and anthropogenic factors on the occupancy of Sumatran tiger, the main prey, and human threats (poaching and logging) using a multi-species occupancy model with residual species correlation (Dorazio & Royle, 2005; Tobler et al., 2019). We used the same set of covariates previously described in Wibisono et al. (2011), including: elevation, distance to roads and to settlements, percent forest cover and rate of deforestation, and percent protected area within each grid cell. For elevation, distance to road, and settlements we calculated the average across each cell from the original data that was at 30 m resolution. We defined the rate of deforestation as an area (ha) of forest that was completely removed between 2000 and 2008.

We standardized the six covariates using a z-transformation and assessed for collinearity. We kept one of two correlated covariates if the absolute value of Pearson's correlation coefficient was greater than ±0.70 (Pusparini et al., 2015). We found distance to roads was highly correlated with elevation, distance to settlements, and percent forest cover. Therefore, we omitted it and kept the other three covariates. In addition, we explored quadratic effects by including the square of elevation and distance to settlements as covariates in our models. For example, a species' occupancy could increase from lower elevations towards higher hilly habitats at mid-elevation, and then decrease again towards high elevations. The final set of covariates were, therefore, elevation, squared elevation, percent forest cover, deforestation, percent protected areas, distance to settlements, and squared distance to settlements. Since occupancy of cells in a landscape block is likely correlated due to similar management and the movement of tigers within the large landscape, we further added the landscape as a random intercept to the model.

As the detection/non-detection data were collected along continuous transects, we have to assume a Markovian dependence among samples, meaning that the probability of detecting signs on a 1 km segment of the transect changes if signs were detected in the previous segment. The model proposed by Hines et al. (2010) specifically deals with this correlated detection process and we extended this model in three ways: 1) we formulated it as a multi-species model with hierarchical regression coefficients to simultaneously model our data from four species and two threats (Dorazio & Royle, 2005), 2) we used an abundance model based on a Poisson distribution for the detection model to address abundance-introduced heterogeneity (Guillera-Arroita et al., 2012; Royle & Nichols, 2003), and 3) we added a latent variable structure to estimate residual correlations among species (Tobler et al., 2019) (Appendix B).

It is reasonable to assume that the abundance of all species and threats varies across the vast landscape surveyed in this study and that a higher abundance leads to higher detection probabilities. Ignoring abundance-induced heterogeneity can lead to an underestimation of occupancy (Guillera-Arroita et al., 2012; Royle & Nichols, 2003). A previous analysis of the tiger data also showed that models accounting for abundance-induced heterogeneity perform better than models ignoring this heterogeneity (Guillera-Arroita & Lahoz-Monfort, 2012; Wibisono et al., 2011). This does not mean that we can estimate actual abundance with this model as other factors such as substrate, small scale habitat preference, weather, animal movement patters etc. can also introduce heterogeneity into the data.

The latent variable structure added to the model allows us to estimate residual correlations among species that can describe patterns not accounted for by the covariates in the model (Tobler et al., 2019; Warton et al., 2015). This could show patterns in co-occurrence between tigers and their prey as well as tigers and some of the main threats. We used three latent variables which should be sufficient for the six species included in the model (Tobler et al., 2019). We formulated our model in the BUGS language and ran it in JAGS 4.3.0 (Plummer, 2003) through R 3.4.2 (R Development Core Team, 2011).

Results

A total of 13,511 (average 34.3±16.5 for each cell) km were surveyed between January 2007 and December 2009. Signs of sambar deer, wild pigs, barking deer, and Sumatran tiger, were found in 325, 312, 277, and 206 of 394 grid cells, respectively, corresponding to the naïve occupancy estimates of 0.83, 0.79, 0.70, and 0.52 respectively. Signs of logging and poaching were found in 151 and 86 cells out of 373 cells surveyed for threats, for a naïve occupancy estimates of 0.40 and 0.23 respectively (Table 6).

Species occupancy and detection

Mean occupancy estimates of Sumatran tiger, wild pigs, Sambar deer, barking deer and across all landscapes were at 0.75±0.05, 0.89±0.03, 0.98±0.01, and 0.90±0.03 ($\widehat{\psi} \pm SE$), respectively. At a landscape level, the highest and the lowest occupancy estimates for Sumatran tiger were in Kerinci Seblat – Batang Hari (0.91±0.04)) and Northern Riau (0.14±0.11). All three ungulate species had occupancy values between 0.84 and 1.00 across most landscapes with wild pigs only showing lower values in Kerinci Seblat – Batanghari (0.67±0.07), and barking deer in Northern Riau (0.30±0.14). This indicated a healthy prey-base across almost all surveyed landscapes

(Table 7) (Figure 3). Probabilities that an individual of a species was present on a specific segment were low but were significantly higher if the species was also present on the previous segment while probabilities of a species being detected if present on a segment were expectedly high (Table 8).

Disturbance

Mean occupancy estimates of illegal logging and poaching across the entire island were at 0.59±0.05 and 0.44±0.10, respectively. The highest and the lowest occupancy estimates for illegal logging were in Way Kambas (0.79±0.10) and Leuser - Ulu Masen (0.55±0.05), while for poaching they were in Way Kambas (0.60±0.19) and Central Sumatra (0.328±0.13), respectively (see Table 7).

Covariates

The occupancy model suggests that the abundance, and therefore occupancy, of Sumatran tiger (β_{ForPct} = 0.201±0.09), sambar deer (β_{ForPct} = 0.213±0.065), and barking deer (β_{ForPct}=0.09±0.077) were higher in grid cells with higher percent forest cover, although not significant for barking deer (Table 9). Tiger and wild pig preferred lower elevations while barking deer were more common at higher elevations. National parks tended to have a positive effect on tigers (β_{NP}=0.158±0.131), while the effect was negative for wild pig (β_{NP}=-0.302±0.119) and barking deer (β_{NP}=-0.282±0.122). Recent forest loss and distance to village had little effect on most species. Logging was more prevalent at lower elevations (β_{Elev}=-0.541±0.128) while poaching had a positive relationship with elevation. Poaching also increased with increasing distance from settlements. There was no significant decrease of poaching (β_{NP}=-0.083±0.219) and logging (β_{NP}=-0.096±0.156) within national parks (see Table 9). When looking at the residual correlation matrix (Figure 4) we can see strong positive correlations between the Sumatran tiger and the two main prey species, the sambar deer and the barking deer as well as among the two ungulate species themselves. We also see a strong residual correlation among logging and poaching, indicating that the two activities often go hand-in-hand.

Discussion

Tiger are dependent on large ungulates as their main food sources (Bagchi et al., 2003; Biswas & Sankar, 2002; K. U. Karanth & Sunquist, 1995; U. Karanth & Stith, 1999). While assessments of the spatial distribution of tiger's principal prey species have been reported from India (Karanth et al., 2010), Laos (Vongkhamheng et al., 2013) and Cambodia (O'Kelly et al., 2012), no assessment has ever been implemented across the island of Sumatra. Previous studies investigated the overlap in activity patterns of Sumatran tigers and their principal prey (Linkie & Ridout, 2011), the relationship between tigers and prey (O'Brien et al., 2003; Wibisono, 2006), and the effect forest patrols have in reducing snare traps set up for tigers and ungulates (Linkie et al., 2015; Risdianto et al., 2016). However, they were carried out only in two national parks, namely Kerinci Seblat and Bukit Barisan Selatan. Our study is the first to quantify the spatial distribution of the Sumatran tiger's principal prey species as well as the main threats of poaching, and illegal logging, in the main tiger habitats across the island of Sumatra, providing the Government of Indonesia with the first robust baseline against which the effectiveness of conservation measures can be evaluated.

Tiger occupancy across the whole survey area was high (0.75 or 75%), agreeing with results from a previous analysis of the same tiger data alone using a slightly different occupancy model, that predicted that 73% of major tiger landscapes in Sumatra was still occupied by the Sumatran tiger (Wibisono et al., 2011). However, at the landscape level occupancy varied widely, ranging from 0.14 to 0.91 with the large landscapes of Kerinci Seblat - Batang Hari together with Central Sumatra as well as Leuser - Ulu Masen being the strongholds with occupancy values of 0.91, 0.84 and 0.76 respectively. The lowest values were found in Southern Sumatra, Way Kambas, and Northern Riau. Yet, a recent tiger density estimate of Sumatran tiger in Southern Sumatra was one of the highest (2.8 adult tigers/100 km^2) among the major landscapes (Pusparini et al., 2017), indicating that tiger occupancy in this landscape might have increased due to effective protection measures taken place over the past decade.

Our results for the Way Kambas landscape along with anecdotal evidence suggests that urgent attention from managers for improved conservation is warranted. While more than 95% of the Way Kambas landscape is managed as a national park, the predicted occupancy of Sumatran tiger was low (0.43±0.18) relative to other major landscapes (average 0.68±0.08). In 1996, tiger density in Way Kambas National Park (WKNP) was predicted at 4.3 adult individuals/100 km^2 or 36 adult tigers in an optimum habitat (Franklin et al., 1999). However, recent communication with the field staff revealed that there might be only 15 adult tigers left in the same monitoring area (Sumianto, *personal communication*). Two possible causes of this potential decrease in Sumatran tiger population in WKNP include illegal logging and poaching, as suggested by this study, which were the highest compared to other landscapes. Our model estimates that illegal logging and poaching impacted 79% and 60% of the park of the Way Kambas landscape, respectively.

We found very high levels of occupancy (>0.90) for all three ungulate species throughout Sumatra, indicating that there is a solid prey base in all tiger priority landscapes and that prey base might not be a limiting factor for tiger populations in most places. The residual correlation analysis shows that tiger occupancy is positively correlated with sambar and barking deer occupancy, but less so with wild pig occupancy (Figure 2). Tiger selectively prey on large-bodied ungulates (Karanth, 1995; Karanth & Sunquist, 1995; Linkie & Ridout, 2011; Wibisono, 2006). In India, Bengal tiger selectively prey on gaur and Sambar deer, and less on smaller ungulates such as chital and barking deer in Nagarahole National Park (Karanth & Sunquist, 1995), while in Ranthambhore National Park they prey on Sambar deer and chital (Bagchi et al., 2003). Other studies in Terai landscape and Bardia National Park, Nepal, also found that Sambar deer (Shrestha, 2004) and chital (Wegge et al., 2008) were important principal prey for tigers. While further diet studies are needed, our results indicate that Sambar deer and barking deer might be the two most important principal prey for Sumatran tiger. Similarly, Wibisono (2006) found a positive correlation between the relative abundance indices of Sumatran tiger and both Sambar deer and barking deer in Bukit Barisan Selatan National Park, Lampung. Further, Linkie and Ridout (2011) found a significant temporal overlap in activity patterns between Sumatran tiger and both Sambar deer and barking deer in Kerinci Seblat National Park. Interestingly, while wild pigs are abundant and have a wide distribution, neither of these two studies found a relationship between Sumatran tiger and wild pig. One possible explanation is that, as large, group-living animal with expanded predator vigilance, wild pigs require a higher energy cost for the tiger to hunt compared to the solitary living Sambar deer and barking deer. On the other hand, wild pigs are wide-ranging, thus make them an unpredictable food source.

Occupancy of Sumatran tiger, wild pig and sambar deer tended to be higher at lower elevations while barking deer had higher occupancy values at higher elevations, although only Sumatran tiger and wild pig were significant. All species, but wild pig, seemed to be forest dependent although the relationship was not significant for barking deer. Compared to higher elevation, lowland forest provides warmer temperatures, more abundant water, less rugged terrain for wildlife movement, and a higher plant diversity as food resources for ungulates. All together lowland forests reduce the energy costs for large carnivores and principal prey for their daily activities (Carbone et al., 2007; Scognamillo et al., 2003). Yet, as our data show, logging is significantly more prevalent in lowland forests and, in Sumatra, most of the remaining lowland forest are inside conservation areas, surrounded by human settlements, agricultural lands, plantations, and road networks (Wibisono et al., 2012; Wibisono & Pusparini, 2010). This close proximity of humans and wildlife increases disturbance, hunting and also increasing the probability of conflict between humans and wildlife and tigers in particular. On the other hand, higher elevations may provide a more secure place for the tiger and principal prey to survive from anthropogenic factors in the long term. A nation-wide study in India found that high elevation facilitated lower probability of extinction of Bengal tiger and several other mammals (Karanth et al., 2010). This highlights the important of Kerinci Seblat and Leuser landscapes as the last stronghold for the Sumatran tiger. These two priority landscapes are the only place in Sumatra with large, intact highlands forests, but they are under a serious threat from road constructions which, if not halted, would fragment them into several smaller unsustainable forest patches (Pusparini et al., 2019).

Poaching of Sumatran tigers for the illegal wildlife trade has long been the major reason for the rapid decline in Sumatran tiger numbers (Linkie et al., 2008). Sheppherd and Magnus (2004) estimated at least 253 tigers were removed from their natural habitats throughout Sumatra between 1998 and 2002, the majority was for illegal trade. On the other hand, selective logging has been identified as the most widespread human disturbance to tropical forests around the globe (Brodie et al., 2015). In Sumatra, Margono et al. (2012) found that between 1990 and 2010 the leading cause of primary forest degradation was uncontrolled illegal logging. Our results provide further insight into the magnitude of illegal logging and poaching, at both an island-wide and site-specific levels of major tiger conservation landscapes. We found that threats from poaching and illegal logging were still widespread throughout the surveyed areas. Logging affected 59% of the surveyed areas while poaching was estimated to occur in 44%. Illegal logging was more prevalent in lower elevation and closer to villages while poaching seemed to be further away from villages.

