

Habitat suitability and connectivity inform the co-management policy of protected area networks for Asian elephants in China

Cheng Huang^{1,2}, Xueyou Li¹, Laxman Khanal³, Xuelong Jiang^{Corresp. 1}

¹ Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China

² Kunming College of Life Sciences, University of Chinese Academy of Sciences, Kunming, China

³ Central Department of Zoology, Institute of Science and Technology, Tribhuvan University, Kathmandu, Nepal

Corresponding Author: Xuelong Jiang

Email address: jiangxl@mail.kiz.ac.cn

Enlarging protected area networks (PANs) is critical to ensure the long-term population viability of Asian elephants (*Elephas maximus*), which are globally threatened by habitat loss and fragmentation. Strict policies of PANs that focus on biodiversity conservation have failed largely in enlarging PANs due to difficulties in meeting the habitat requirements of Asian elephants and persuading the participation of stakeholders. A co-management policy that promotes sustainable use of natural resource, wildlife conservation, and stakeholder participation may have greater feasibility than strict policies in enlarging PANs in a “developing” world. Here, we elucidated this issue from the standpoints of elephant habitat suitability and socio-economic background of the habitat. We identified suitable habitat of Asian elephants in human-dominated landscapes using maximum entropy models (MaxEnt) and examined whether habitat suitability was indirectly associated with local economic development. We found that (1) Asian elephant suitable habitat was mainly distributed in areas of forest matrix with multiple land-use (50% natural forest cover) rather than relatively intact forest and in proximity to community settlements (mean distance 2 km) and (2) habitat suitability and local economic development were negatively associated ($p=0.04$). Thus, our results indicate that co-management is more feasible than the strict approaches for enlarging PANs. Additionally, our results provide on-ground information for elephant corridor design in southern China.

Habitat suitability and connectivity inform the co-management policy of protected area networks for Asian elephants in China

Cheng Huang^{1,2}, Xueyou Li¹, Laxman Khanal³ and Xuelong Jiang¹

¹ Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, Yunnan, China

² Kunming College of Life Sciences, University of Chinese Academy of Sciences, Kunming, Yunnan, China

³ Central Department of Zoology, Institute of Science and Technology, Tribhuvan University, Kathmandu, Nepal

Corresponding Author:

Xuelong Jiang

32 Jiaochang Donglu, Kunming, 650223, China

E-mail address: jiangxl@mail.kiz.ac.cn

ABSTRACT

Enlarging protected area networks (PANs) is critical to ensure the long-term population viability of Asian elephants (*Elephas maximus*), which are globally threatened by habitat loss and fragmentation. Strict policies of PANs that focus on biodiversity conservation have failed largely in enlarging PANs due to difficulties in meeting the habitat requirements of Asian elephants and persuading the participation of stakeholders. A co-management policy that promotes sustainable use of natural resource, wildlife conservation, and stakeholder participation may have greater feasibility than strict policies in enlarging PANs in a “developing” world. Here, we elucidated this issue from the standpoints of elephant habitat suitability and socio-economic background of the habitat. We identified suitable habitat of Asian elephants in human-dominated landscapes using maximum entropy models (MaxEnt) and examined whether habitat suitability was indirectly associated with local economic development. We found that (1) Asian elephant suitable habitat was mainly distributed in areas of forest matrix with multiple land-use (50% natural forest cover) rather than relatively intact forest and in proximity to community settlements (mean distance 2 km) and (2) habitat suitability and local economic development were negatively associated ($p=0.04$). Thus, our results indicate that co-management is more feasible than the strict approaches for enlarging PANs. Additionally, our results provide on-ground information for elephant corridor design in southern China.

INTRODUCTION

Protected area networks (PANs), which are comprised of core protected areas (PAs) and corridors, are the cornerstones for ensuring long-term population viability of wildlife by safeguarding contiguous habitat for dispersal and gene flow (Wilson & MacArthur, 1967,

