

Prioritizing habitat core areas and corridors for a large carnivore across its range

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Abstract

With increasing loss and fragmentation of habitats driving the emerging global extinction crisis, paired with limited resources for conservation, there is an immense need to identify and prioritize the most important areas for conservation actions. The goal of this study was to measure, map and rank core areas and corridors for mainland clouded leopard (a forest indicator species) across its entire range in Southeast Asia. We used an empirically based landscape resistance model developed from range-wide camera survey data, cumulative resistant kernel analysis to define core areas and least-cost network analysis to identify corridors for long-distance dispersal. We then ranked core areas based on their strength and size, and corridors based on their strength and the strength of core areas they connect. We found that the most important core areas and corridors are concentrated in Southeast Asia, largely in Myanmar, Laos and Malaysia. Myanmar contains nearly the entirety of the first and third highest ranked core areas, as well as the most important network of corridors in SE Asia. Almost the entire territory of Laos constitutes one large potential core area, ranked as the second most important across the clouded leopard's range. A large number (22) of very small (<8000 km²) and fairly isolated core areas are in China. Only 24% of clouded leopard core areas and 17% of corridors are protected. This is the first example of using empirical models to prioritize conservation actions across the full range of a large carnivore. Our analysis identifies the location, size and connectivity of the most important remaining habitats of the clouded leopard across its range, which could provide quantitative guidance in the efforts to maximize the efficacy of regional conservation initiatives to conserve this species and the ecosystems it inhabits.

Introduction

Wildlife conservation efforts have mainly focused on establishing networks of protected areas (Naughton-Treves, Holland & Brandon, 2005). However, many existing protected areas are small in size and do not support viable populations of many native species, particularly large mammals (Opdam, Steingröver & Van Rooij, 2006). Viability of wildlife populations requires protection of core population areas and dispersal linkages between them (Cushman, 2006; Keyghobadi, 2007). Connectivity protects metapopulations from demographic stochasticity and prevents inbreeding depression (e.g. Packer *et al.*, 1991). With very limited financial resources for protecting landscapes, and with rapidly expanding human populations and economies putting increasing pressure on land use across Asia, it is crucial to identify and prioritize core habitats and ecological corridors for endangered wildlife. To provide the scientific rigor needed for political support, these efforts should be based on extensive empirical

data on species occurrence, movement or genetic differentiation (e.g. Rudnick *et al.*, 2012; Cushman *et al.*, 2018). Furthermore, it should be based on approaches providing strong spatial predictions of conservation value of all locations in the study system, such as spatially synoptic methods to predict and rank the importance of both core areas and corridors (e.g. Cushman, Landguth & Flather, 2013b; Cushman *et al.*, 2018).

Rapid destruction of tropical forest ecosystems is a major threat to biodiversity (Giam, 2017). Southeast Asia has the highest deforestation rate worldwide, and the region may lose three-quarters of its original forests and up to 42% of its biodiversity within 100 years (Sodhi *et al.*, 2004). The clouded leopard *Neofelis nebulosa* ranges across Southern and Southeast Asia and is highly affected by rapidly changing landscapes and growing human pressure. Direct exploitation and habitat loss (particularly of primary evergreen tropical rainforest) resulted in a population decline of at least 30% between 1993 and 2014 (Grassman *et al.*, 2016). This

rate will likely to grow with accelerating land use change in the region (Cushman *et al.*, 2017; Macdonald *et al.*, 2018). The species is listed as Vulnerable on the IUCN Red List of Threatened Species (Grassman *et al.*, 2016), and has been recently added to Indian Recovery Programme for Critically Endangered Species (National Board for Wildlife 2018). In addition to its vulnerability, the clouded leopard is also a highly charismatic species (Macdonald *et al.*, 2015), with high capacity to serve as a conservation umbrella for other felids (Dickman *et al.*, 2015) and with great ambassadorial potential for conservation of Southeast Asian forest and its fauna (Macdonald *et al.*, 2017). This makes the clouded leopard a potentially useful focal species for conservation of forest ecosystems in the region.