In Sumatra, villagers normally set traps for ungulates inside the forest further away from villages where wildlife is more abundant. In national parks where awareness programs have been implemented, the villagers also set traps in more remote areas to avoid law enforcement patrols. For hunting wild pig on the other hand, they usually used trained dogs to drive pig groups into a long net set up on their crop lands. Surprisingly, whether an area is within a national park or not seemed to have little effect on the prevalence of poaching and illegal logging. While routine law enforcement patrols have been intensified in most national parks in recent years, during the survey period they were mostly conducted on a case-by-case basis and either in or close to villages. This might have caused most poaching and illegal logging activities inside the national park boundaries to go undetected. Future surveys will show if the significant increase in patrol activities since this study was able to reduce poaching and illegal logging.

The high occupancy of illegal logging in Northern Riau is not surprising given the non-protected status of this landscape. On the other hand, the level of poaching and illegal logging in Kerinci Seblat landscape was worrisome. As one of only three global priority TCL (Sanderson et al., 2010), containing Kerinci Seblat National Park, the largest protected area in Sumatra, more than 60% of this landscape seemed to be affected by poaching and illegal logging. This corroborates findings by a study by (Linkie et al., 2015) that reported that a total of 4,433 snare traps were dismantled between 2000 and 2010 in KSNP. Furthermore, (Linkie et al., 2006) found that densities of Sumatran tiger in Kerinci Seblat National Park were substantially higher in primary forests compared to selectively logged or degraded forests. Interestingly we found no negative correlation between tiger occupancy and logging and poaching even after accounting for environmental covariates. One reason for that could be that both activities are continuously expanding into intact tiger habitat.

Recommendation

As a solid prey base is crucial for sustaining viable tiger populations (Karanth et al., 2004). However, robust analyses on tiger principal prey are lacking. Therefore, surveys to monitor the status of Sumatran tiger's principal prey over time should be taken place. For large landscapes such as Kerinci Seblat and Leuser Ulu Masen, large scale detection/non-detection survey following patch occupancy approach is proven to be the best approach to implement. The multi-species occupancy models used in this study can be used to look at changes in occupancy across different regions. Although efforts to reduce logging and poaching have been strengthened in recent years, logging and poaching were still prevalent throughout the majority of the surveyed landscapes, including the two largest priority TCLs of Kerinci Seblat and Leuser Ecosystem. Evaluation and improvement of the current protections need to be taken place to reduce major threats in prime tiger habitats. Our results show that tigers still occupy many areas outside protected areas where conservation investments are lacking. The loss of tigers in these areas has reached alarming levels. A total of 130 tiger individuals (10 tigers per year) were killed due to retaliatory killing in these smaller landscapes over the last 16 years (Kartika, 2016). Long-term conservation strategies for Sumatran tigers need to consider both the priority landscapes as well as the adjacent buffer areas. This is critical especially in small unsustainable landscapes in order to maintain sufficiently large, connected populations. Since most protected areas are too small relative to the size needed for viable tiger populations, better protection from poaching and habitat loss outside of protected areas is critical.

TABLES

Table 6 The global status of surveyed landscapes, survey efforts, and naive occupancy of Sumatran tiger, sambar deer, wild pigs, and barking deer in Sumatra, Indonesia. The dataset was collected through detection/non-detection surveys along transects carried out in a total of 394 grid cells of 17 by 17 km each by various organizations covering approximately 60% of the remaining tiger habitats between 2007 and 2009. Naïve occupancy is equal to the number of grid cells with tiger signs divided by the total grid cells.

Landscape	TCL Status	Survey Dates	# Grid Cells	# Km Walk	# Grid Cells with Response Variable (Naïve occupancy)					
					Sumatran Tiger	Sambar Deer	Wild Pig	Barking Deer	Logging	Poaching
Southern Sumatra	II + III	24/03/07 - 25/06/08	51	1,687	21 (0.41)	48 (0.94)	51 (1.00)	30 (0.59)	22 (0.43)	13 (0.25)
Way Kambas	NA	06/01/08 - 11/03/08	10	33	2 (0.20)	9 (0.90)	10 (1.00)	10 (1.00)	5 (0.50)	6 (0.60)
Eastern Sumatra	NA	26/04/07 - 21/11/09	15	845	10 (0.67)	12 (0.80)	15 (1.00)	12 (0.80)	6 (0.40)	7 (0.47)
Central Sumatra	I + II + III	09/04/07 - 15/10/09	31	1,533	21 (0.68)	24 (0.78)	29 (0.94)	27 (0.87)	13 (0.42)	5 (0.16)
Kerinci Seblat - Batanghari	I	09/01/07 - 10/09/09	110	3,493	76 (0.69)	91 (0.83)	51 (0.46)	89 (0.81)	39 (0.35)	28 (0.25)
Northern Riau	NA	09/06/09 - 22/12/09	18	739	0 (0.00)	9 (0.50)	18 (1.00)	2 (0.11)	0 (0.00)	0 (0.00)
Leuser - Ulu Masen	I	02/05/07 - 01/03/09	159	4,884	76 (0.48)	132 (0.83)	138 (0.87)	107 (0.67)	66 (0.42)	27 (0.17)
Total			394	3,511	206 (0.52)	325 (0.82)	312 (0.79)	277 (0.70)	151 (0.38)	86 (0.22)

* TCL = tiger conservation landscapes (Dinerstein et al., 2006)

Table 7 Estimated occupancy values (mean(SD)) estimated with a multi-species occupancy model for different landscape across Sumatra. The occupancy dataset was collected through detection/non-detection surveys along transects carried out in a total of 394 grid cells of 17 by 17 km each by various organizations covering approximately 60% of the remaining tiger habitats in Sumatra between 2007 and 2009.

Landscape	Grid cells (N)	Sumatran tiger	Wild pig	Sambar deer	Barking deer	Illegal logging	Poaching
Southern Sumatra	51	0.60 (0.09)	1.00 (0.00)	1.00 (0.00)	0.89 (0.05)	0.56 (0.08)	0.46 (0.14)
Way Kambas	10	0.43 (0.18)	1.00 (0.00)	1.00 (0.00)	0.97 (0.04)	0.79 (0.1)	0.60 (0.19)
Eastern Sumatra	15	0.80 (0.09)	1.00 (0.00)	0.98 (0.02)	0.84 (0.09)	0.59 (0.11)	0.59 (0.18)
Central Sumatra	31	0.84 (0.06)	1.00 (0.00)	0.99 (0.01)	0.99 (0.01)	0.56 (0.09)	0.28 (0.13)
Kerinci Seblat - Batang Hari	110	0.91 (0.04)	0.67 (0.07)	0.99 (0.01)	0.96 (0.02)	0.63 (0.06)	0.61 (0.13)
Northern Riau	18	0.14 (0.11)	1.00 (0.00)	0.89 (0.07)	0.30 (0.14)	0.76 (0.17)	0.47 (0.26)
Leuser - Ulu Masen	159	0.76 (0.06)	0.95 (0.02)	0.99 (0.01)	0.91 (0.04)	0.55 (0.05)	0.32 (0.10)
Island-wide	394	0.75 (0.05)	0.89 (0.03)	0.98 (0.01)	0.90 (0.03)	0.59 (0.05)	0.44 (0.10)

Table 8 Probabilities that an individual of a species is present on a transect segment when the species was not present on the previous segment (θ) or when the species was present on the previous segment (θ’) as well as the detection probability of a species if it is present on the segment (p), estimated using a multi-species patch occupancy framework. The occupancy dataset was collected through detection/non-detection surveys along transects carried out in a total of 394 grid cells of 17 by 17 km each by various organizations covering approximately 60% of the remaining tiger habitats in Sumatra between 2007 and 2009.

Species	θ	θ'	p
Sumatran tiger	0.0326 (0.0058)	0.1435 (0.0336)	0.6086 (0.1259)
Wild pig	0.0321 (0.0060)	0.0861 (0.0164)	0.9340 (0.0132)
Sambar deer	0.0245 (0.0053)	0.1454 (0.0274)	0.5907 (0.0242)
Barking deer	0.0348 (0.0075)	0.1209 (0.0291)	0.5708 (0.0660)
Illegal logging	0.0303 (0.0052)	0.2481 (0.0419)	0.8125 (0.0460)
Poaching	0.0120 (0.0040)	0.1326 (0.0417)	0.8282 (0.0406)

Table 9 Species and threats-wise and beta parameters of site covariates used in the analysis. Elevation2 and Dist.Settlement2 are squared terms of elevation and distance from settlements. Values show mean ± sd and 95% credible intervals, estimated using a multi-species patch occupancy framework. The occupancy dataset was collected through detection/non-detection surveys along transects carried out in a total of 394 grid cells of 17 by 17 km each by various organizations covering approximately 60% of the remaining tiger habitats in Sumatra between 2007 and 2009.

Species	Elevation	Elevation2	Forest Perc.	Forest Lost	National Park	Dist. Settlement	Dist. Settlement 2
Sumatran tiger	-0.235±0.096	0.030±0.055	0.201±0.09	-0.072±0.067	0.158±0.131	0.027±0.070	-0.039±0.035
	(-0.424-0.043)*	(-0.075-0.143)	(0.027-0.38)*	(-0.229-0.04)	(-0.095-0.414)	(-0.115-0.164)	(-0.105-0.033)
Wild Pig	-0.301±0.087	0.062±0.056	-0.028±0.074	-0.031±0.046	-0.302±0.119	-0.019±0.069	-0.069±0.033
	(-0.477-0.129)*	(-0.038-0.176)	(-0.172-0.119)	(-0.124-0.059)	(-0.537--0.07)*	(-0.16-0.108)	(-0.139--0.007)*
Sambar Deer	-0.044±0.073	-0.017±0.044	0.213±0.065	-0.012±0.048	0.01±0.093	0.058±0.059	-0.06±0.03
	(-0.187-0.097)	(-0.107-0.066)	(0.089-0.34)*	(-0.103-0.086)	(-0.172-0.191)	(-0.055-0.178)	(-0.119--0.002)*
Barking Deer	0.172±0.091	-0.007±0.051	0.090±0.077	-0.017±0.055	-0.282±0.122	0.033±0.067	-0.064±0.034
	(-0.006-0.355)	(-0.113-0.086)	(-0.064-0.245)	(-0.123-0.098)	(-0.531--0.049)*	(-0.094-0.168)	(-0.134-0)
Logging	-0.541±0.128	-0.039±0.085	-0.112±0.105	-0.049±0.067	-0.096±0.156	0.003±0.085	-0.098±0.054
	(-0.796-0.294)*	(-0.239-0.094)	(-0.321-0.091)	(-0.200-0.071)	(-0.403-0.213)	(-0.181-0.162)	(-0.223--0.014)*
Poaching	0.270±0.172	0.005±0.078	-0.103±0.162	0.031±0.107	-0.083±0.219	0.167±0.15	-0.014±0.061
	(-0.061-0.62)	(-0.164-0.159)	(-0.451-0.184)	(-0.118-0.308)	(-0.522-0.351)	(-0.046-0.508)	(-0.111-0.124)

* significant at $\alpha = 0.05$

FIGURES

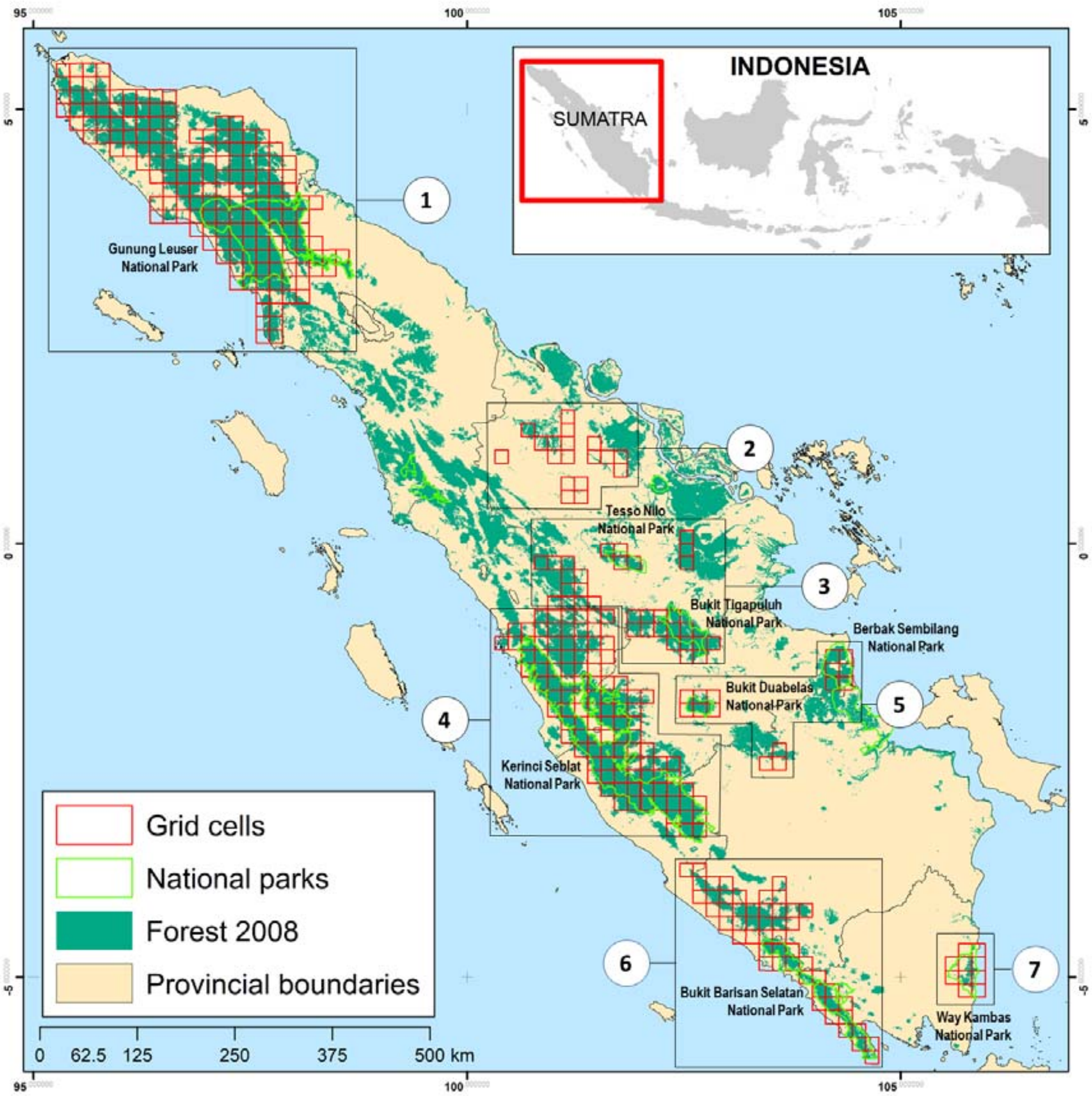

Figure 2 Grid cells, national parks, and predefined landscapes, including: 1. Leuser – Ulu Masen, 2. Northern Riau, 3. Central Sumatra, 4. Kerinci Seblat - Batanghari, 5. Eastern Sumatra, 6. Southern Sumatra, and 7. Way Kambas. The grid cells were used as a framework of the detection/non-detection patch occupancy surveys along transects carried out in a total of 394 grid cells of 17 by 17 km each by various organizations covering approximately 60% of the remaining tiger habitats in Sumatra between 2007 and 2009.