Bennett & Mulongoy, 2006, Geldmann et al., 2013). Although PANs coverage was markedly increased over the past century with 15% of global land protected in 2018 (<https://liverport.protectedplanet.net/chapter-2>), some half of PAs were established primarily for biodiversity conservation similar to PAs of IUCN categories I–IV, i.e., nature reserves (NRs), wilderness areas, national parks, natural monuments, and habitat/species management areas (McDonald & Boucher, 2011), where human activities are strictly restricted. These strict policies generate three concerns from conservation field. First, the habitat suitability in strict PAs might be decreased for some species or taxa over time due to lack of landscape heterogeneity (Wharton, 1968, Mudappa et al., 2007, Evans et al., 2018). Second, the PA-oriented efforts lead to increased isolation of PAs and wildlife (DeFries et al., 2005, Laurance et al., 2012) because while strict PAs are often established in areas with intact primary vegetation and low human pressure, fragmented primary and secondary vegetation in human-dominated landscapes are continually eroded (Joppa & Pfaff, 2009, Acharya et al., 2017, Evans et al., 2018). Third, encouraging local stakeholder participation is difficult especially in developing countries because the establishment of strict PAs and local economic development are commonly regarded as competing issues by them (Bennett & Mulongoy, 2006, McDonald & Boucher, 2011). In this context, a co-management policy, that promotes sustainable use of natural resource, wildlife conservation, and stakeholder participation, potentially provides a more feasible mean for expanding PANs for a focal species or taxa in human-dominated landscapes (Zhang et al., 2006, Goswami et al., 2014, Evans et al., 2018).

South and Southeast Asia contain global hotspots of biodiversity (Myers et al., 2000), but are areas where wildlife is increasingly threatened by human activities (Ceballos & Ehrlich, 2002, Hansen et al., 2013). Agriculture and infrastructure expansions are among the most devastating threats (Edwards et al., 2010, Hansen et al., 2013, Clements et al., 2014). Large animals are particularly affected because of their considerable home range requirements (Ceballos & Ehrlich, 2002; Robert et al., 2006) and negative interactions with villagers (Acharya et al., 2017, AsERSM, 2017). Asian elephants (*Elephas maximus*) are endangered flagship species in their native regions. Despite their importance in ecosystem function (e.g., seed dispersal and nutrient recycling), culture, and fundraising for wildlife conservation (Campos-Arceiz et al., 2008; Ritchie & Johnson, 2009; Verissimo et al., 2011), only 29% of their distribution range is legally protected in 13 countries (Hedges et al., 2008), and thus most Asian elephants inhabit human-dominated landscapes (Jathanna et al., 2015, Calabrese et al., 2017). Enlarging PANs was identified as a priority for ensuring their long-term population viability (AsERSM, 2017). However, economic development is the current top priority in many regions, and thus expanding PANs for Asian elephants under strict policies is likely to fail socially in human-dominated landscapes (Bennett & Mulongoy 2006, Zhang et al., 2006, Evans et al., 2018) as well as fail to meet habitat requirements.

Asian elephants are extreme habitat generalists and occur in primary and secondary forests, scrubland, grassland, and farmland (Choudhury et al., 2008). They have context-dependent strategies to utilize resources and avoid mortality risks. For instance, the Cangyuan population

(20–23 individuals) in China mostly stays within an area of ~33 km² in an NR (Liu et al., 2016); the Mengla-Shangyong population (88–98 individuals) is located within two subdivisions (1 239 km²) of an NR and its periphery (Chen et al., 2013); the Menghai-Lancang population (15) and most of the Xishuangbanna-Pu'er population (98–109 individuals) frequently use human-dominated landscapes (Fig. 1). Despite these differences, there is mounting evidence that Asian elephants are “forest-edge specialists” at the fine spatial scale (Sitompul et al., 2013; Wadey et al., 2018). However, strict PAs substantially reduce human resource extractions and fires (Nelson & Chomitz, 2011), resulting in intact closed forests, which are less suitable for Asian elephants than moderately disturbed forests (Sitompul et al., 2013, Evans et al., 2018, Wadey et al., 2018). On the other hand, Asian elephants are conflict-prone and cause extensive loss to villages by raiding crops, damaging property, and even killing people (Gubbi, 2012, Chen et al., 2016). Villages in damage hotspots (or areas frequently used by elephants) are typified by hilly terrain in regions with traditional farming practices within a forest matrix and relatively far from major roads (Wilson et al., 2013, Chen et al., 2016). These areas are generally less developed economically than villages, with flat terrain that produce large cash-crop plantations in proximity to major roads. Thus, alternative support for these villages is necessary to offset the elephant-caused loss and encourage villager participation in enlarging PANs for Asian elephants. To enlarge PANs for Asian elephants, we propose that co-management policy, that integrates sustainable resource use, wildlife conservation, and stakeholder participation, is more feasible than strict policies which focus on wildlife conservation. This proposition is supported by two key pieces of evidence: (1) the areas covered by relatively intact forest are less suitable for Asian elephants than forest matrix with multiple land-use in human-dominated landscapes and (2) habitat suitability are negatively associated with local economic development, in other words, poorer village areas likely provide more suitable habitat for Asian elephants than relatively rich villages. Our study provides useful information to guide conservation policy for enlarging PANs and for elephant corridor design.

MATERIALS & METHODS

Field permit

Field studies were conducted under the permission from the Yunnan Forestry and Grassland Administration.