The overall goal of this paper was to use empirically based, synoptic modelling to optimize the allocation of limited resources for biodiversity conservation in Southeast Asia. In this paper, we model and rank core habitats and corridors for the mainland clouded leopard across its range to provide a quantitative basis for conservation prioritization in Southeast Asia. We based our analysis on spatially optimized habitat models derived from an extensive dataset of clouded leopard occurrences collected across the entire range of the species (e.g. Macdonald *et al.*, 2019), and on synoptic approaches (*sensu* Cushman, Lewis & Landguth, 2014) to model landscape connectivity.

Materials and methods

Resistance surface

The resistance surface that underpins our analysis was based on clouded leopard habitat suitability (Macdonald *et al.*, 2019). The authors built a scale-optimized (*sensu* McGarigal *et al.*, 2016) habitat suitability model based on presence/absence data from 2948 camera stations, set within 45 sampling grids in nine countries across clouded leopard range. To test relationships between clouded leopard detection and 46 biologically informative variables at eight spatial scales (250 m–32 km), the authors used a scale-optimized generalized linear mixed-effect model. The final model included 10 variables: camera effort, percentage of forest cover, percentage of closed forest, percentage of mosaic habitat, mean annual precipitation, mean compound topographic index, slope position (mean and standard deviation), correlation length (i.e. extent) of protected areas and grassland/shrubland habitats (Macdonald *et al.*, 2019). The model revealed that clouded leopard occurs in areas of extensive forest cover, often within protected areas, and prefers upland or ridge locations and high precipitation.

We used a negative exponential transformation of the habitat suitability layer to produce a resistance surface for connectivity modelling. The negative exponential transformation is widely regarded as the best way to transform habitat suitability to resistance to movement (Mateo-Sánchez *et al.*, 2015; Keeley, Beier & Gagnon, 2016). The exponential transformation used was:

$$\text{Exp}(-1 \times \text{Habitat suitability}/1.5) + 0.78.$$

Dispersal source points

We distributed 10 000 points (reflecting the estimated clouded leopard population size in SE Asia – IUCN Red List 2017) probabilistically with a density proportional to the landscape suitability for clouded leopard (e.g. Cushman *et al.*, 2016). This was done in several steps. First, we rescaled the habitat suitability layer between 0 and 1. Second, we produced a raster layer with randomly and uniformly distributed values between 0 and 1. We then subtracted the random raster from the rescaled suitability layer and assigned all pixels with positive value as potential occurrences. Finally, we randomly selected 10 000 points from these potential occurrence pixels.

Connectivity analysis

We applied cumulative resistant kernel (Compton *et al.*, 2007) and factorial least-cost path (Cushman, McKelvey & Schwartz, 2009) approaches to the source points and resistance surface described above using UNICOR (Landguth *et al.*, 2012). The cumulative resistant kernel produces a prediction of the total movement density across the landscape, and identifies the main pattern of synoptic connectivity and core habitat areas (Kaszta *et al.*, 2018). The surface is calculated by summing all individual least-cost kernels from all dispersal source points (Compton *et al.*, 2007). The factorial least-cost path method complements the resistant kernels by defining narrow linkages in the landscape where the movement pattern is constrained in the network of least-cost paths connecting all source points. The final paths are computed by summing the least-cost paths between all possible pairs of points (Cushman *et al.*, 2013a).

Both cumulative resistant kernels and factorial least-cost paths account for species dispersal abilities, which is essential for accurate prediction of landscape-scale connectivity patterns (Cushman *et al.*, 2013b, 2016). Dispersal distances are uncertain for clouded leopards; however, a number of studies have found relationships between maximum dispersal distances and home range size (Bowman, Jochen & Fahrig, 2002; Whitmee & Orme, 2013). With the average home range of *N. nebulosa* varying between 23 and 45 km², clouded leopard dispersal ability is estimated to be 160–252 km (Macdonald *et al.*, 2018). We therefore chose a threshold of 250 000 cost units for cumulative resistant kernels, reflecting a plausible upper end of natal dispersal distances for the species, and 1 250 000 for least-cost paths to model long-distance connections beyond the extent of locally connected populations (Hearn *et al.*, 2018; Macdonald *et al.*, 2018).

Identifying and ranking core areas and corridors

To define core areas, we used a threshold value of the 70th percentile of the cumulative kernel surface. This was chosen to exclude the bottom tail of the kernel distribution, which corresponds to areas of very low predicted rate of clouded

leopard movement. We ranked these key patches based on their strength (sum of kernel values) and size (e.g. Cushman *et al.*, 2018). The final ranking value for the core areas prioritization represented the averaged values of these sub-rankings. We then identified the networks of corridors linking core areas and we ranked them based on their strength (sum of least-cost path values outside of core areas) multiplied by the average strength of the core areas they link (Cushman *et al.*, 2018).