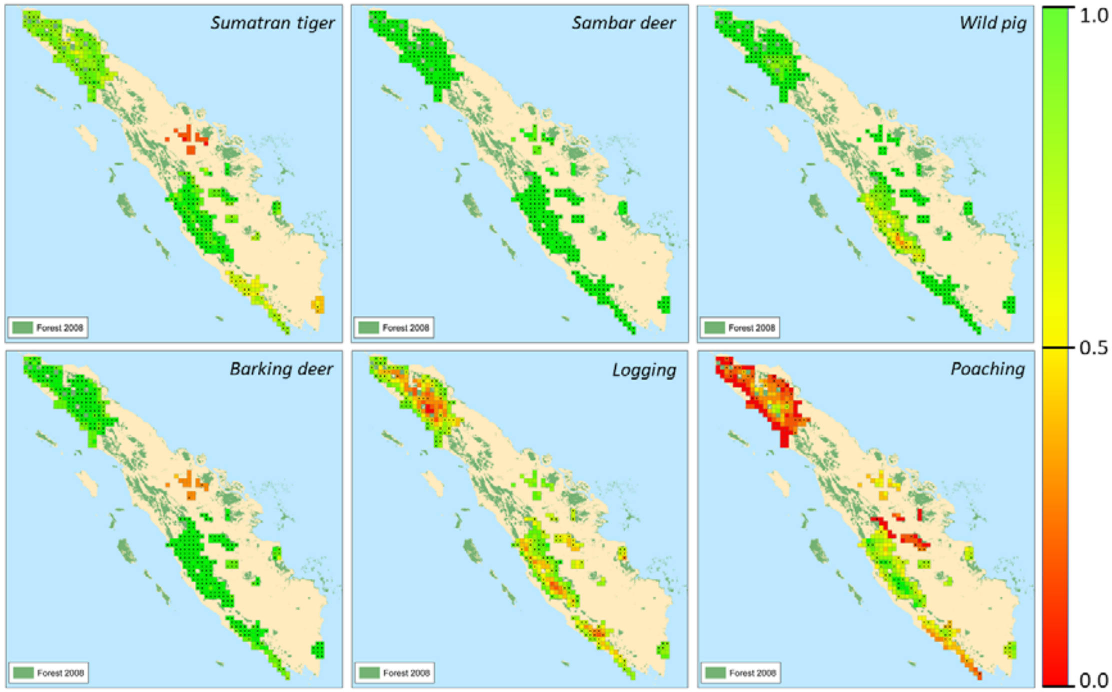

Figure 3 Occupancy of four species and two threats predicted with a multi-species co-occurrence model. Black dots are sites with actual indirect tiger sign detections. The grid cells were used as a framework of the detection/non-detection patch occupancy surveys along transects carried out in a total of 394 grid cells of 17 by 17 km each by various organizations covering approximately 60% of the remaining tiger habitats in Sumatra between 2007 and 2009.

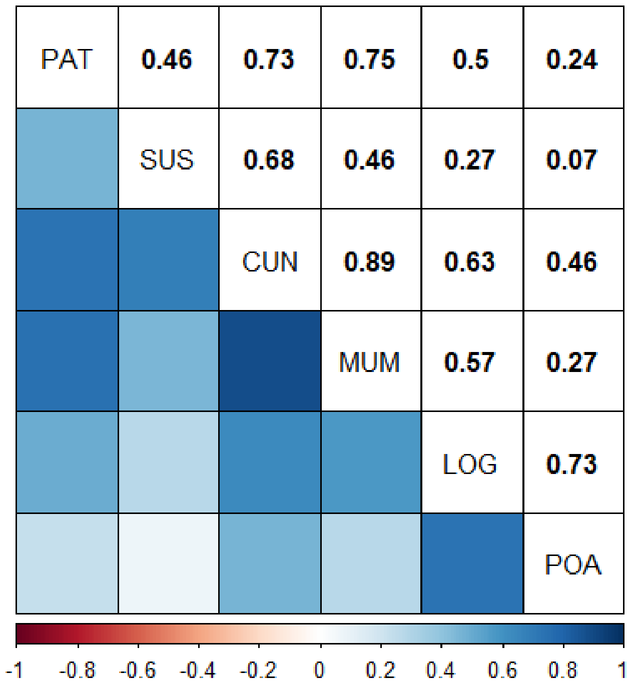

Figure 4 Residual correlation among four species and two types of threats estimated with a latent-variable co-occurrence model predicted with multi-species co-occurrence model. The occupancy dataset was collected through detection/non-detection surveys along transects carried out in a total of 394 grid cells of 17 by 17 km each by various organizations covering approximately 60% of the remaining tiger habitats in Sumatra between 2007 and 2009. Species and threats included Sumatran tiger (PAT), wild pigs (SUS), Sambar deer (CUN), barking deer (MUM), logging (LOG), and poaching (POA).

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Chapter 3

MODELING POTENTIAL CONNECTIVITY OF FRAGMENTED HABITATS OF SUMATRAN TIGER IN WEST SUMATRA, INDONESIA

Introduction

Many protected areas around the world are within human dominated landscapes, small in size, and isolated (Chundawat et al., 2016; DeFries et al., 2005). This situation does not match with the requirement of large carnivores having large home ranges and long dispersal movements (Chundawat et al., 2016). Conservationists propose two main strategies to improve wildlife persistence in these human-dominated landscapes, 1) conserving areas which act as "steppingstones" between two or more habitat patches and 2) restoring connectivity to facilitate wildlife movement between wildlife habitats (McRae et al., 2012). Several approaches are proposed to improve connectivity between protected areas, including protecting existing corridors, restoring deforested habitats, setting up mitigation structures, and land-purchasing to secure lands along the corridors (McRae et al., 2012). Prior to any of these approaches, a robust assessment should be carried to identify areas of the most potential for landscape connectivity.

Over the past decade, conservation investments have been focused on tiger populations in priority Tiger Conservation Landscapes (Walston et al., 2010). In Sumatra, this has been translated into the protection of six priority Tiger Conservation Landscapes, namely Bukit Barisan, Kerinci Seblat, Berbak–Sembilang, Bukit Tiga Puluh, Leuser Ulu Masen, and Kampar – Kerumutan (Ministry of Forestry of

Indonesia, 2010). However, many Sumatran tigers live in human-dominated landscapes, leading to prolific human–tiger conflicts. Indeed, most tigers that were killed in the same time frame were located in human-dominated landscapes where conservation investments are lacking. Between 2001 and 2016, 130 tigers were killed due to conflict with local communities; 75 (58%) were in human-dominated landscapes (Kartika, 2016).

The recent population viability analyses led by the Ministry of Environment and Forestry of Indonesia identifies only four of 23 landscape patches containing Sumatran tigers that are viable to support tigers for the next 100 years. The probability of extinction of tiger populations in these fragmented, isolated, landscapes can only be minimized if their dispersal is facilitated (Pusparini et al., 2019). Therefore, improving and maintaining connectivity among these landscapes is critical. A successful strategy for conserving the Sumatran tiger will therefore rely on protecting the source population while providing dispersal opportunities with sink populations through maintaining connectivity (McRae et al. 2012).

The previous Sumatran tiger action plan focused on securing source areas within larger priority tiger conservation landscapes (Soehartono et al., 2007; Walston et al., 2010). In specific, Indonesia's National Tiger Recovery Plan (NTRP) targets to double the Sumatran tiger populations in six priority landscapes by 2022 (Global Tiger Initiative, 2010; Ministry of Forestry of Indonesia, 2010). This strategy jeopardizes Sumatran tiger populations in many neglected, non-priority, landscapes, as conservation investments over the past decade have mostly been allocated in the priority landscapes documented in the NTRP.

In its new action plan, the Government of Indonesia has substantially revised the previous action plan (KLHK, 2019a). The revised action plan defines a set of conservation actions for small, isolated, and neglected landscapes, where tigers still exist and are in need of novel conservation measures. This includes 13 small forest patches; mostly in North Sumatra and West Sumatra provinces. Among priority actions are research on landscape connectivity in isolated and neglected landscapes, translocation, and implementation of metapopulation management.

The goal of our study is to provide a model of landscape connectivity in human – dominated landscapes, which will be used by management authorities to improve the management of Sumatran tiger populations in non-priority landscapes across the island of Sumatra. To reach this goal we applied circuit theory and least-cost path metrics to: i) identify and map the least-cost pathways and areas of importance which potentially facilitate movements of the Sumatran tigers between the three protected areas (core area), ii) identify the level of importance of the core areas and linkages, relative to one another, for conservation, and iii) identify critical areas along the least-cost pathways where further loss would threaten the potential connectivity.

Our study is focused on a human-dominated landscape in the West Sumatra region, within which seven protected areas are located, including: Barumun Wildlife Reserve, Batang Gadis National Park, Malampah – Alahan Panjang Wildlife Reserve, Maninjau Nature Reserve, Batang Pangean I and II Nature Reserve, Bukit Rimbang – Bukit Baling Wildlife Reserve, and Barisan Nature Reserve adjacent to the North Kerinci core tiger area in Kerinci Seblat landscapes (Walston et al., 2010). Source-sink dynamics are likely present and important in these degraded landscapes. By identifying and maintaining connectivity among tiger subpopulations we can improve the long-term survival of the Sumatran tigers in this region.

This study is in urgent need for at least three reasons, including: 1) to address the action plan mandate for research on connectivity, 2) to establish a model for landscape connectivity which can be replicated island-wide, and 3) to provide baseline data for further development of tiger metapopulation management strategies in Sumatra.

Methods

Study Site

Our study focuses on a human-dominated landscape in the West Sumatra region. The spatial extent of this study is arbitrary to include seven protected area in the region, including Barumun Wildlife Reserve (BWR, 400 km^2), Batang Gadis National Park (BGNP, 657 km^2), Malampah – Alahan Panjang Wildlife Reserve (392 km^2), Maninjau Nature Reserve (219 km^2), Barisan Nature Reserve (1,317 km^2), Batang Pangean I and II Nature Reserve (481 km^2), and Bukit Rimbang – Bukit Baling Wildlife Reserve (1,482 km^2) (Figure 5). These protected areas and adjacent forests (here in after “forest patches”) may provide important corridors for tigers between Batang Gadis and Kerinci Seblat landscapes (Dinerstein et al., 2006). These forest patches represent sites where tigers have coexisted with people for decades despite the potential of source-sink dynamics with the adjacent prime tiger habitats. BNR, in particular, is located next to the North Kerinci Core Tiger Area of the Kerinci Seblat landscape (Walston et al., 2010).

The assessed landscape expands between 0 and 2,972 m asl. The mean elevation across all forest patches is 871.7 (*SD*±341.2) m asl, with the lowest and highest are in Bukit Rimbang – Bukit Baling Wildlife Reserve (43 m asl) and Batang Pangean I and II Nature Reserve (2,972 m asl) respectively. More than 90% of site landcover was dominated by primary and secondary forests. A small portion of site landcover was dominated by agriculture (4.7%) indicating that illegal activities did occur inside the protected areas (Table 10). The project landscape is dominated by agricultures (31%), secondary forests (21%), and plantations (20%). Only 9% is primary forests, most of them (49%) are within highly isolated protected areas. All landscape patches have much larger *SD*s compared to their means, indicating that the distribution of patch sizes is skewed toward small areas (Table 11).

Most forest-edge communities living in the region are composed of subsistence farmers that are largely dependent on the harvest of their main cash crop and livestock for basic living (Anonymous, 2014; West Sumatra Statistic Agency, 2018). In a situation where human habitations are adjacent to forest edges, the risk of encounter between villagers and Sumatran tiger was higher (Inskip & Zimmermann, 2009; Wati, 2021). As a result, the index of tiger mortality in West Sumatra was among the highest (0.26 tigers/incident) across all Sumatra provinces (Kartika, 2016). Traditionally, Minang, the native tribe and the majority of West Sumatra's population, respect tigers and therefore could be important members of tiger friendly community groups. The Minang believe tigers have feelings and help guard the villages from bad matters. Despite this, the severity of human-tiger conflict (HTC) in this region was magnified by high human density (126 people/km^2), habitat conversion to agricultural lands (34% of land), and high livestock density, including pigs, cattle, and buffaloes (1.790/km^2) (West Sumatra Statistic Agency, 2018).