Study area

This study was conducted within the range of the Xishuangbanna-Pu'er population in Xishuangbanna and Pu'er, Yunnan, southwest China, bordering Vietnam and Laos (Fig. 1). This population consists of five subpopulations, i.e., Liushun, Yunxian, Simaogang, Jiangcheng, and Mengyang (Fig. 1). The region ranges from 495 m to 1 851 m above sea level, with an annual mean temperature of 21 °C and annual precipitation of ~1 500 mm (Liu et al., 2018). Natural forests (mainly subtropical evergreen broad-leaved forest) are fragmented by production forests (e.g., *Pinus kesiya* and *Eucalyptus* spp.), cash-crop plantations (e.g., rubber, coffee, and tea), and traditional farmlands (e.g., corn, rice, and sugarcane) (Chen et al., 2010). Three corridors (I, II, and III) were proposed by Zhang et al. (2015) to connect the (a) Menghai-Lancang and

Xishuangbanna-Pu'er population and (b) subpopulations of the Xishuangbanna-Pu'er population (Fig. 1). However, a hydro-power dam raised the water level of the Mekong River, isolating the Menghai-Lancang population from the Xishuangbanna-Pu'er population since 2005 (Chen et al., 2010). The study area includes 32 villages, each of which comprises several community settlements (251 in total). A town is the social center of villages and usually comprises several adjacent settlements. The primary industries are agriculture and agroforestry (Chen et al., 2010).

Data collection

In the confirmed range of the elephants, we collected data on the presence of Asian elephants and land-cover type along with 91 line transects (307 km) from December 2016 and March 2017, with the assistance of forest rangers. These line-transects were designed to traverse all types of land-cover (Fig. 1 and 2). Dung piles and footprints within a 20 m width of the line-transects were recorded, with intervals of at least 200 m (Dataset S1). Land-cover was categorized into seven types: i.e., natural forest, pine plantation (i.e., *Pinus kesiya*), cash-crop plantation, shrubland, traditional farmland, infrastructure site (e.g., settlements and roads), and water body (i.e., rivers, reservoirs, and ponds) (Chen et al., 2010).

We treated the per-capita annual income of villages as a proxy for economic development, with higher incomes representing higher levels of economic development. We collected the data from the Digital Village of Yunnan (<http://www.ynszxc.gov.cn/>).

Data analysis

The analysis included five steps. First, environmental variables were selected for habitat suitability models. Second, a land-cover map was developed from remote-sensing images. Third, the maximum entropy model (MaxEnt) was used to describe the presence probability of Asian elephants and generate a habitat suitability map, after which the characteristics of suitable habitat were summarized. Fourth, the possible negative association between habitat suitability and level of economic development was examined by linear regression. Fifth, a habitat resistance surface was used to simulate the pathways of Asian elephants by least-cost and circuit models.

Environmental variables

Asian elephants frequently occur in areas of low altitude, flat terrain, and low human disturbance and feed natural foods or crops in proximity to forest (Jathanna et.al., 2015, Lin et.al., 2015, Liu et.al., 2016). Hence, we initially selected thirteen environmental variables in three categories with potential associations with elephant presence (Table 1): i.e., geographic and topographic (altitude and terrain roughness index), land-cover (distance to, edge density of, and percentage of natural forest, pine plantation, and traditional farmland), and human disturbance (distance to town and distance to community settlement).

Land-cover classification

We used Landsat 8 OLI_TIRS images (30-m resolution from the Data Cloud of CAS, <http://www.csdb.cn/>) to develop a land-cover map. We added ancillary layers to improve classification accuracy, including ASTER GDEM grids (Data Cloud of CAS), slope and its texture, and Normalized Difference Vegetation Index and its texture (Wegmann et al., 2016). We

performed a supervised classification using the random forest algorithm with 25% of land-cover points left to validate the classification (Leutner & Horning, 2017).