We calculated the percentage of each SE Asian nation that was covered by core dispersal areas and corridors. Furthermore, we compared the strength of the core areas and corridors across countries by calculating the ratio of the sum of kernel values/least-cost paths within each country to the sum of kernel values/least-cost paths in all of SE Asia. Finally, we also calculated the percentage of core dispersal areas and corridors within protected areas classified by IUCN as category I–IV, using the official shapefile of protected areas provided by IUCN and updated on January 2019.

Results

Core areas ranking

We identified 42 core areas (Fig. 1), of which 15 are larger than 5000 km², and 10 are larger than 10 000 km². The largest and most important core areas are in Myanmar, Laos and Peninsular Malaysia. The most fragmented part of the clouded leopard range is in China, with only one predicted core area exceeding 8000 km². 24.2% of the predicted core areas in SE Asia are covered by IUCN-protected area categories I–IV (Fig. 1).

The first and third most important core areas, based on size and strength, lie almost entirely within Myanmar's borders. Laos contains almost the entirety of the second most important core area, which is also partly in Myanmar. The highest number of core areas (22) falls within China; however, all of them are of low rank as a result of small size and low summed kernel value (Figs 2 and 3a).

Among the SE Asian countries, Laos has the highest percentage of its territory comprising predicted core area for clouded leopard (78.4%), followed by Myanmar (44.9%) and Bhutan (44.9%). In contrast, only very small proportions of China and India are classified as core areas for clouded leopard dispersal (0.6% and 4%, respectively) (Fig. 4a).

Myanmar substantially outranks the other countries based on core areas strength, containing 46.8% of the total cumulative kernel density. Second in importance, based on predicted cumulative kernel value, is Laos with 21.2%. The weakest core areas (the lowest predicted density of movement proportionally to the total density of movement in SE Asia) were predicted to be those within China (0.8%), Bhutan (1.8%), Bangladesh (1.8%) and Cambodia (1.9%) (Fig. 4b).

Corridor ranking

We delineated 54 corridor networks linking core areas, all of which were larger than 1000 km², with 10 larger than 50 000 km² (Fig. 5). 17.7% of these corridors fall within protected areas. The most important corridor network, based on the combination of its strength (sum of least-cost paths values) and the strength of the core areas it connects, lies mainly in Myanmar and partly in China, linking the two most important core dispersal areas (Fig. 5). The network of corridors ranked second links two parts of the most important core area in its weakest point, enhancing connectivity within that key area. The corridors network ranked third links the second most important predicted core area with the eastern part of SE Asia, through Vietnam to China. Networks of corridors with the lowest predicted ranks lie in China, as they link sets of relatively small core areas with weak networks of local corridors (Figs 4b and 5).

Vietnam contains extensive networks of predicted corridors, which represent 33% of the country's territory and 9.3% of the total corridor strength in SE Asia. In contrast, although corridors in China occupy only 10.4% of its territory, the total strength of these corridors represents 35.6% of the total sum of the least-cost path values in entire SE Asia.

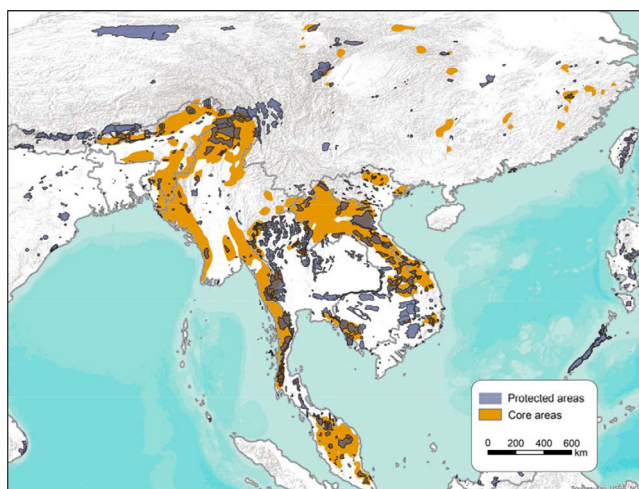


Figure 1 Clouded leopard core dispersal areas and network of protected areas.
[Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