Datasets

Our analyses required two main datasets, 1) tiger localities obtained from detection/non-detection surveys following a patch occupancy sampling design previously implemented on Sumatran tiger (Wibisono et al., 2011) and 2) spatially explicit landscape characteristics, including major infrastructure, topography, land cover, and land cover types.

Tiger Detection: Between October 2018 and June 2019, two well-trained field teams carried out a series of detection/non-detection surveys in all habitat types likely to support tigers, from lowland to montane habitat (see Table 10) (Wibisono et al., 2011). A total of 36 grid cells of 289 km^2 (17 x 17 km), each composed of at least 10% potential tiger habitat, have been surveyed. The cell size was based on the putative home range size of an adult male Sumatran tiger to allow for changes in the distribution of resident tigers to be reflected in the proportion of the cells occupied. Within each of the grid cell's quadrants, one randomly selected cell of 4.5 km^2 (2.125 by 1.125 km) was then applied to introduce the element of randomization. The field teams were required to walk through the random cells while maintaining spatial coverage of the overall grid cells, haphazardly selected animal trails likely to contain signs of tiger and primary prey, including sambar deer, barking deer, and wild pig. These animal trails were irregular by nature and typically found along ridgelines, riparian corridors, valleys, and human trails. The detection (otherwise non-detection) of tiger and prey based on their signs was established based on 1-km walking distance, representing one spatial replicate. Therefore, the field teams recorded only the first sign of each species they found on the trail in every 1-km segment walked. Each recorded sign was georeferenced using the UTM48N coordinate system. Tiger signs included pugmarks, scrape marks, claw marks, and feces. we limited prey signs to footprints, feces, and rooting (wild pig), to avoid misidentification of other types of non-typical signs (tree twists, rubbing, wallows, beds, etc.). To reduce heterogeneity in detection probability, the number of replicates per cell was proportionate to the extent of forest habitat in the cell, with a minimum of 4 and a maximum of 40 of 1 km segments when the grid cell was 10% and 100% forested, respectively.

Landscape Characteristics: we classified landscape characteristics into three categories, i.e.: 1) terrain, including rivers (vector) (KLHK, 2019b), elevation, slope, and aspect (raster: 30 m resolution) (USGS, 2017), 2) land cover, including percent tree cover (raster: 1 km resolution) (Hansen et al., 2013) and land cover (vector) (KLHK, 2011), and 3) infrastructures, including land cover (vector) (KLHK, 2011), protected/non-protected area (vector) (Protected Planet, 2019), and road (vector) (OpenStreetMap©).

We generated slope and aspect layers from the digital elevation model (DEM) (USGS, 2017). The original land cover layer contained 21 classes. For better interpretation, we generalized the land cover layer into 10 classes (primary forest, secondary forest, plantation, agriculture, shrub, swamp, settlement, bare land, mining, water body) based on their similar characteristics. We employed Euclidian distance from rivers to generate the distance from roads and rivers layers, respectively. We selected four types of concessions from the land cover layer to identify forest management regimes which may serve as corridors to facilitate tiger movement between the modelled core areas (e.g., fiber, timber, oil palm, and social forestry). The main idea behind this is that the management of these land covers are under the authority of the Ministry of Environment and Forestry (MoEF). Therefore, the MoEF may apply specific regulations to 'force' the concessionaires to allocate part their concessions as tiger corridors. For further analyses, we then converted all vector datasets into rasters using the DEM as a mask to make sure all the output rasters are in the same spatial extent and resolution (30 m). We processed all spatial data using a licensed ArcGIS 10.7 (ESRI, Redlands).

Analyses

The analyses required two main spatial datasets, i.e. a shapefile containing core area polygons and a resistance raster layer which specifies the resistance to movement at each cell in a landscape. We defined core habitats of Sumatran tigers in the target landscape using Maxent v3.4.1 (Phillips et al., 2004, 2006). Maxent has been widely used for presence only dataset over other techniques due to its robustness against autocorrelated environmental predictors (Elith et al., 2010; Phillips et al., 2006), lower sensitivity to small sample sizes (Elith et al., 2006), and being less affected by spatial errors (Graham et al., 2008). Maxent output is an ASCII format covering the spatial extent of the study site (in this case, West Sumatra landscape), where each pixel contains a predicted logistic probability value of species presence ranging between 0 and 1.0 (Elith et al., 2006; Phillips, 2008).

Further, using circuit theory and least-cost path analysis (Dutta et al., 2016; McRae & Beier, 2007; McRae et al., 2008), We developed a spatially explicit model of potential structural connectivity between the core habitats based on geographical characteristics, infrastructures, and landcovers (Calabrese & Fagan, 2004). A circuit is defined as a network of nodes connected by resistors. Resistors are electrical components that facilitate current. In the circuit, current represents a random walk. In wildlife ecology, nodes represent core habitats, current represents random wildlife movement, and resistors represent different types of landscape matrices where the animal should traverse through between the core habitats. The ability of resistors to conduct current is called as conductance. Opposite to conductance, is resistance, the inhibition of the resistors to conduct current. Therefore, in wildlife ecology, conductance represents habitat permeability to facilitate animal movement, and, in contrast, resistance represents landscape friction. Thus in short, the circuit theory measures all possible pathways for the animal to move between two core habitats (Brad H McRae, 2006; Brad H McRae et al., 2008). The least-cost path (LCP) is used complementary to the circuit theory in two ways. Among all possible pathways measured by the circuit theory, the LCP determines a single optimal pathway and presumably reflects a route preferred by a disperser once it has a thorough knowledge about the landscape it is going to travel through (Brad H McRae et al., 2008). The analytical procedures included modelling: i) core areas, ii) resistance layers, iii) linkage pathways, iv) core centrality, v) linkage priority, and vi) pinch point maps. Details of each procedure are described below:

Core Areas: We performed Maximum Entropy modeling, in the program MaxEnt version 3.4.1 (Phillips et al., 2006; Elith et al., 2011), to delineate tiger core areas. First, we predicted habitat suitability based on the tiger detection (response variable) obtained from the detection/non-detection surveys against several environmental variables (predictors). The response variable consisted of 183 Sumatran presence points. We performed a Pearson's correlation analysis to test for correlations between nine landscape variables, from which a pair of variables was removed if the coefficient correlation was > 0.50 (Mccarthy et al., 2015; Wibisono et al., 2011). The final set of predictors used in the analysis included elevation, slope, aspect, percent tree cover (Hansen et al., 2013), land cover, protected/non-protected area, and distance from river. We defined the protected areas and land cover as categorical variables and the remaining covariates as continuous variables. We performed a Bootstrap procedure with 25% random tests, ten replicates, and 5,000 iterations, and kept the other settings at the default options in program Maxent. We further performed Jackknife tests to assess consistency in variable importance between the training and test gains (Phillips, 2008). The overall model performance was measured by the area under the curve (AUC) of the receiver operating characteristic (ROC) curve (Phillips et al., 2006). We estimated the relative importance of each predictor to the Maxent model using the percent contribution and permutation importance, averaged over ten replicates. We investigated the response curves to explore how the environmental predictors effected the Maxent prediction.

We defined the core habitats based on a tenth percentile training presence logistic threshold. This threshold excludes all areas with predicted suitability less than that of the lowest 10% of recorded presence points. We used this threshold to reduce noise in the final core area model. We kept model pixels with logistic probabilities equal or larger than the threshold and omitted if otherwise (Wibisono et al., 2018). This procedure produced a raster layer containing a range of individual pixels, i.e., isolated habitat, to large groups of pixels, i.e., contiguous habitat patches. For further analysis, we converted the raster layer to a polygon vector layer. To arrive at ecologically meaningful core habitats, we kept polygons equal to 250 km^2 and larger and eliminated if otherwise. That size represents the known largest home range size of an adult male tigers in Sumatra (Wibisono & Pusparini, 2010). We then used GIS processes to fill hollows inside the polygons. The final core habitat data layer was then a vector of spatial polygons which have the potential habitat within to support at least one adult male tiger.

Resistance Layer: We applied Gnarly Landscape Utilities (McRae et al., 2008) on four landscape categories, land cover, roads, slope, and elevation, to develop the resistance layer. To assign resistance values, each landscape category must be classified into appropriate classes (Appendix C). We reclassified elevation into five classes based on eco-floristic characteristics of the Sumatra Island (e.g. ≤300 m asl, >300 - ≤800 m asl, >800 - ≤1,300 m asl, >1,300 - ≤2,500 m asl, >2,500 m asl) (Laumonier et al., 2010), and slope into four classes using natural breaks (Jenks) method (e.g. $\leq 7.9^0$, $>7.9^0 – 17.4^0$, $>17.4^0 – 28.9^0$, $>28.9^0$). We used the 10 generalized land cover classes (see landscape characteristics section) and maintained the original road classes, e.g. primary (national roads), secondary (provincial roads), tertiary (pathway), and tertiary (typically in settlements, towns, or cities).

We used several published papers to assign a resistance value to each class and our own experience in tiger ecology if published information was not available. For our study, we arbitrarily set up the resistance values ranging between 0 (the lowest) and 100 (the highest) (Beier et al., 2008; Dutta et al., 2016; McRae et al., 2008). A study in Riau, Central Sumatra, revealed a naïve occupancy of Sumatran tiger in forested area was at 0.73, 0.00 at agricultures, and a mean of 0.25 in various plantations, including oil palm, rubber, and acacia (Sunarto et al., 2012). The naïve occupancy at forested area was comparable to the predicted island-wide tiger's occupancy in Sumatra (0.72±0.05 *SE*) (Wibisono et al., 2011). Therefore, we assigned a resistance value of 100 for agricultures (i.e. tigers are very unlikely to traverse through agricultures). Assuming the naïve occupancy of 0.73 in the forest is equal to '0' resistance (e.g. tigers can freely move through forests) (Dutta et al., 2016), then the resistance value for plantations was $100 * \left(1 - (\frac{pla}{for})\right)$ or equal to 67, where 100 is the maximum resistance, *pla* is the mean naïve occupancy of plantations and *for* is the naïve occupancy of forested area respectively. For shrub, bare land, and settlement, we assigned resistance values of 2, 6, and 100 respectively (Dutta et al., 2016). In contrast to Dutta et al (2016), we assigned a resistance value of 90 for waterbody because in the land cover layer it is mostly major rivers, ponds and lakes, where there was a little chance for the tigers to swim through. Sumatran tiger densities range between 0.30 (FFI, *unpublished*) to 2.8 tigers/100 km^2 (Pusparini et al., 2017) in higher and lower elevation respectively. Therefore, we assigned resistance values of 0 for low (≤800 m asl), 20 for lower elevation (> 800 to ≤1,300 m asl), 60, and 80 for higher elevation (≥1,300 asl). We set up the resistance values for slope classes linear to elevations or steeper slope at higher elevation, i.e., 0 for flat and sloping, 20 for tilting, and 60 for steep. After calculating the resistance layer, we added 1 to the layer to account for Euclidean distance (McRae et al., 2009). We set up the resistance calculation method to 'Sum' to allow cumulative values of overlapped layers to be accounted for. Each pixel in the resistance raster, therefore, reflects a value of energy cost, impediment, and risk of mortality an animal should pay to cross that pixel (Adriaensen et al., 2003).

Linkage pathways: We used the Linkage Pathway tool of Linkage Mapper's ArcGIS toolbox to map corridors and least-cost path (LCP) between pairs of core areas using circuit theory. The LCP is a single path defined as a minimum cost-weighted distance (CWD) between two core areas, which represent the source and the destination (Adriaensen et al., 2003). Linkage pathways run cost-weighted distance analyses to produce accumulated least-cost linkages between core habitat networks using a core habitat vector and a raster of resistance to movement. We considered the number of linkages to be 'Unlimited' to allow any possible pathways of all pairwise cores. The tool clips the paths based on a user-specified cutoff width before injecting current. Here we used 50 km for the cutoff, representing the known farthest tiger movement in Sumatra based on cameratrap dataset (e.g. 42 km, rounded up) (WCS, *unpublished*). Therefore, to truncate the corridor and limit the corridor distance to the farthest tiger movement, we used 50,000 (map unit in meter) for the 'Cost-Weighted Distance Threshold', and 'Maximum Euclidean Corridor Distance'.

The Linkage Pathway tool calculates two metrics to describe the quality of each linkage. First, the ratio between the CWD and the Euclidean distance (ED) of each pair of cores, expressed by CWD divided by ED (CWD:ED). The quality of a linkage is higher when the ratio between the CWD and ED is lower and vice versa. Therefore, the highest possible quality of the linkage is equal 1. This indicates the level of difficulty to move between two cores relative to their proximity. Second, the ratio between CWD and LCP (CWD:LCP), which provides the mean resistance travelled along the optimum path between cores.

Core centrality and linkage priority: We used Centrality Mapper and Linkage Priority tools of the Linkage Mapper's ArcGIS toolbox to calculate current flow centrality (CFC) through the linkage networks. The CFC is a measure of contribution of individual core areas and linkages relative to one another in facilitating ecological flows across the overall network connection. Therefore, this analysis allows us to set up core areas and linkages that are of conservation priority (Dutta et al., 2018). The core areas and linkages with higher CFC values are thought to have more important contribution in maintaining the overall network connection (Carroll et al., 2012).