MaxEnt modeling

For habitat suitability models with presence-only data, the MaxEnt outperforms other existing approaches (Ferrier et al., 2006, Phillips et al., 2006). MaxEnt contrasts environment of wildlife presences against the available background (Elith et al., 2011). In this study, the background was represented by 10 000 points randomly generated in buffer zones of average home range size (113 km²) around the presence points (Dataset S2) (Fernando et al., 2008; Amirkhiz et al., 2018). To identify important variables describing habitat suitability of Asian elephants and build a model with high accuracy, we performed an optimized selection of environmental variables and MaxEnt features and β multiplier based on Akaike information criteria (AIC) following the workflow of Amirkhiz et al. (2018). First, we excluded the variables that were highly correlated ($|r| > 0.7$) and contributed less than 5% to the model and then step-wise optimized the β multiplier (0–15 by 0.5 intervals). Second, as MaxEnt calculates five models for each environmental variable, known as features (i.e., linear (L), quadratic (Q), product (P), threshold (T), and hinge (H): Phillips et al., 2017), we selected the feature set by the lowest AIC among “L”, “H”, “LQ”, “LQT”, “LP”, “HP”, “LQP”, and “LQTP”, then used the optimized model to predict a habitat suitability map. The prediction was evaluated by threshold-independent (Area Under the Curve of the Receiver Operating Characteristic plot, AUC) and threshold-dependent omission rate. Third, a 10% training presence threshold was used for delineating suitable from unsuitable habitat (Escalante et al., 2013, Hughes, 2017), after which we summarized the characteristics of the suitable habitat. The modeling was performed in R with MaxentVariableSelection and ENMeval package (Team 2013, Muscarella et al., 2014, Jueterbock, 2016).

Association between habitat suitability and level of economic development

In the study area, the level of economic development of a village is related to its altitude, terrain, and land-use pattern, and thus may be indirectly associated with habitat suitability of Asian elephants. The habitat suitability of a village for Asian elephants was calculated by averaging the habitat suitability of community settlements, which was extracted from the habitat suitability map by the locations of the community settlements. We used linear regression to examine the direction and significance of the association between the habitat suitability of a village and its level of economic development.

Pathway mapping

Least-cost and circuit models are two widely used approaches for corridor design (Ruiz-González et al., 2014, Wang et al., 2014). We simulated the pathways of Asian elephants by least-cost and circuit models using Linkage Mapper and Circuitscape software (McRae & Shah, 2009; Wang et al., 2014; Mcrae et al., 2008), with the length and movement resistance of the least-cost pathways calculated. The resistance surface was calculated by one minus the habitat suitability layer. As we focused on mapping pathways around the previously-proposed corridors (I, II, and III) by Zhang et al. (2015), the least-cost model was constructed with three core

ranges, i.e., Mengyang, Liushun and Simaogang, and Jiangcheng (Fig. 1). All presence points were used to produce a connectivity map for the entire study area by the circuit model.

RESULTS

In total, we collected 245 presence points of Asian elephants. The overall accuracy of the land-cover classification was 0.91.

The model with the lowest AIC had a β multiplier=1; linear, quadratic, threshold, and product features ("LQTP"); and eight uncorrelated variables with a contribution of >5%, including terrain roughness index, distance to town, community settlement, natural forests, and traditional farmlands, and percentage of natural forest, pine plantation, and traditional farmland. The percentage of natural forests (23%), distance to town (23%), and distance to community settlement (16%) were among the most strong predictors of the Asian elephants' presence.

In general, the model accurately discriminated presence points from the background environment (mean AUC=0.86). The low AUC difference (0.05) suggested that the model did not over-fit the presence points. Threshold-dependent measures indicated that the model had low over-fitting and high discriminatory ability at 10% omission rate (0.20) and lowest presence threshold (< 0.001). The threshold value of the suitable habitat was 0.28. In our study, the Asian elephant suitable habitat was mainly distributed in areas of forest matrix with multiple land-use (50% natural forest cover) rather than relatively intact forest, away from towns (mean distance 10 km), near community settlements (mean distance 2 km), and with flat terrain (mean terrain roughness index 4.83) (Fig. 2).

~~There was a significant negative correlation between the habitat suitability for Asian elephants and the level of economic development ($p=0.04$)~~

The least-cost model (Fig. 3) revealed that the shortest pathway is #3 (29 km) and the longest pathway is #2 (47 km), while the pathway #1 had the lowest habitat resistance. The connectivity map of the study area supported the pathway #1 as a potential corridor to connect the Mengyang and Jiangcheng subpopulation (Fig. 3). Besides, the connectivity map showed that the area of the white rectangle on Fig. 3 is important to connect the subpopulations of Mengyang to Liushun and Simaogang because of its location and relatively high habitat connectivity.

DISCUSSION

For elephants, habitat selection reflects a trade-off between resource use and mortality risk avoidance (Munshi-South et al., 2008, Basille et al., 2009). The percentage of natural forest was the strongest variable affecting the presence of Asian elephants. This finding is consistent with a previous study on the Cangyuan population in China (Liu et al., 2016) and demonstrated the substantial role of natural forests for Asian elephants in regard to providing food, refuge, and thermoregulation (Kumar et al., 2010, Goswami et al., 2014, Evans et al., 2018). In particular, our study revealed that forest matrix habitats with multiple land-use are more suitable for Asian elephants than the relatively intact forest in human-dominated landscapes, which is supported by previous studies (Sitompul et al., 2013, Evans et al., 2018, Wadey et al., 2018). Forest edges provide better light conditions for *Ficus* spp. and gramineous plants, which are primary natural foods of Asian elephants (Chen et al., 2006, Sitompul et al., 2013, Wadey et al., 2018).