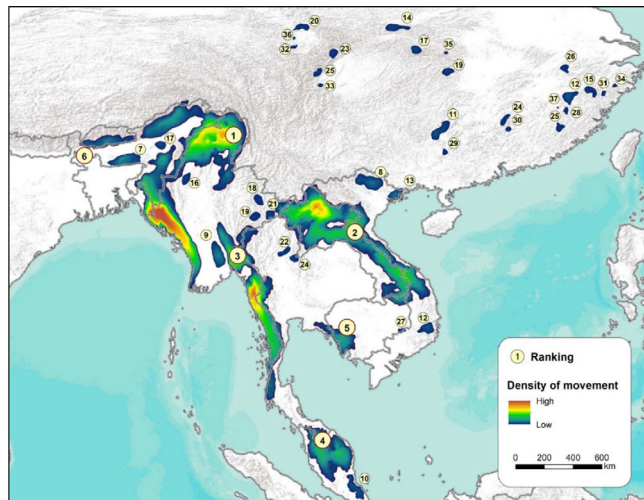


Figure 2 Ranking of core habitat areas for clouded leopard across the species range, with strength of core areas expressed as density of movement. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

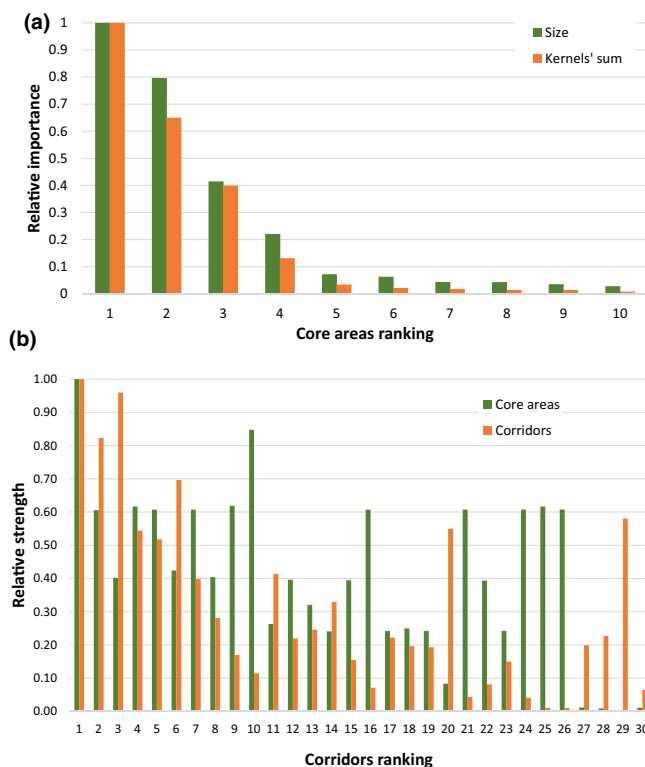


Figure 3 (a) Relative size and sum of kernel values of each core area and (b) components of the corridors networks' ranking, including strength of core areas linked by corridors (averaged sum of kernel values) and strength of each corridor network (sum of least-cost path values). [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

This is the highest among all considered countries, reflecting the great extent of China and the cumulative value of many weak corridors. Myanmar, after China, is second in the strength of corridors lying within its borders, representing 24% of the total strength of corridors in SE Asia (Fig. 4).

Discussion

Growing human population paired with pressure for development drives accelerating loss of habitat across Southeast Asia

(Cushman *et al.*, 2017; Macdonald *et al.*, 2018). Given the combination of very high biodiversity value, rapidly increasing human impacts on ecosystems, and limited economic and political ability for large-scale conservation initiatives, it is essential to optimize conservation actions so to achieve the greatest biodiversity benefits. Spatial ranking of core areas and corridors across large, multi-national extents is a powerful framework to accomplish this (e.g. Cushman *et al.*, 2016, 2018). Spatial planners and policy-makers in Southeast Asia should prioritize conservation actions by grounding