Centrality Mapper goes through the LCP vectors and stick maps from the Linkage Mapper and calculates the CFC using the Circuitscape (McRae & Shah, 2009). Each core is held as a node and each linkage is assigned with a resistance value equivalent to the CWD of the associated LCP. It iterates over all pairwise core areas, injects 1 Amp into one core area while defining another as the "ground" in electrical terms. A centrality score is the sum of results across all cores and linkages.

Linkage Priority weights a combination of many factors, including core area values (CAV: core's size and shape, mean resistance values, and 'other core area value' [see below]), and permeability of each linkage, the proximity, and how central the linkage against the entire core network. It assumes that a linkage of two very important core habitats has a higher conservation priority than the one that connects two marginal core habitats. In addition, it can accommodate expert opinion to weight either or both the cores and the linkages. For the CAV, we weighted four of six required parameters, i.e., normalized mean resistance (Resistance Weight, RW), normalized size (Size Weight, SW), normalized ratio between area and perimeter (Area/Perimeter Weight, APW), and other core area value (Other Core Area Value, OCAV). Each weight contains a decimal value between 0 and 1 to be multiplied by the given parameter of which all together should be summed to 1. Therefore, we weighted the RW, SW, APW, and OCAV with 0.25, 0.25, 0.25, and 0.25 respectively, and the other two parameters with 0.00. The OCAV weight needs core area rasters to work. To be ecologically more meaningful, therefore, we supplied the optional 'Other

Core Area Value Raster' with the core area's raster produced using Maxent (i.e. Core Area section) whose the raster's logistic values within each core area was averaged.

Pinch point map: We used the Centrality Mapper tool of Linkage Mapper's ArcGIS toolbox to identifies pinch points. Pinch points are locations within the least-cost corridors that are critical for the conservation of landscape connectivity. These pinch points identify bottle necks for movement of the target species along the corridors where alternative pathways are not present. Pinch points are a narrowing low resistance land cover types due to physical features which should be of conservation priorities. Further degradation of quality of these areas and the surroundings can disproportionately compromises the quality of the connectivity. We supplied the 'Circuitscape mode for raster centrality calculations' parameter with 'Pairwise', which calculates current between all pairwise cores, one pair per run, and sums the results. To better describe the spatial distribution of the pinch point locations, we reclassified the pinch point raster into nine classes using Reclassify tool of ArcGIS, applied *Natural Breaks* statistics to select the highest pinch point values of 1.81 or larger, converted into polygon.

Results

Tiger detection: We obtained 183 verified Sumatran tiger signs. The most common signs detected were scratches (31%) while the least was scentmarks (1.6%). Most signs were detected in secondary (49.7%) and primary forests (48.6%), and at higher elevation (80.3%; 1,087.5 ±373.2 m asl). However, a larger portion of signs were detected in non-protected area (59.0%) (Table 12).

Characteristics of landcover resistance: The mean resistance of bare land (13.2±15.1) was the lowest for tiger movement across all land cover types. As expected, settlement (137.9±40.4) had the highest mean resistance value across all land cover types. Although intuitively thought as the best tiger habitat, the mean resistance value of primary forest (47.2±30.6) was high. This makes sense because most of primary forests in this region are at higher elevation (970.5±484.1), thus rugged terrain. Higher elevation and steeper slopes (tilting and steep) were assigned with a resistance value of 60 and 80, respectively, meaning higher resistant for tiger movement. The use of sum in the resistance calculation allowed other overlapping layers to reduce the cumulative resistance values of agriculture, mining, and settlement; three land uses with maximum resistance values. However, the mean resistance of agriculture (114.2±21.5), mining (116.5±22.7), and settlement (137.9±40.4) were still the highest of all land cover types, indicating that it was very unlikely for the tiger to move across these land covers (Table 13).

Core areas: Maxent analysis identified elevation as providing the single most important contribution (62.4%) and permutation importance (55.4%) to the predicted Sumatran tiger suitable habitat. Together with land cover (15.9%) and forest (9.3%), these three variables contributed nearly 90% of the overall Maxent model prediction (Table 14). In agreement, elevation had the highest gain when used in isolation, which decreased most when it was omitted from other candidate models in Jacknife test for variable important using regularized training gain, test gain, and AUC on test data. The response curve of elevation was unimodal, indicating that the Sumatran tiger detections were highest in medium elevations, while decreasing at lower and higher elevations. The species distribution model performed well with a mean AUC of 0.95±0.004. Using the ten-percentile logistic threshold, we then classified the core areas as a set of model pixels with a logistical probability of 0.34 or greater. A total of nine core areas were produced for the connectivity analysis, here we named them from South to North: Batang Pangean (BPA: 7,058 km^2), Barisan (BAR: 9,659 km^2), Bukit Rimbang – Bukit Baling (BRB: 2,800 km^2), Maninjau I (MAN I: 1,134 km^2), Maninjau II (MAN II: 601 km^2) , Malampah – Alahan Panjang I (MAP I: 3,129 km^2), Malampah – Alahan Panjang II (MAP II: 3,128 km^2), Batang Gadis (BGA: 14,881 km^2), and Barumun (BRU: 8,633 km^2) The CFC values of core areas MAP I (23.6) and MAP II (22.8) were the highest among all nine core areas, indicating that these two cores might be the most important to maintaining the overall linkage network in West Sumatra province (Table 15) (Figure 6).

Connectivity: Thirteen links were produced between pairwise core areas across the study site. The mean ± SD of ED, CWD, and LCP, were 21.1 (16.9), 904.3 (790.2), and 32.9 (24.5), respectively. The ED, CWD, and LCP were the lowest for Link ID 10 (MAN I – MAN II, 3.5), Link ID 4 (MAP I – MAP II, 36.6), and Link ID 1 (BRU – BGA, 5.3) and the highest for Link ID 2 (BRU – MAP I, 48.8), Link ID 12 (BRB – BAR, 2,393.0), and Link ID 13 (BAR – BPA, 135.1), respectively. The ratio between CWD and ED (CWD:ED) and between CWD and LCP (CWD:LCP) were the lowest both for Link ID 4 (10.3 and 50.8) and the highest for Link ID 13 (135.1) and Link ID 10 (50.4), respectively. The CFC value was the highest for Link ID 4 (16.5). Altogether, MAP I and MAP II possessed three of the best connectivity attributes, i.e. the highest core centrality, the highest linkage quality, the lowest mean resistance travelled, and thus the highest quality in maintaining the overall linkage network. In contrast, the CFC value for Link ID 2 (4.2) was the lowest, indicating the least important linkage for the overall linkage network (Table 16) (Figure 7).

Characteristic of linkage habitat: We identified a total of 1,978.1 km^2 linkages connecting nine core areas in West Sumatra Province. Most of them consisted of secondary forests (59.5%), shrub (18.7%), and agriculture (13.6%), indicating the importance of these land cover types as habitat corridor to facilitate tiger movement in the region. Primary forest (3.7%) contributed less to the overall linkage network (Table 17). Most linkages skewed to gentler slopes (23.5 ± 7.2^0) and at higher elevation (1,113.7±70.6 m asl). However, there is no obvious pattern of the altitudinal distribution of the overall linkages (Figure 8).

Pinch point: Pinch points were identified in eight of twelve LCPs. The lowest number of pinch point (1) was at Link ID 4 (MAP I – MAP II) and the highest (16) at Link ID 8 (MAP II – BRP). No obvious pinch point was identified in Link ID 1, 2, 7, and 10 (Table 18). There was an indication of correlation between the length of Link ID and the number of pinch points although not significant (n = 12, $r = 0.53$, $p > 0.05$). This provides a complementary information about important linkages of which at high risk of further human disturbances, Figure 9).

Discussion

In human-dominated landscapes, the long-term survival of a wide-ranging species depends on the movement of the animals through physical corridors between core habitat patches (Dutta et al., 2016). This study is the first attempt to identify and characterize the potential connectivity among tiger habitat patches in a human dominated landscape in Sumatra. We detected tigers in 25 (64%) of 35 surveys grid cells covering all remnant forest in West Sumatra. This indicated that tigers could survive even in these highly disturbed landscapes. The proportion of grid cells with tiger presence in the study site was even higher than four of the six priority tiger landscapes in Sumatra set up by the Government of Indonesia for tiger recovery, including Leuser Ecosystem, Bukit Barisan Selatan, Berbak – Sembilang, and Kampar – Kerumutan (Ministry of Forestry of Indonesia, 2010).

This study is specifically aimed to fill the scientific gaps required to implement the newly developed Strategic and Action Plan for the Conservation of Sumatran Tiger: 2020 – 2030. (hereinafter is referred to as “action plan”). The action plan mandates the management authority to strengthen Sumatran tiger management in small populations (e.g. ≤ 20 mature individuals) and neglected habitats (Pusparini et al., 2019). Furthermore, the framework of this study will benefit not only for the Sumatran tiger but also for other key wildlife species on the island, including the Sumatran elephant (*Elephas maximus sumatranus*), Sumatran rhinoceros (*Dicerorhinus sumatrensis*), and Sumatran orangutan (*Pongo abelii* and *P. tapanuliensis*). Analytical approaches used in this study can be replicated for these critically endangered species which share common habitats and anthropogenic threats across their geographical ranges on the island.

Studies on habitat connectivity across the tiger range countries have increased over the past decade, mostly to assess the ongoing habitat fragmentation, to anticipate the demand for inevitable infrastructure developments, and to facilitate genetic flow among fragmented tiger populations (Hilty et al., 2020). These studies of habitat connectivity designated core areas using various approaches, i.e. protected area boundaries, arbitrary buffers added to protected area boundaries, and protected areas where tigers had a high probability of occupancy (Dutta et al., 2018; Joshi et al., 2013; Yumnam et al., 2014). Here we used a quantitative approach by applying output from Maximum Entropy modelling of observed tiger sign to define tiger core areas and to weight individual core areas according to their logistic probability of the habitat suitability prediction. This provided a more meaningful parameter to describe the ecological characteristic of individual core areas, in addition to size, area, and other core area parameter values. As an example, a smaller core area with a higher logistical probability may be ecologically more important than a larger area with lower logistical probability in maintaining the overall linkage network. While a study on a proposed corridor network in Central Sumatra named Rimba corridor has been done to investigate effective governance sustainability (Sulistyawan et al., 2017), our study was the first to quantify the potential of different land cover types in serving as physical linkages for the Sumatran tiger to move between two core tiger habitats.

Non-protected primary and secondary forests may provide the last refuge for the tiger in this human-dominated landscape as shown by the highest record of tiger signs in these forest habitats. In this region, however, tigers were likely forced to use sub optimum habitats at higher elevation (1,300 – 2,500 m asl), in contrast to other studies where tiger occurrence was the highest at optimum lowland and hilly habitats (0 – 1,300 m asl) (Linkie et al., 2006; Pusparini et al., 2019). This might be an avoidance mechanism in response to high human disturbance in a human-dominated landscape, which otherwise, would lead to prolific conflict between tigers and humans. Indeed, an index of tiger mortality due to conflict with human was among the highest (0.26 tigers/incident) in West Sumatra among all Sumatra mainland provinces (Kartika, 2016). The severity of conflict between tigers and humans was magnified by high human population densities (126 people/km^2), habitat conversion to agricultural lands (34% of total land area) (West Sumatra Statistic Agency, 2018), and high livestock density, all together including pigs, cattle, and buffaloes (1,790 individuals/km^2) (Robinson et al., 2014).

Our results suggest that in a heavily fragmented landscape, secondary forest and shrub have become the most important land cover types to facilitate connectivity among habitat patches and provide habitat extensions, additional sub optimum habitats adjacent to prime habitats where tigers may live or go through, for a landscape-wide species like the Sumatran tiger. These land cover types along gentler slopes at higher elevation seemed to have the highest potential for linkage pathways among core habitats. The mean value of resistance layer over agriculture was among the highest of all land cover types. However, the fact that up to 13% of the overall linkages was agriculture might explain that this land cover type is important to facilitate tiger movement where it is the only option to get between two core areas. In an area dominated by coffee plantations, a Sumatran tiger was photographed in a forest patch as small as 0.02 km^2, 2 km away from Bukit Barisan Selatan National Park boundary (Weiskopf et al., 2019). Wibisono and Pusparini (2010) recorded a tiger – human conflict incident as far as 5.6 km from forest boundary ($n = 24$, 2.1 ± 1.3), indicating that the tiger did roam across multiple-use landscapes as far as several kilometers away from the nearest forested habitat. Our study corroborates these findings in that heavily degraded, human-dominated, landscapes may have the potential to serve as buffer zones for the Sumatran tiger population living in core tiger habitats. Our study has also provided the first strong evidence that forest patches in human dominated landscapes can serve as a biodiversity-rich habitat network for the entire West Sumatra landscape (SINTAS, *unpublished report*). This study, therefore, provides a critical baseline information for the government's national initiative to identify and protect critical areas outside protected area networks to be designated as structural corridors and essential ecosystem areas (Arumingtyas, 2017). Effective and local specific management strategies are urgently needed to stop further loss of tiger individuals from these buffer areas.