Furthermore, ~~palatable~~ crops in forest matrix are attractive to the elephants, with 68% of feeding sites ~~found~~ in such areas during the rainy season (Zhang et al., 2003). On the other hand, elephants ~~do~~ suffer mortality at the hands of humans, both directly and indirectly, from ditches, electrocution, and retaliatory killing (Chen et al., 2013; Palei et al., 2014; AsERSM, 2017). Therefore, Asian elephants are less likely to occur ~~in the proximity of towns characterized by~~ dense human infrastructure, plantations, and management (Fig. 2). Although we focused on habitat suitability patterns of Asian elephants in human-dominated landscapes, similar patterns can be found in NRs and their peripheries. For example, the Mengla-Shangyong population mostly inhabits the buffer and experimental zones of an NR and its peripheries with moderately-disturbed landscapes (Fig. 1) (Hongpei Yang pers. comm.).

Based on quantitative analysis, conservation efforts on establishing corridors for the elephants ~~could~~ be concentrated on the predicted pathways and areas of high connectivity. With the greatest length and largest movement resistance, pathway #2 was rarely ~~utilized~~ by Asian elephants **based on long-term monitoring (Chen et al., 2010, Zhang et al., 2015)**; despite having the shortest length, the resistance of pathway #3 was only slightly ~~smaller~~ than that of pathway #2 and traversed tracts of rubber plantations (Fig. 2), where stakeholders are unlikely to restore contiguous natural habitat for the elephants; pathway #1 was the most consistent with the connectivity map calculated by the circuit model and has the lowest resistance. Thus, ~~the~~ pathway #1 should be allocated ~~higher~~ conservation priority than either pathway #2 or #3. Also, efforts are needed to protect the connective habitat of the area with the white rectangle on Fig. 3. Our study provides more precise information for corridor design than Zhang et al. (2015).

Habitat suitability of Asian elephants is affected by many factors. Our study is limited by our reliance on presence-only data and variables extracted from remote sensing images to determine the habitat suitability, from which the resistance layer was generated for simulating pathways. Incorporating movement data of the elephants recorded by telemetry techniques and on-ground variables (e.g., food abundance and forest structure) could improve habitat suitability models and provide straightforward movement trajectories for corridor design.

In China, PANs include NRs (~15% of the national territory), world natural and cultural heritage sites, scenic zones, wetland parks, forest parks, geological parks, and water conservancy scenic locations (Cao et al., 2015). While most NRs are managed as socially exclusive landscapes (Zhang et al., 2006, Cao et al., 2015), including the Xishuangbanna National Nature Reserve (soft green area in Fig. 1), Asian elephants need forest matrix with open lands and are flexible to human disturbance. Conservation policies allowing considerable interventions in NRs could enlarge Asian elephant habitat without great loss of biodiversity. For example, selectively logged forests appear to maintain ~90% of the original biodiversity compared to primary forest (Berry et al., 2010, Brodie et al., 2014), and retention forestry, whereby a proportion of original vegetation is left unlogged, further reduces the negative impacts on biodiversity (Gaveau et al., 2013, Fedrowitz et al., 2014). Among NRs, efforts should be paid to protect community-owned forests, which represent a major proportion of natural forests and are critical for the elephants (Kumar et al., 2010, Evans et al., 2018) and other wildlife (Rodrigues et al., 2017, Rodrigues &

Chiarello, 2018). Meanwhile, integrating traditional farmlands into PANs can fulfill human needs and encourage the participation of villagers. Generally, the less-developed villages are more suitable to Asian elephants than are the more-developed villages. Thus, supporting sustainable economic development and reducing elephant-caused loss are needed to encourage human-elephant coexistence, and may include developing ecotourism, encouraging wildlife-friendly products, and compensating the loss (Mishra et al., 2003; Chen et al., 2013; Huang et al., 2018).

CONCLUSIONS

Asian elephants are affected globally by habitat fragmentation and loss. Thus, enlarging PANs is a priority for their conservation (AsERSM, 2017). Using presence data from an on-ground survey in human-dominated landscapes combined with habitat suitability models, we found that: (1) Asian elephants suitable habitat was mainly distributed in areas of forest matrix with multiple land-use rather than relatively intact forests and in proximity to community settlements; and (2) habitat suitability and level of economic development had an indirectly negative association. From the standpoints of elephant habitat and local socio-economic background, these results suggest that a co-management policy would be more feasible than the current strict policies for enlarging PANs to protect contiguous habitat for Asian elephants. Such a policy would also be suitable for other areas with similar land-cover patterns and socio-economic contexts, such as northeastern India and northern Laos (Kumar et al., 2010, Wilson et al., 2013, AsERSM, 2017).