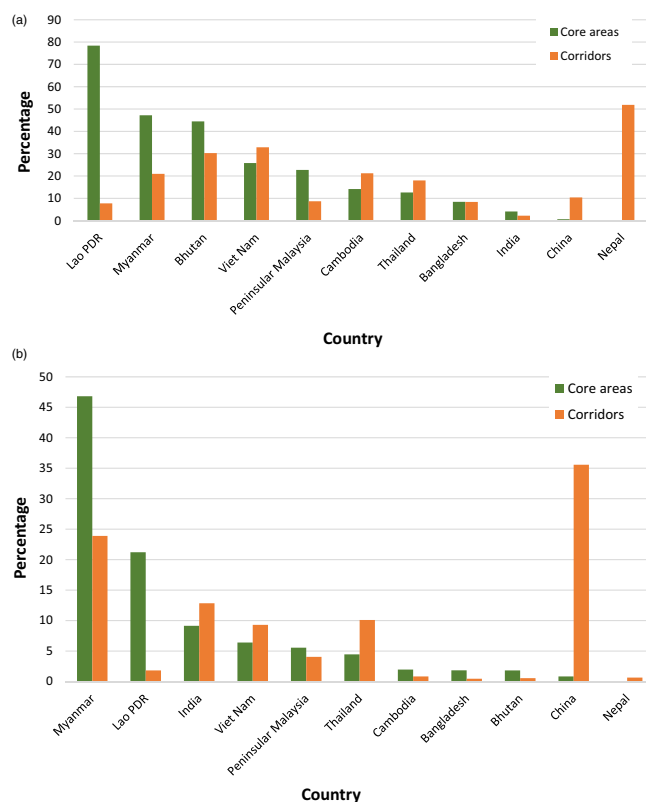


Figure 4 (a) Percentage of countries' territory represented by clouded leopard core dispersal areas and corridors and (b) proportion of core areas and corridor strength (sum of kernel values and sum of least-cost paths) in each country to the total strength of core areas and corridors. [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://onlinelibrary.wiley.com).]

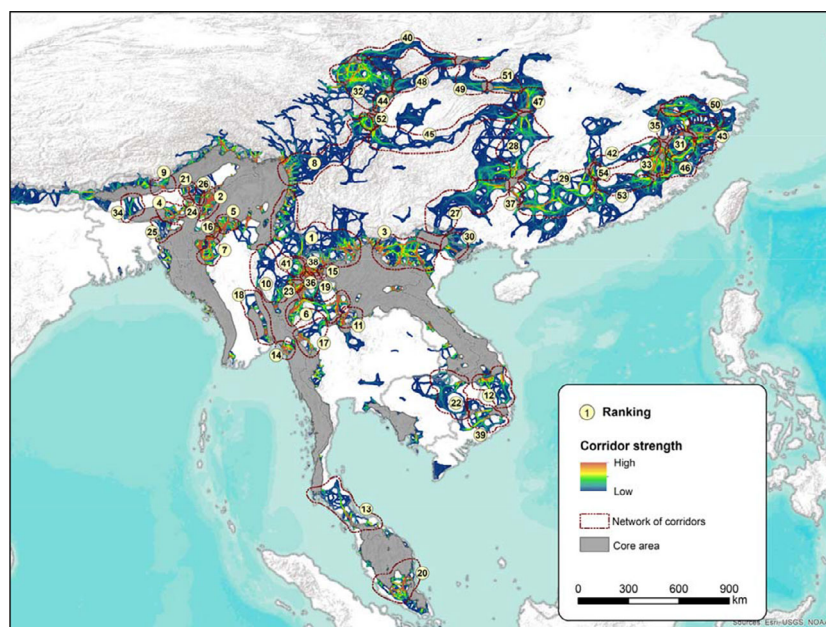


Figure 5 Ranking of corridors' networks linking clouded leopard core areas across whole species range. [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

them in thorough scientific evidence and robust assessments of the risks, benefits and trade-offs of different alternative actions (e.g. Kaszta *et al.*, 2019). This work presents the first comprehensive, empirically based evaluation of core habitat and connectivity areas for any large carnivore across its

entire range, combining connectivity modelling with spatial prioritization of core areas and corridors.