MAP I and MAP II, located at the center of the overall core area network, have the highest centrality scores with only one pinch point along the linkage pathway in between. More than half of these two cores are Malampah – Alahan Panjang Wildlife Reserve (MAPWR) and within two larger side-by-side forested areas of a total of 1,694,2 km^2 (hereinafter is referred as MAP landscape). Assuming a density of 1 adult tiger/100 km^2, then the MAP landscape could support up to 17 adult tigers; thus, may serve as the most important tiger habitats in West Sumatra. The MAP landscape is, however, bisected by a provincial road running between Bukit Tinggi City in the Southeast to Padang Sidempuan City in the Northwest. The pinch point indicated a section where further development should be avoided. On the other hand, the pinch point also indicated locations as to where the provincial and central government could consider the development of artificial wildlife corridors, such as wildlife flyovers or underpasses, to facilitate wildlife movement between the two forest sections. At a minimum, wildlife signboards can be installed along the pinch point and in its vicinity to reduce wildlife road killing accidents. The signboards, however, could increase threats from wildlife poachers as they may use them as signs for hunting spots. Roadblocks, therefore, need to be established in both sides of the entrance to the MAPWR by reactivating the existing guard posts in concert with surveillance and intensive law enforcement patrol along the road within the wildlife reserve.

While our study has identified the MAP I and MAP II as the two most important core areas, unless the management of other core areas is improved, the function of MAP I and MAP II in maintaining the overall core networks will not be optimal. Our study included eight major protected areas in West Sumatra as core areas. Unlike a national park, which is managed as an independent management unit, other types of protected areas are managed by a provincial conservation agency. As a result, one provincial conservation agency can have many protected areas to manage. The provincial conservation agency of West Sumatra itself must manage 20 protected areas sized between < 0.01 km^2 - 950 km^2 spreading across the province. Limited human resources and a restricted budget of the provincial conservation agency, along with the spatial arrangement of the protected areas, has made the management of these protected areas far from ideal. Therefore, effective and local specific management strategies are urgently needed to strengthen the management of other core tiger habitat areas in West Sumatra region. This includes provincial regulations regarding the improvement of protected area management and the conservation of wild fauna outside of the protected areas.

The government of West Sumatra has established provincial wildlife conflict mitigation units through a governor regulation No. 522.5-417-2018 regarding human – wildlife conflict management and mitigation. However, the teams are not yet in working order, mainly due to a complex structural load. It is, therefore, necessary to evaluate and simplify the regulation to be more practical, to allow the mitigation teams implementing the regulation on the ground. West Sumatra province is among a few provinces in Sumatra where customs are still firmly maintained by most local tribes, the largest forest edge communities in the region. Traditionally, west Sumatran tribes, called Minang, respect the tigers as their grandparents who protect their life and livelihood. It is, therefore, necessary to recognize and reinforce customary laws, again through provincial regulation.

The regulations should be supported by an effective awareness program which takes into account the Minang culture and local wisdom as the center of knowledge. Most importantly, the West Sumatra government should allocate state budget to support the implementation of these regulations. A stronger and effective collaboration between the central and provincial government must be initiated as a guarantee to save the Critically Endangered Sumatran tiger and other key wildlife species, and forest habitats in human-dominated landscapes, not only in West Sumatra, but also in other Sumatra provinces.

Recommendation

While the importance of habitat connectivity to improve wildlife management has been increasingly recognized over the past several years (Arumingtyas, 2017; Sulistyawan et al., 2017), attempts to quantify potential connectivity for existing fragmented wildlife habitats in human-dominated landscapes are still lacking. Part of this lack is due to gaps of the relevant government agencies in connectivity assessment techniques and knowledge on wildlife ecology in human-dominated landscapes. Conservation tools and analytical procedures demonstrated in our study provide a "user friendly" yet robust approach for government officers to conduct similar analysis for fragmented wildlife habitats in other human-dominated landscapes across the Sumatra Island and beyond. It is, therefore, a necessity to develop and implement a hands-on training program on habitat connectivity assessment for members of relevant government bodies. Results of the assessment will provide a baseline for government regulations regarding identification and establishment of essential ecosystem areas in Sumatra. Lastly, ground surveys may be needed to validate if tigers actually disperse through the modelled linkages.

TABLES

Table 10 Protection status, altitudinal ranges, and land cover types of the remaining Sumatran tiger habitats in West Sumatra, Indonesia of which structural connectivity analyses were modelled. The analyses required two main spatial datasets, i.e. a shapefile containing core area polygons and a resistance raster layer which specifies the resistance to movement at each cell in a landscape. The core habitats of Sumatran tigers were modelled using Maxent v3.4.1, while the land cover layers, along with other geographic layers, including slopes, elevations, and road networks were use d to develop the resistance layer. The area indicates the size of the protected area only. The land cover layer was obtained from the Ministry of Environment and Forestry of Indonesia of year 2011, generalized from a total of 21 types to ten land cover types based on similarities for better interpretation.

Area	Status	Area (km^2)	Elevation (m asl)			Land Cover (km^2)						
			Mean (*SD*)	Min	Max	Primary Forest	Secon-dary Forest	Shrub	Plan-tation	Agricul-ture	Settle-ment	Others
Barumun	Wildlife Reserve	400	973 (292.7)	262	1,996	246.9	96.8	20.0	0.1	35.9	0.0	0.5
Batang Gadis	National Park	657	925.9 (379.1)	96	2,141	365.6	209.8	50.9	0.0	29.3	0.0	1.8
Malampah - Alahan Panjang	Nature Reserve	392	992.7 (430.9)	74	2,892	90.6	264.4	18.8	0.9	14.8	2.1	0.2
Maninjau	Nature Reserve	219	972.7 (320.2)	124	1,728	73.0	72.0	23.3	0.0	50.5	0.1	0.0
Barisan	Nature Reserve	1,317	1,204.0 (440.5)	87	2,685	1115.6	96.9	23.7	0.0	80.1	0.3	0.0
Batang Pangean I & II	Nature Reserve	481	631.3 (293.9)	294	2,972	0.0	428.3	29.2	0.7	22.3	0.3	0.0

Area	Status	Area (km^2)	Elevation (m asl)			Land Cover (km^2)						
			Mean (*SD*)	Min	Max	Primary Forest	Secon-dary Forest	Shrub	Plan-tation	Agricul-ture	Settle-ment	Others
Bukit Rimbang Bukit Baling	Wildlife Reserve	1,482	402.6 (231.4)	43	1,304	517.6	912.8	43.5	0.5	1.6	0.0	5.5
Total						2,409.3	2,081.0	209.3	2.2	234.5	2.8	8.0
Percent						48.7%	42.1%	4.2%	0.0%	4.7%	0.1%	0.2%

Table 11 Major land covers of the overall landscape extent in West Sumatra, generalized from a total of 21 land cover types based on similarities in land cover characteristics for better interpretation. The land cover layer, along with other geographic layers, including slopes, elevations, and road networks were used to develop a resistance layer required for a structural connectivity analysis of this study, between Sumatran tiger's core habitats in West Sumatra, Indonesia. The core areas of Sumatran tiger were modelled using Maxent 3.4.1. The land cover layer was obtained from the Ministry of Environment and Forestry of Indonesia of year 2011. The core habitats of Sumatran tigers were modelled using Maxent v3.4.1.

Land Cover	# Patches	Area (km^2)						Elevation (m asl)			
		Sum	%	Mean	SD	Min	Max	Mean	SD	Min	Max
Primary Forest	76	5,220.8	8.8%	68.7	153.3	$1.0*10^{-7}$	663.1	970.5	484.1	22.0	2,892.0
Secondary Forest	489	12,621.8	21.3%	25.8	168.3	$2.6*10^{-9}$	2,567.9	639.6	425.5	0.0	2,972.0
Shrub	2498	8,169.4	13.8%	3.3	18.6	$2.4*10^{-8}$	405,9	234.9	301.4	0.0	2,834.0
Plantation	285	11,222.3	18.9%	3,9.4	232.9	$1.5*10^{-9}$	3,311.7	73.9	99.1	0.0	1,762.0
Agriculture	448	18,345.4	30.9%	41.0	347.9	$8.4*10^{-11}$	6,958.6	316.3	339.1	0.0	2,362.0
Settlement	355	796.7	1.3%	2,2	7.7	$2.0*20^{-6}$	121.2	165.0	256.0	0.0	1,588.0
Bare land	758	1,756.8	3.0%	2.3	11.1	$6.5*10^{-7}$	247.1	115.9	168.1	0.0	2,742.0
Mining	41	139.0	0.2%	3.4	6.5	$1.1*10^{-4}$	35.8	84.0	112.2	0.0	677.0
Swamp	120	538.5	0.9%	4.5	14.5	$4.5*10^{-5}$	127.8	31.3	20.6	0.0	260.0
Waterbody	139	522.1	0.9%	3.8	17.9	$9.1*10^{-10}$	123.8	274.7	331.0	0.0	1,759.0

Table 12 Distribution of tiger signs found during the detection/non-detection survey in West Sumatra, Indonesia, based on elevation, land protection status, and land cover. Tiger sign localities found during the surveys were used to model tiger core areas required for a subsequent structural analysis of this study. The core areas of Sumatran tiger were modelled using Maxent 3.4.1. Five prominent tiger signs, including scratch, scrapemark, pugmark, scat, and scentmark, were used to identify the presence of Sumatran tiger during a series of detection/non-detection surveys carried out between October 2018 and July 2019 in 39 of 289 km^2 grid cells, in West Sumatra province.

Class \ Sign		Scratch	Scrape-mark	Pugmark	Scat	Scent-mark	Total	%
	Total	57	51	46	26	3	183	
	%	31.1%	27.9%	25.1%	14.2%	1.6%		100.0%
Land cover	Primary forest	14	35	25	14	1	89	48.6%
	Secondary Forest	43	13	21	12	2	91	49.7%
	Agriculture	0	1	0	0	0	1	0.5%
	Shrub	0	2	0	0	0	2	1.1%
Protection Status	Protected Area	5	29	27	13	1	75	41.0%
	Non-Protected Area	52	22	19	13	2	108	59.0%
Elevation	Lowland	1	1	0	1	0	3	1.6%
	Hilly	12	13	8	0	0	33	18.0%
	Lower Montane	36	22	27	15	3	103	56.3%
	Montane	8	15	11	10	0	44	24.0%

Table 13 Mean resistance of each land cover type in Western Sumatra, across a resistance layer developed for use in Circuit Theory and Least Cost Path analysis for Sumatran tiger habitat connectivity. The mean resistance value was the sum of resistance values of all pixels in each land cover type divided by the total number of pixels in the given land cover type. The standard deviation (SD) implies the variation of resistance in each land cover type given other overlapped variables, including slopes, elevations, and roads.

Land Cover	Mean Resistance	
	Mean	SD
Bare land	13.2	15.1
Shrub	14.3	18.8
Secondary Forest	29.6	26.6
Swamp	31.7	7.4
Primary Forest	47.2	30.6
Plantation	73.0	13.9
Waterbody	92.1	21.2
Agriculture	114.2	21.5
Mining	116.5	22.7
Settlement	137.9	40.4

Table 14 The percent relative contribution and permutation importance of each variable calculated by Maxent 3.4.1 to predict tiger distribution in West Sumatra, Indonesia. The Maxent output was used to model tiger core areas required for subsequent structural analysis of this study. Tiger core areas were defined using a 10-percentile training presence logistic threshold. This threshold excluded all areas with predicted suitability less than that of the lowest 10% of recorded presence points. Values were averaged over 10 replicates and normalized to give the percentages. The permutation importance was used to assess variable importance of the final Maxent model output.

Variable	Contribution (%)	Permutation Importance (%)
Elevation	62.4	55.4
Land cover	15.9	16.3
Forest	9.3	12.0
Slope	5.3	7.0
Aspect	3.0	3.8
Protected Area	2.2	0.1
River	2.0	5.4

Table 15 Current flow centrality of nine core habitats in West Sumatra, Indonesia, identified using Centrality Mapper tool of the Gnarly Utilities. The current flow centrality is a measure of contribution of individual core areas relative to one another in facilitating ecological flows across the overall network connection. CFC is the current flow centrality. Higher CFC indicates more important cores in maintaining the overall linkage network. The table was sorted down from the highest to the lowest current flow centrality values.

Protected Area	Area (km^2)	CoreID	Core Area	Area (km^2)	CFC
Malampah - Alahan Panjang	391.7	3	Malampah - Alahan Panjang I	3,127.7	23.6
		4	Malampah - Alahan Panjang II	3,129.4	22.8
Barisan	1,316.7	8	Barisan	9,659.3	17.3
Maninjau	218.9	5	Maninjau I	600.7	15.4
		6	Maninjau II	1,134.0	15.0
Batang Gadis	657.4	2	Batang Gadis	14,881.0	12.8
Bukit Rimbang Bukit Baling	1,481.5	7	Bukit Rimbang Bukit Baling	2,799.6	10.4
Barumun	400.3	1	Barumun	8,633.1	10.0
Batang Pangean	480.8	9	Batang Pangean	7,058.4	8.0
Mean (±SD)				5,669 (4,729)	15 (6.0)

Table 16 Current flow centrality of 13 least-cost paths in West Sumatra, Indonesia, identified using Linkage Priority tool of the Gnarly Utilities. The current flow centrality is a measure of contribution of individual linkages relative to one another in facilitating ecological flows across the overall network connection. Higher CFC indicates more important linkages in maintaining the overall linkage network. The table was sorted out from the highest to the lowest current flow centrality values.