ACKNOWLEDGMENTS

We are grateful to Pu'er Forestry Bureau, Xishuangbanna National Nature Reserve, and Jinghong Forestry Bureau for field support. We thank Hongpei Yang and Wei Cha for sharing their experiences, and Zhonghua Li, Li He, and Dan Yan for their assistance in the field.

REFERENCES

- Acharya, K.P., Paudel, P.K., Jnawali, S.R., Neupane, P.R., Koehl, M., 2017. Can forest fragmentation and configuration work as indicators of human-wildlife conflict? Evidences from human death and injury by wildlife attacks in Nepal. *Ecol. Indic.* 80, 74–83.
- Adams, W.M., Aveling, R., Brockington, D., Dickson, B., Elliott, J., Hutton, J., Roe, D., Vira, B., Wolmer, W., 2004. Biodiversity conservation and the eradication of poverty. *Science*. 306, 1146–1149.
- Amirkhiz, G.R., Frey, J.K., Cain Iii, J.W., Breck, S.W., Bergman, D.L., 2018. Predicting spatial factors associated with cattle depredations by the Mexican wolf (*Canis lupus baileyi*) with recommendations for depredation risk modeling. *Biol. Conserv.* 224, 327–335.
- AsERSM, 2017. Report: Asian elephant range states meeting. Jakarta, Indonesia. Retrieved from https://elephantconservation.org/iefImages/2018/03/AsERSM-2017_Final-Report.pdf.
- Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D.C., Odden, J., Andersen, R., Arild Høgda, K., Gaillard, J.M., 2009. What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography*. 32, 683–691.

- 320 Bennett, G., Mulongoy, K.J., 2006. Review of experience with ecological networks, corridors
321 and buffer zones, in: Secretariat of the Convention on Biological Diversity, Montreal,
322 Technical Series 23:5–6.
- 323 Berry, N.J., Phillips, O.L., Lewis, S.L., Hill, J.K., Edwards, D.P., Tawatao, N.B., Ahmad, N.,
324 Magintan, D., Khen, C. V, Maryati, M., Ong, R.C., Hamer, K.C., 2010. The high value of
325 logged tropical forests: lessons from northern Borneo. *Biodivers. Conserv.* 19, 985–997.
- 326 Brodie, J.F., Giordano, A.J., Zipkin, E.F., Bernard, H., Mohd-azlan, J., Ambu, L., 2014.
327 Correlation and persistence of hunting and logging impacts on tropical rainforest mammals.
328 *Conserv. Biol.* 29, 110–121.
- 329 Calabrese, A., Calabrese, J.M., Songer, M., Wegmann, M., Hedges, S., Rose, R., Leimgruber, P.,
330 2017. Conservation status of Asian elephants: the influence of habitat and governance.
331 *Biodivers. Conserv.* 26, 2067–2081.
- 332 Campos-Arceiz, A., Larrinaga, A.R., Weerasinghe, U.R., Takatsuki, S., Pastorini, J.,
333 Leimgruber, P., Fernando, P., Santamaria, L., 2008. Behavior rather than diet mediates
334 seasonal difference in seed dispersal by Asian elephants. *Ecology* 89, 2684–2691.
- 335 Cao, M., Peng, L., Liu, S., 2015. Analysis of the network of protected areas in China based on a
336 geographic perspective: Current status, issues and integration. *Sustain.* 7, 15617–15631.
- 337 Ceballos, G., Ehrlich, P.R., 2002. Mammal population losses and the extinction crisis. *Science*.
338 296, 904–907.
- 339 Chen, J., Deng, X., Zhang, L., Bai, Z., 2006. Diet composition and foraging ecology of Asian
340 elephants in Shangyong, Xishuangbanna, China. *Acta Ecol. Sin.* 26, 309–316.
- 341 Chen, M., Hong, G., Li, Z., Dong, Y., Yang, Y., 2013. Studies of conflict between elephant and
342 human being in China. Yunnan Science and Technology Press, Kunming, Yunnan, China.
- 343 Chen, M., Li, Z., Guo, X., Yang, Z., Dong, Y., 2010. Asian elephant conservation corridors in
344 China. Yunnan Science and Technology Press, Kunming, Yunnan, China.
- 345 Chen, S., Yi, Z., Campos-Arceiz, A., Chen, M., Webb, E.L., 2013. Developing a spatially-
346 explicit, sustainable and risk-based insurance scheme to mitigate human–wildlife conflict.
347 *Biol. Conserv.* 168, 31–39.
- 348 Chen, Y., Marino, J., Chen, Y., Tao, Q., Sullivan, C.D., Shi, K., Macdonald, D.W., 2016.
349 Predicting hotspots of human-elephant conflict to inform mitigation strategies in
350 Xishuangbanna, Southwest China. *PLoS One* 11, e0162035.
- 351 Choudhury, A.L., Choudhury, D.K., Desai, A., Duckworth, J.W., Easa, P.S., Johnsingh, A.J.T.,
352 Fernando, P., Hedges, S., Gunawardena, M., Kurt, F., 2008. *Elephas maximus*. IUCN Red
353 List of Threatened Species.
- 354 Clements, G.R., Lynam, A.J., Gaveau, D., Yap, W.L., Lhota, S., Goosem, M., Laurance, S.,
355 Laurance, W.F., 2014. Where and how are roads endangering mammals in Southeast Asia’s
356 forests? *PLoS One* 9, 1–25.
- 357 DeFries, R., Hansen, A., Newton, A.C., Hansen, M.C., 2005. Increasing isolation of protected
358 areas in tropical forests over the past twenty years. *Ecol. Appl.* 15, 19–26.