We mapped and ranked 42 core areas and 54 networks of corridors linking the core areas across Southeast Asia. Macdonald *et al.* (2019) identified 24 habitat patches for clouded

leopard across Southeast Asia. We refined and extended those predictions in this study. There are several important differences between the Macdonald *et al.*'s (2019) paper and its findings and the approach and the results presented in this study. Most importantly, the Macdonald *et al.*'s (2019) paper did not consider connectivity *per se*, but based core areas and linkages only on habitat suitability predictions, without accounting for species movement and dispersal. Several past studies have shown that habitat quality alone is a relatively weak proxy for population size (Van Horne, 1983; Cushman *et al.*, 2008), movement patterns (Cushman *et al.*, 2014; Shirk *et al.*, 2015) and long-term population connectivity (Wasserman *et al.*, 2010). Therefore, it is preferable to use empirically based, spatially synoptic approaches to infer population core areas and connectivity among them (Cushman *et al.*, 2013a).

Accordingly, we used spatially synoptic movement and connectivity modelling approaches to quantitatively map and rank both core areas and corridors across the full range of the mainland clouded leopard. This use of formal connectivity modelling is theoretically much stronger than using habitat suitability maps directly for answering questions about core areas for movement and corridors linking them (e.g. Shirk *et al.*, 2015). Although we identified many of the same core areas as Macdonald *et al.* (2019), our ranking is not only based on their size (as in Macdonald *et al.*, 2019) but also on the kernel value, which provides the best spatial prediction (incidence function) of movement through each pixel (Kaszta *et al.*, 2018). Finally, and most importantly, our analysis identified and mapped many (dozens) corridors, which were formally ranked based on their strength and importance. These corridors are spatially explicit and optimized by the factorial least-cost-path algorithm, which gives the ability to assess both their strength and to delineate precisely where they run through the landscape, which is not possible from an assessment based solely on habitat quality in the absence of formal connectivity modelling (e.g. Macdonald *et al.*, 2019).

We found that the largest and most important core areas and corridors are concentrated in Myanmar, Laos, Peninsular Malaysia, Vietnam, Assam (India) and Bhutan, which collectively correspond to the Indo-Burma biodiversity hotspot (Myers *et al.*, 2010). Myanmar stands out as disproportionately important to clouded leopard habitat extent (Macdonald *et al.*, 2019), and to the core areas and corridors identified in this paper. Specifically, Myanmar contains the core areas ranked as first and third in our analysis, as well as the northern part of the core area ranked as second. Furthermore, these areas are linked by networks of corridors in the eastern part of the country, including what we predicted to be the most important corridor network for clouded leopards in all of SE Asia. It is worth noting that the core area ranked first and third overlap with states struggling with armed ethnic conflict, in particular: Rakhine, Kachin and Kayah states (Uppsala Conflict Data Program, 2019), which poses a major obstacle to conservation efforts.

Kaszta *et al.* (2020) predicted that growing development pressure in Myanmar, fuelled by the international

investments mainly from China (e.g. foreseen by the Belt and Road Initiative) and India (e.g. Indian Highway), is a potential huge threat to the clouded leopard population and the forest ecosystems on which it depends. The simulations conducted by Kaszta *et al.* (2020) predicted that major developments in the country (some already under construction like the Indian Highway) may lead to a 36% decrease in clouded leopard landscape connectivity and a 29% decrease in clouded leopard population size, accompanied by a substantial reduction in its genetic diversity.

Our results show that almost the entire territory of Laos constitutes one extensive potential core area for clouded leopards, ranked as second most important in SE Asia. It is important to note that our analyses do not directly include poaching pressure or the historical and current geopolitical situation of the different nations in the region. Estimates for clouded leopard population in Laos are largely unknown. There are only a few local studies from Nakai-Nam Theun NPA (Coudrat *et al.*, 2014) and Nam Et-Phou Louey NPA (Johnson, Vongkhamheng & Saithongdam, 2009) documenting presence of clouded leopard in these parks. Although there is limited scientific evidence, it is believed that the population of clouded leopards across Laos has been greatly reduced due to high hunting and poaching pressure (especially from neighbouring Vietnam) (Harrison *et al.*, 2016). Our analysis shows extensive habitat potential to rebuild clouded leopard populations in Laos, and at the same time identifies the areas of highest conservation importance and connections to key core areas in neighbouring countries which can form the foundation for a data-driven conservation strategy.