Link ID	Linkage		ED (km)	CWD (weighted km)	LCP (km)	CWD : ED	CWD : LCP	CFC
	From	To						
4	MAP I	MAP II	3.6	**36.6**	6.3	**10.3**	**5.8**	***16.5***
3	BGA	MAP I	27.4	417.2	48.8	15.2	8.5	9.8
10	MAN I	MAN II	**3.5**	269.2	5.3	78.0	***50.4***	9.5
11	MAN II	BAR	15.1	1,013.0	20.9	67.0	48.5	8.8
13	BAR	BPA	14.5	1,962.0	44.5	***135.1***	44.1	8.0
8	MAP II	BRB	43.7	1,081.1	***69.2***	24.7	15.6	7.9
1	BRU	BGA	3.5	51.4	**5.3**	14.6	9.8	7.7
5	MAP I	MAN I	9.5	317.1	13.4	33.3	23.7	7.1
6	MAP II	MAN I	7.0	355.0	13.2	50.6	26.9	5.5
9	MAP II	BAR	38.0	2,055.1	46.8	54.1	44.0	4.9
12	BRB	BAR	42.7	***2,393.0***	66.4	56.1	36.1	4.8
7	MAP II	MAN II	16.6	795.1	23.4	47.9	34.0	4.4
2	BRU	MAP I	***48.8***	1,010.2	64.1	20.7	15.8	**4.2**
Mean (±*SD*)			21.1 (16.9)	904.3 (790.2)	32.9 (24.5)	46.7 (34.2)	27.9 (16.0)	7.6 (3.3)

ED = Eucledian Distance, CWD = Cost-weighted Distance, LCP = Least-cost Path, BPA = Batang Pangean, BAR = Barisan, BRB = Bukit Rimbang – Bukit Baling, MAN I = Maninjau I, MAN II = Maninjau II, MAP I = Malampah – Alahan Panjang I, MAP II = Malampah – Alahan Panjang II, BGA = Batang Gadis, BRU = Barumun. Bolded values are the lowest, bolded values in Italic are the highest.

Table 17 Contribution of each land cover type to the overall modelled linkages aimed for the Sumatran tiger in West Sumatra, Indonesia, based on circuit theory and least-cost path analyses. It represents the total area of each land cover type composing the overall predicted linkages. The larger the area, the more important the land cover to the overall predicted linkages, thus for the tiger movement, and vice versa.

Land Cover	Area_(km^2)	%
Secondary Forest	1,177.4	59.5
Shrub	370.8	18.7
Agriculture	269.7	13.6
Primary Forest	73.1	3.7
Waterbody	45.9	2.3
Plantation	21.4	1.1
Settlement	10.9	0.5
Bare land	8.9	0.5
	1,978.1	100.0

Table 18 Number of pinch points in each linkage modeled using circuit theory and least-cost path analyses, in West Sumatra, Indonesia. Pinch points are locations within the least-cost corridors that are critical from disturbances for the conservation of landscape connectivity for the Sumatran tiger to traverse between two core tiger habitats. These pinch points identify bottle necks for Sumatran tiger movement, i.e., a narrowing low resistance land cover types due to physical features which should be of conservation priorities.

Link ID	LCP Length (km)	# Pinch Point
1	5.3	0
10	5.3	0
7	23.4	0
2	64.1	0
4	6.3	1
5	13.4	3
11	20.9	3
9	46.8	3
12	66.4	3
6	13.2	4
3	48.8	6
8	69.2	16
Total	383.0	39

FIGURES

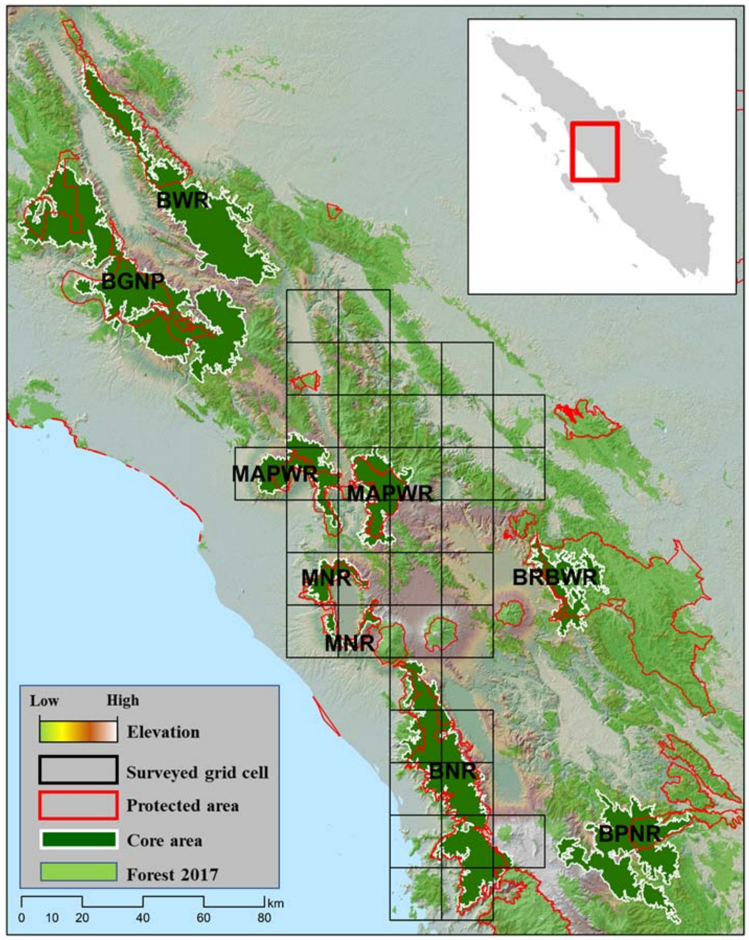

Figure 5 Project landscape in West Sumatra, Indonesia, which shows their function as potential structural connectivity (corridors) to facilitate Sumatran tigers' movement between North Kerinci Tiger Core Area and Batang Gadis National Park and adjacent protected areas. BWR = Barumun Wildlife Reserve, BGNP = Batang Gadis National Park, MAPWR = Malampah – Alahan Panjang Wildlife Reserve (i.e. MAP I and MAP II), MNR = Maninjau Nature Reserve, BRBWR = Bukit Rimbang Bukit Baling Wildlife Reserve, BNR = Barisan Nature Reserve, BPNR = Batang Pangean I and II Nature Reserve.

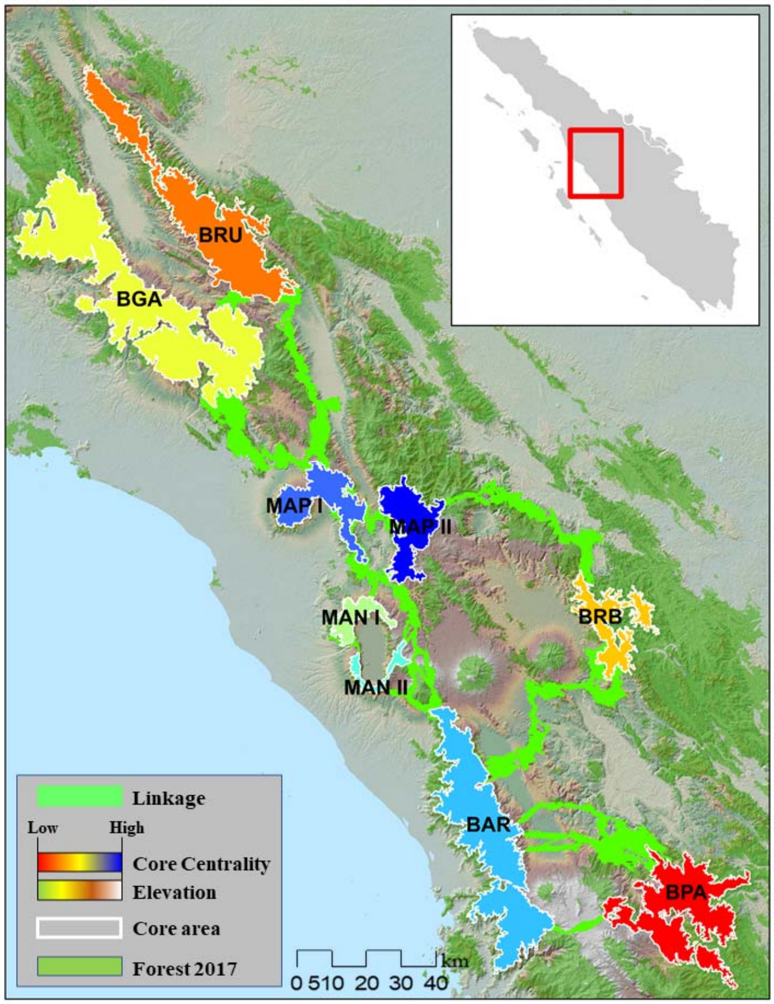

Figure 6 Core area centrality in West Sumatra, Indonesia, where warmer colors indicate more important cores to maintain the entire core network for the Sumatran tiger to move between tiger core areas and all possible linkage pathways (1,978.1 km^2) truncated by and within an Euclidean distance cutoff of 50 km. MAP I and MAP II of the Malampah – Alahan Panjang Wildlife (MAPR) Reserve were the two most important core areas in maintaining the integrity of the entire core area network when linkages were present. BWR = Barumun Wildlife Reserve, BGNP = Batang Gadis National Park, MNR = Maninjau Nature Reserve, BRBWR = Bukit Rimbang Bukit Baling Wildlife Reserve, BNR = Barisan Nature Reserve, BPNR = Batang Pangean I and II Nature Reserve.

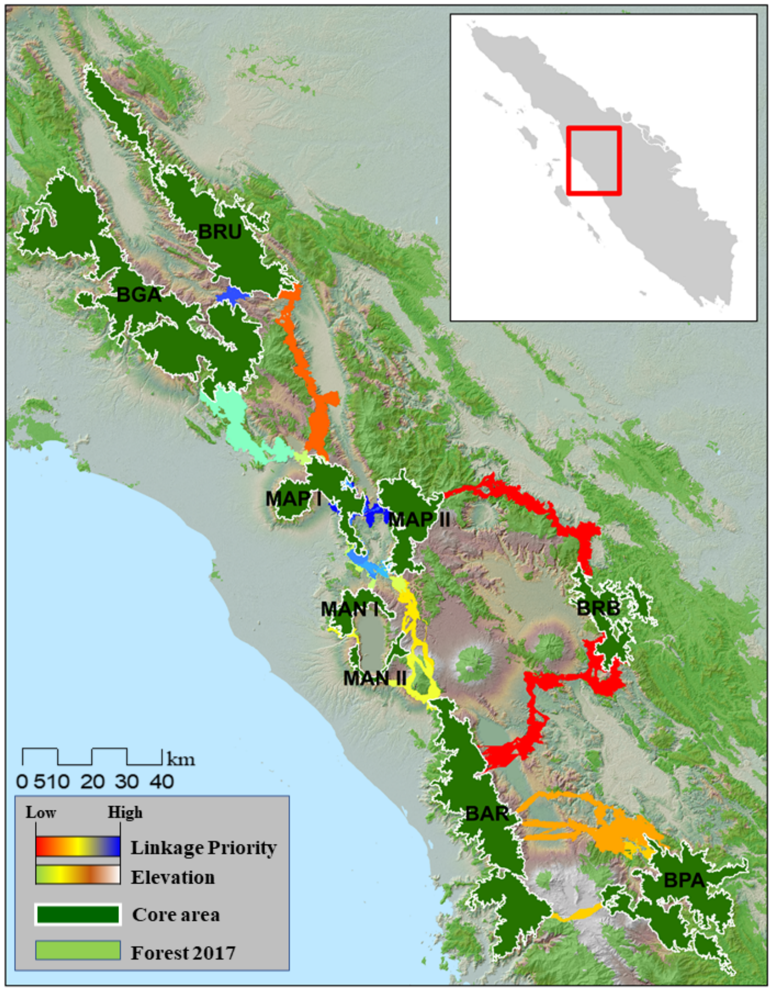

Figure 7 Linkage priority for Sumatran tigers in West Sumatra, Indonesia, modelled using a circuit theory and least-cost path analyses. Warmer colors indicate more important linkage to maintain the entire core network. Thirteen potential linkages were identified between pairwise core areas across the landscape where the linkage between MAP I and MAP II was the most important in maintaining the entire core area network. BRU = Barumun Wildlife Reserve, BGA = Batang Gadis National Park, MAN I and MAN II = Maninjau Nature Reserve, BRB = Bukit Rimbang Bukit Baling Wildlife Reserve, BAR = Barisan Nature Reserve, BPA = Batang Pangean I and II Nature Reserve.

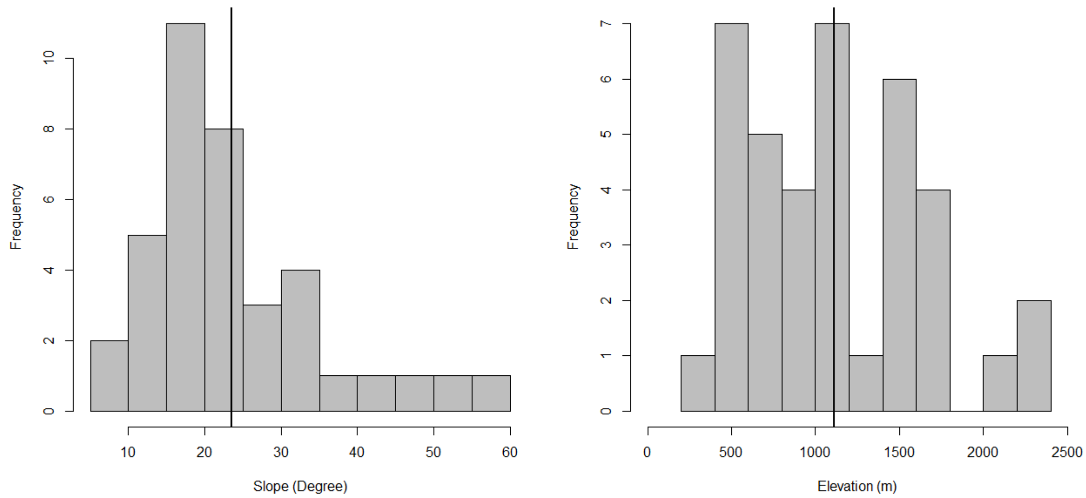

Figure 8 Geographic characteristics of the predicted habitat linkages of Sumatran tiger in West Sumatra, Indonesia. The overall linkages skewed to gentler slopes and at higher elevation with no obvious pattern in altitudinal distribution.