- Desai, A.A., Riddle, H.S., 2015. Human-elephant conflict in Asia. United State Fish and Wildlife Service. Retrieved from <https://www.fws.gov/international/pdf/Human-Elephant-Conflict-in-Asia-June2015.pdf>.
- Edwards, D.P., Hodgson, J.A., Hamer, K.C., Mitchell, S.L., Ahmad, A.H., Cornell, S.J., Wilcove, D.S., 2010. Wildlife-friendly oil palm plantations fail to protect biodiversity effectively. *Conserv. Lett.* 3, 236 – 242.
- Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17, 43–57.
- Escalante, T., Rodríguez-Tapia, G., Linaje, M., Illoldi-Rangel, P., González-López, R., 2013. Identification of areas of endemism from species distribution models: threshold selection and Nearctic mammals. *TIP* 16, 5–17.
- Evans, L.J., Asner, G.P., Goossens, B., 2018. Protected area management priorities crucial for the future of Bornean elephants. *Biol. Conserv.* 221, 365–373.
- Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., 2014. Can retention forestry help conserve biodiversity? A meta-analysis. *J. Appl. Ecol.* 51, 1669–1679.
- Fernando, P., Wikramanayake, E.D., Janaka, H.K., Jayasinghe, L.K.A., Gunawardena, M., Kotagama, S.W., Weerakoon, D., Pastorini, J., 2008. Ranging behavior of the Asian elephant in Sri Lanka. *Mamm. Biol.* 73, 2–13.
- Ferrier, S., Guisan, A., Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-pereira, R., Schapire, R.E., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Gaveau, D.L.A., Kshatriya, M., Sheil, D., Sloan, S., Molidena, E., Wijaya, A., Wich, S., Ancrenaz, M., Hansen, M., Broich, M., Guariguata, M.R., Pacheco, P., Potapov, P., Turubanova, S., Meijaard, E., 2013. Reconciling forest conservation and logging in Indonesian Borneo. *PLoS One* 8, e69887.
- Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M., Burgess, N.D., 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biol. Conserv.* 161, 230–238.
- Goswami, V.R., Sridhara, S., Medhi, K., Williams, A.C., Chellam, R., Nichols, J.D., Oli, M.K., 2014. Community-managed forests and wildlife-friendly agriculture play a subsidiary but not substitutive role to protected areas for the endangered Asian elephant. *Biol. Conserv.* 177, 74–81.
- Gubbi, S., 2012. Patterns and correlates of human-elephant conflict around a south Indian reserve. *Biol. Conserv.* 148, 88–95.

397 Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, Sa., Tyukavina, A., Thau,
398 D., Stehman, S. V, Goetz, S.J., Loveland, T.R., 2013. High-resolution global maps of 21st-
399 century forest cover change. *Science*. 342, 850–853.

400 Hedges, S., Fisher, K., Rose, R., 2008. Range-wide mapping workshop for Asian elephants
401 (*Elephas maximus*). Rep. to US Fish Wildl. Serv. Cambodia.

402 Huang, C., Li, X.Y., Shi, L.J., Jiang, X.L.. 2018. Patterns of human-wildlife conflict and
403 compensation practices around Daxueshan Nature Reserve, China. *Zool. Res.* 39, 406–412.

404 Hughes, A.C., 2017. Mapping priorities for conservation in Southeast Asia. *Biol. Conserv.* 209,
405 395–405.

406 Jathanna, D., Karanth, K.U., Kumar, N.S., Karanth, K.K., Goswami, V.R., 2015. Patterns and
407 determinants of habitat occupancy by the Asian elephant in the Western Ghats of
408 Karnataka, India. *PLoS One* 10, e0133233.