Apart of the three largest core areas, clouded leopard habitat is highly fragmented across SE Asia. Our results show that the Cardamom core area in Cambodia (fifth in the core area ranking) is disconnected from any other clouded leopard core areas. The highly degraded state of forest ecosystems in southern China is reflected in our predictions of very low size and high fragmentation of core areas in that country. Specifically, we identified 22 areas in China that qualified as 'core habitats' by our criteria, all of which were below 8000 km², and which collectively represent a very small proportion of the Chinese territory. Furthermore, only three of these are partially protected. The Chinese core areas are fairly isolated from the larger core areas in Southeast Asia. Our analysis shows that the only link between Chinese key habitats and the set of large core areas in the southwest is through a network of corridors in Northern Yunnan and Sichuan and indirectly through two sets of corridors in the northern part of Guangxi province and in Vietnam. However, the latter corridors are relatively weak. We believe that these sets of corridors (in particular the one in Yunnan and Sichuan), which are currently protected only to a very small extent, are extremely important in maintaining clouded leopard populations in China.

Our analysis indicates substantial differences in the structure and strength of landscape connectivity between countries, which has important implications for the conservation priorities in each of the countries, and for regional, trans-boundary conservation efforts (e.g. Cushman *et al.*, 2018).

For example, Laos has very extensive and well-connected forest-dominated landscapes. However, there are very low population densities of a wide range of wildlife in Laos compared to the habitat carrying capacity due to hunting and poaching pressure. Our analysis suggests that conservation effort in this country should focus on fighting illegal poaching, while protecting critical core and linkage habitats, such as those prioritized in this study.

In contrast, our results show that China has experienced severe loss of habitats and a high degree of habitat fragmentation reflected in small and poorly connected core areas. Therefore, we believe that conservation actions in China should focus on habitat restoration and expansion of protected areas in strategic locations to expand the existing core areas and preserve the connectivity between the most important ones. Moreover, the rapid economic development and accelerating urban migration in China also provide a globally unique opportunity for ecological restoration. Specifically, as China grows more wealthy and the human population increasingly abandons rural villages for cities, China could achieve vast improvements in the ecological condition of its ecosystems and potentially recovery of its native wildlife populations. An analogous recovery of forest ecosystems occurred in the Eastern United States in the 20th century. The many small core areas and the vast network of weak linkages we predicted across southern and eastern China may provide the nuclei and network for effective, regional-scale ecological restoration in the region.

Myanmar emerged from our analysis as a critical nation for conservation of clouded leopard habitat core areas and corridors. Our results identify clear conservation priorities in Myanmar, including protection of the most important core areas and corridor linkages in all of Southeast Asia. In addition, like in Laos and elsewhere in the region, it is essential to rapidly reduce direct losses of clouded leopards and other wildlife through illegal wildlife trade and poaching while protecting large and well-connected core areas of habitat.

While our analysis provides useful information for conservation prioritization within each nation individually, perhaps its greatest strength is its regional and range-wide scope, which enables the analysis to observe patterns without artificial distortion of national boundaries and the edge effects analyses limited to political jurisdictions create. Trans-boundary conservation prioritization based on empirical models and synoptic connectivity assessments are essential to conserve populations of wide-ranging species that exist at low densities and have large dispersal abilities (e.g. Cushman *et al.*, 2016, 2018).

Our results showed that only 1/4 of the clouded leopard core habitats and <1/5 of corridors in SE Asia are currently protected by any form of legal conservation status (IUCN and UNEP-WCMC, 2019). This shows a large mismatch between the existing protected area network and the most important forest habitats for this species, and argues for a large and ambitious expansion of protected areas, ideally prioritizing the highest ranked core areas and corridors. Furthermore, even within protected areas, management, law enforcement and level of corruption greatly varies across SE

Asian countries (D'Cruze & Macdonald, 2015), and often severely degrades the effectiveness of protected areas.

Conservation of large carnivores, clouded leopard among them, requires a combined strategy incorporating the preservation of remaining core habitats and linkages between them, with reduction of direct losses of populations from poaching (Cushman *et al.*, 2018). Protecting large core areas and the key dispersal linkages among them is critical to support long-term viability by providing gene flow to reduce inbreeding depression as well as demographic rescue and potential recolonization, which are key processes in metapopulation conservation.