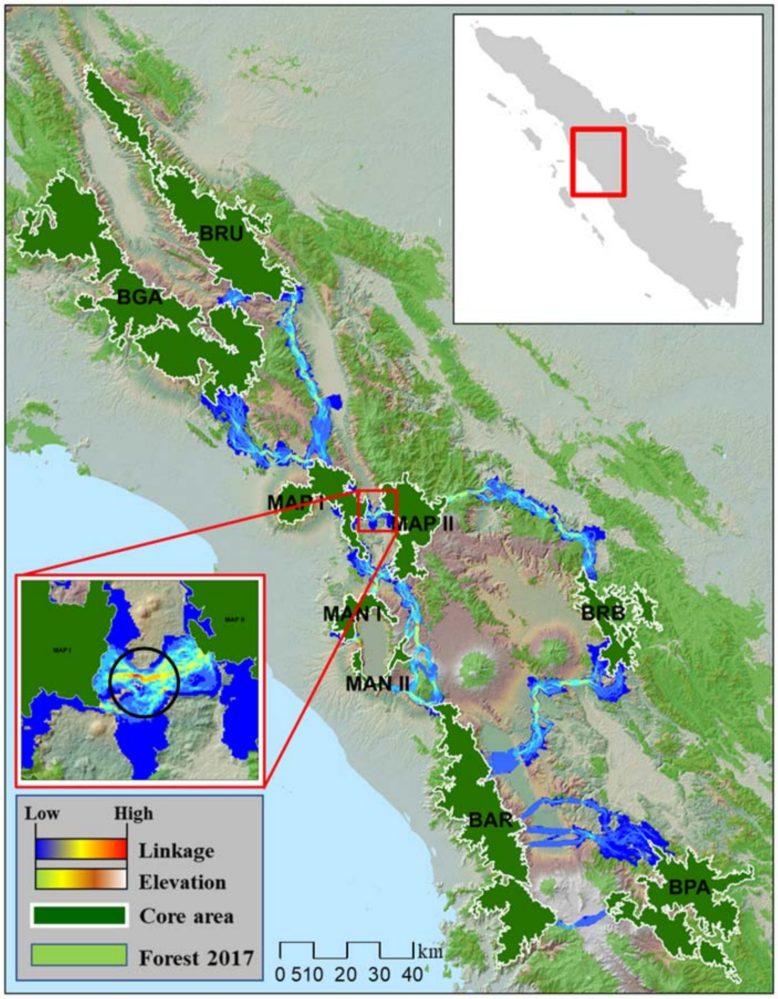

Figure 9 Pinch point map modelled for Sumatran tiger using a circuit theory and least-cost path analyses in West Sumatra, Indonesia. Warmer colors indicate that further degradation of quality of these areas and the surroundings can disproportionately compromise the quality of the connectivity. For an example, the black circle shows the location of pinch point between MAP I and MAP II (Malampah – Alahan Panjang Wildlife Reserve). BRU = Barumun Wildlife Reserve, BGA = Batang Gadis National Park, MAN I and MAN II = Maninjau Nature Reserve, BRB = Bukit Rimbang Bukit Baling Wildlife Reserve, BAR = Barisan Nature Reserve, BPA = Batang Pangean I and II Nature Reserve

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Appendix A

MODEL SELECTION BASED ON AIC_C VALUES FOR SUMATRAN TIGER DENSITIES IN 29 CAMERA TRAP SAMPLING SESSIONS FROM 16 SITES ACROSS THE SUMATRAN ISLAND, INDONESIA, COLLECTED BETWEEN 1999 AND 2017.

Model	Detection Function	npar	logLik	AIC	AICc	dAICc	AICcwt
D(group,protection),g0(sex,group), σ(sex,group)	Hazard halfnormal	16	-2167.68	4367.36	4370.19	0	0.5589
D(group,protection,forest),g0(sex,group), σ(sex,group)	Hazard halfnormal	17	-2167.68	4369.36	4372.56	2.369	0.171
D(group), g0(sex, group), σ(sex,group)	Hazard halfnormal	15	-2170.10	4370.21	4372.70	2.503	0.1599
D(habitat,protection), g0(sex,group), σ(sex, group)	Hazard halfnormal	15	-2170.48	4370.95	4373.44	3.246	0.1103
D(session), g0(sex,group), σ(sex,group)	Hazard halfnormal	40	-2156.90	4393.80	4413.33	43.133	0
D(session), g0(sex), σ(sex)	Hazard halfnormal	34	-2194.16	4456.32	4470.00	99.809	0
D(session), g0(sex,habitat), σ(sex,habitat)	Hazard halfnormal	38	-2189.51	4455.02	4472.46	102.267	0
D(session, g0(.),σ(.)	Hazard halfnormal	32	-2209.55	4483.09	4495.09	124.898	0

npar is number of parameters modelled
logLik is logit link
AIC is Akaike Information Criterion
AICc is AIC for small sample
ΔAICc is the different between a model with the best model
AICcwt is AIC weight

Appendix B

AN ABUNDANCE MODEL BASED ON A POISSON DISTRIBUTION FOR THE DETECTION MODEL TO ADDRESS ABUNDANCE-INTRODUCED HETEROGENEITY ASSUMING A MARKOVIAN DEPENDENCE AMONG SAMPLES.

Let's consider a case where data are collected along transects at $j=1,2,\ldots J$ independent sites in a large landscape. Let's further assume that each transect is subdivided into $k=1,2,\ldots K$ segments of equal length (e.g. 1 km) and for each segment the presence or absence of each species $i=1,2,\ldots I$ is recorded. These segments are considered our replicates that allow us to estimate a detection probability. If all the segments were sampled randomly and independently, the detection probability for each segment would be the product of (1) Pr(species present on segment) and (2) Pr(species detected | species present on segment) (Hines et al., 2010). Given this confusion between presence and detection we cannot estimate occupancy at the segment level, but we can still estimate overall detection probability for the site. However, for our transect, segments are not independent, and we expect a correlation between adjacent segments as can be seen in cluster sampling. This correlation can be caused by individual animals walking along a trail covering multiple segments or by animal populations occurring in clusters within a site due to small-scale resource availability. We therefore need to account for this correlation in our model in order to avoid biased estimates (Hines et al., 2010).

Our data h_{ijk} consists of detections/non-detections for each species in each segment at each site. We define the latent variable a_{ij} as the abundance of species i at site j (we don't assume that is a true measure of abundance but rather an indicator for frequency of use of the site by a species) and model a_{ij} as a Poisson distribution with rate parameters λ_{ij}.

$$a_{ij} \sim Poisson(\lambda_{ij})$$

$$\log(\lambda_{ij}) = Xobs_j \beta obs_i$$

where $Xobs_j$ is a vector of environmental covariates for site j with the first element set to 1 for the intercept, and βobs_i is the corresponding vector of species-specific regression coefficients for species i. The regression coefficients were modelled hierarchically and species-level parameters were treated as random effects, e.g., $\beta_i \sim$ Normal(μ, σ^2), where μ and σ^2 are the mean and the variance of coefficient β in the wider community of species from which the study species were drawn.

A second latent variable y_{ijk} indicates whether a species is present on a particular segment (y_{ijk}=1 for present) with θ_{ij} being the probability of a single individual of that species being present and the expression $1 - (1 - \theta_{ij})^{a_{ij}}$ defining the probability that at least one individual is present given abundance a_{ij} and the segment therefore is occupied. To model the spatial dependency we define two cases: θ_{ij} the probability that the species is present in a segment if it was not present in the previous segment ($y_{ij(k-1)} = 0$) and θ'_{ij} the probability that the species is present if it was also present in the previous segment ($y_{ij(k-1)} = 1$).

$$y_{ijk} \sim Bernoulli(1 - (1 - ((1 - y_{ij(k-1)})\theta_{ij})(y_{ij(k-1)}\theta'_{ij}))^{a_{ij}})$$

Finally, p_{ij} is the probability that signs are detected when a species is present on a segment present and

$$h_{ijk} \sim Bernoulli(p_{ij} y_{ij})$$

Both θ_{ij} and p_{ij} can be modeled as a function of covariates.

The occupancy probability ψ_{ij} is derived from the abundance as the probability that at least one individual is present in the sampling unit:

$$\psi_{ij} = 1 - \exp(-\lambda_{ij})$$

Appendix C

RESISTANCE LAYER PARAMETERS DEVELOPED FOR CONNECTIVITY ANALYSIS BETWEEN NINE SUMATRAN TIGER'S CORE AREAS IN A HUMAN-DOMINATED LANDSCAPE OF WEST SUMATRA, INDONESIA.

Data Layer	Class ID	Class Description	Extra Info	Habitat Value	Resistance	Expand Cells
landcover	1	Primary Forest	KLHK (2011)	0	0	0
landcover	2	Secondary Forest	KLHK (2011)	0	0	0
landcover	3	Plantation	KLHK (2011)	0	67	0
landcover	4	Agriculture	KLHK (2011)	0	100	0
landcover	5	Shrub	KLHK (2011)	0	2	0
landcover	6	Bare land	KLHK (2011)	0	6	0
landcover	7	Swamp	KLHK (2011)	0	30	0
landcover	8	Settlement	KLHK (2011)	0	100	0
landcover	9	Mining	KLHK (2011)	0	100	0
landcover	10	Waterbody	KLHK (2011)	0	90	0
road	1	Primary	OpenStreetMap©	0	100	1
road	2	Secondary	OpenStreetMap©	0	100	1
road	3	Settlement	OpenStreetMap©	0	100	1
road	4	Tertiary	OpenStreetMap©	0	60	1
slope	1	Flat (up tp 7.9 degree)	Natural break	0	0	0
slope	2	Sloping (>7.9 - 17.4 degree)	Natural break	0	0	0
slope	3	Tilting (>17.4 - 28.9 degree)	Natural break	0	0	0
slope	4	Steep (>28.9 degree)	Natural break	0	60	0
elevation	1	Low elevation (up to 300 m asl)	Laumonier et al. (2008)	0	0	0
elevation	2	Low elevation (>300 - 800 m asl)	Laumonier et al. (2008)	0	0	0
elevation	3	Lower elevation (>800 - 1,300 m asl)	Laumonier et al. (2008)	0	0	0

Data Layer	Class ID	Class Description	Extra Info	Habitat Value	Resistance	Expand Cells
elevation	4	Higher elevation (>1,300 - 2,500 m asl)	Laumonier et al. (2008)	0	60	0
elevation	5	Higher elevation (>2,500 m asl)	Laumonier et al. (2008)	0	80	0

AUTHORSHIP

CHAPTER 1. REVISITING THE EXISTING ESTIMATES OF SUMATRAN TIGER POPULATIONS FROM MULTIPLE STUDIES.

Hariyo T. Wibisono[1,2,3], Kyle P. McCarthy[1], Mathias Tobler[2], Yoan Dinata[4], Donny Gunaryadi[5], William Marthy[6], Irene Margareth Romaria Pinondang[3], Rizki Amalia Adinda Putri[3], Febri Anggriawan Widodo[7]

[1]Department of Entomology and Wildlife, University of Delaware, DE, USA
[2]Population Sustainability, San Diego Zoo Wildlife Alliance, San Diego, CA, USA
[3]SINTAS Indonesia, Bogor, West Java, Indonesia
[4]Zoological Society of London – Indonesia Programme, Bogor, Indonesia
[5]Fauna & Flora – International – Indonesia Programme, Jakarta, Indonesia
[6]Wildlife Conservation Society – Indonesia Program, Bogor, Indonesia
[7]WWF Indonesia, Jakarta, Indonesia

CHAPTER 2. AN ISLAND-WIDE ASSESSMENT OF THE DISTRIBUTION OF THE SUMATRAN TIGER IN RELATION TO ITS MAIN PREY SPECIES AND MAYOR THREATS IN SUMATRA, INDONESIA.

Hariyo T. Wibisono[1,2,3], Kyle P. McCarthy[1], Mathias Tobler[2], Yoan Dinata[4], Donny Gunaryadi[5], William Marthy[6], Rizki Amalia Adinda Putri[3], Febri Anggriawan Widodo[7].

[1]Department of Entomology and Wildlife, University of Delaware, DE, USA
[2]Population Sustainability, San Diego Zoo Wildlife Alliance, San Diego, CA, USA
[3]SINTAS Indonesia, Bogor, West Java, Indonesia
[4]Zoological Society of London – Indonesia Programme, Bogor, Indonesia
[5]Fauna & Flora – International – Indonesia Programme, Jakarta, Indonesia
[6]Wildlife Conservation Society – Indonesia Program, Bogor, Indonesia
[7]WWF Indonesia, Jakarta, Indonesia

CHAPTER 3. MODELING POTENTIAL CONNECTIVITY OF FRAGMENTED HABITATS OF SUMATRAN TIGER IN WEST SUMATRA, INDONESIA.

Hariyo T. Wibisono[1,2,3], Kyle P. McCarthy[1]

[1]Department of Entomology and Wildlife, University of Delaware, DE, USA
[2]Population Sustainability, San Diego Zoo Wildlife Alliance, San Diego, CA, USA
[3]SINTAS Indonesia, Bogor, West Java, Indonesia