There are several examples of successful application of analyses to identify key core and connectivity areas for wildlife populations. The approach presented in this work to map and identify core habitats and corridors for conservation was first developed by Cushman & Landguth (2012) to assess and prioritize core areas and corridor linkages for three species of conservation concern across a vast extent in the United States Great Plains. More recently, the approach was improved and successfully applied to prioritize areas for lion conservation in the Kavango-Zambezi Transfrontier Conservation Area (Cushman *et al.*, 2018). That project has been used as a primary source of information in the official effort by the Botswana Government to develop their national spatial plan. In India, a broad-scale connectivity analysis (Puyravaud *et al.*, 2017) using cumulative resistant kernels and factorial least-cost paths re-evaluated previously delineated movement corridors for the Asian elephant in Nilgiri Biosphere Reserve, the largest protected forest area in India. The results of that study were a primary source of information in a ruling by the Indian Supreme Court to protect the Sigur Plateau corridor from development. Finally, Kaszta *et al.* (2019) used connectivity analysis similar to that employed in this paper to map and quantify the potential impacts of development and forest restorations in Sabah (Borneo) projected in the Sabah Structure Plan for 2033 on populations of clouded leopard, and Kaszta *et al.* (2020) used these methods to evaluate the potential impacts of Belt and Road and other large potential developments across Myanmar.

The prioritization of core habitats and corridors presented in this work is based exclusively on biological criteria and does not include economic, societal and political aspects which are also crucial when deciding whether, where and how much to protect (Cushman *et al.*, 2018). Future research should focus on integrating robust, data-based analyses with political and social structured decision-making to improve the utility and effectiveness of conservation prioritization.

The camera traps used to develop the models upon which this analysis was based were located across the entire range of the clouded leopard to account for the full range of ecological, climatic and anthropogenic conditions that affect the species across its range. However, to maximize the efficiency of the trapping effort in detecting clouded leopards and sampling the gradient of conditions over which their occurrence probability changes from high occurrence to low occurrence rates, the majority (but not all) of the camera grids were

placed in or adjacent to protected areas. We recognize that habitat models built largely on data from protected areas, such as Macdonald *et al.* (2019), may not reliably predict occurrence probabilities across the wider landscape or the region. However, this camera trap dataset is the most extensive set of clouded leopard occurrence data collected globally. The Macdonald *et al.*'s (2019) model does show strong sensitivity to extent of protected areas and human footprint, suggesting it sampled a sufficient range of landscape conditions to identify and predict response in relation to protected area status, human impacts and forest cover across a range of scales.

This study focuses on habitat prioritization for clouded leopards, which might serve as a good indicator and focal species to focus limited resources for immediate biodiversity conservation actions to conserve forest ecosystems and forest-dependent biodiversity in Southeast Asia. However, the approach presented here can be applied also to other species of high conservation importance. For example, Samuel A. Cushman *et al.* (2013b) applied similar methods to assess core areas and corridors for three species and evaluate the degree to which efficient multi-species conservation strategies could be optimized. Similarly, Cushman & Landguth (2012) used multi-scale resistant kernel modelling to assess core areas and connectivity for a large number of focal species and evaluate feasibility of multi-species conservation strategies and how well carnivore umbrella species could serve as focal species for conservation planning. We suggest that future research in Southeast Asia focus on extending the results of this analysis to develop conservation decision-making based on broad-scale, multi-species integrated prioritization of key habitats and corridors to allow gene flow and dispersal across subpopulations (e.g. Cushman & Landguth, 2012; Cushman *et al.*, 2013b).

We also recommend that future research be undertaken to combine connectivity analyses with simulation modelling of population-level impacts of different conservation and development scenarios (e.g. Kaszta *et al.*, 2019, 2020). Specifically, while the current analysis of the baseline condition of core areas and corridors for clouded leopard across Southeast Asia may be critical to focus immediate and urgent conservation action in the areas of highest importance, it is insufficient to fully inform decision-makers as to the optimal trade-off between development options and conservation actions. For example, it would be useful to explicitly evaluate realistic alternative development and conservation scenarios to assess how they impact the extent, strength and integrity of core areas and corridors, and also to evaluate how these changes are likely to affect predicted population size and genetic diversity (e.g. Kaszta *et al.*, 2019, 2020). Furthermore, simulation modelling of conservation and development planning scenarios can be used to modify proposed plans to maximize their conservation benefits while minimizing negative impacts to biodiversity. We hope this initial baseline assessment of core habitats and corridor importance will enable such spatial optimization of alternative scenarios to be conducted across the full extent of Southeast Asia, for a number of focal species, including the clouded leopard.

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