409 Joppa, L.N., Pfaff, A., 2009. High and far: biases in the location of protected areas. *PLoS One* 4,
410 e8273.

411 Jueterbock, A., Smolina, I., Coyer, J.A., Hoarau, G., 2016. The fate of the Arctic seaweed *Fucus*
412 *distichus* under climate change: an ecological niche modeling approach. *Ecol. Evol.* 6,
413 1712–1724.

414 Kioko, J., Kiffner, C., Ndibalema, V., Hartnett, E., Seefeld, C., 2015. Maasai people and
415 elephants: values and perceptions. NISCAIR-CSIR, India.

416 Kumar, M.A., Mudappa, D., Raman, T.R.S., 2010. Asian elephant *Elephas maximus* habitat use
417 and ranging in fragmented rainforest and plantations in the Anamalai Hills, India. *Trop.*
418 *Conserv. Sci.* 3, 143–158.

419 Laurance W.F., Carolina Useche D., Rendeiro J., Kalka M, Bradshaw C.J.A., Sloan S.P.,
420 Laurance S.G., Campbell M., Abernethy K., Alvarez P., Arroyo-Rodriguez V., Ashton P.,
421 Benítez-Malvido J., Blom A., Bobo K.S., Cannon C.H., Cao M., Carroll R., Chapman C.,
422 Coates R., Cords M., Danielsen F., De Dijn B., Dinerstein E., Donnelly M.A., Edwards D.,
423 Edwards F., Farwig N., Fashing P., Forget P.M., Foster M., Gale G., Harris D., Harrison R.,
424 Hart J., Karpanty S., John Kress W., Krishnaswamy J., Logsdon W., Lovett J., Magnusson
425 W., Maisels F., Marshall A.R., McClearn D., Mudappa D., Nielsen M.R., Pearson R.,
426 Pitman N., van der Ploeg J., Plumptre A., Poulsen J., Quesada M., Rainey H., Robinson D.,
427 Roetgers C., Rovero F., Scatena F., Schulze C., Sheil D., Struhsaker T., Terborgh J.,
428 Thomas D., Timm R., Nicolas Urbina-Cardona J., Vasudevan K., Joseph Wright S., Carlos
429 Arias-G. J., Arroyo L., Ashton M., Auzel P., Babaasa D., Babweteera F., Baker P., Banki
430 O., Bass M., Bila-Isia I., Blake S., Brockelman W., Brokaw N., Brühl C.A.,
431 Bunyavejchewin S., Chao J.T., Chave J., Chellam R., Clark C.J., Clavijo J., Congdon R.,
432 Corlett R., Dattaraja H.S., Dave C., Davies G., de Mello Beisiegel B., de Nazaré Paes da
433 Silva R., Di Fiore A., Diesmos A., Dirzo R., Doran-Sheehy D., Eaton M., Emmons L.,
434 Estrada A., Ewango C., Fedigan L., Feer F., Fruth B., Giacalone Willis J., Goodale U.,
435 Goodman S., Guix J.C., Guthiga P., Haber W., Hamer K., Herbinger I., Hill J., Huang Z.,
436 Fang Sun I., Ickes K., Itoh A., Ivanauskas N., Jackes B., Janovec J., Janzen D., Jiangming

M., Jin C., Jones T., Justiniano H., Kalko E., Kasangaki A., Killeen T., King H., Klop E., Knott C., Koné I., Kudavidanage E., Lahoz da Silva Ribeiro J., Lattke J., Laval R., Lawton R., Leal M., Leighton M., Lentino M., Leonel C., Lindsell J., Ling-Ling L., Eduard Linsenmair K., Losos E., Lugo A., Lwanga J., Mack A.L., Martins M., Scott McGraw W., McNab R., Montag L., Myers Thompson J., Nabe-Nielsen J., Nakagawa M., Nepal S., Norconk M., Novotny V., O'Donnell S., Opiang M., Ouboter P., Parker K., Parthasarathy N., Pisciotto K., Prawiradilaga D., Pringle C., Rajathurai S., Reichard U., Reinartz G., Renton K., Reynolds G., Reynolds V., Riley E., Rödel M.O., Rothman J., Round P., Sakai S., Sanaiotti T., Savini T., Schaab G., Seidensticker J., Siaka A., Silman M.R., Smith T.B., de Almeida S.S., Sodhi N., Stanford C., Stewart K., Stokes E., Stoner K.E., Sukumar R., Surbeck M., Tobler M., Tscharrntke T., Turkalo A., Umapathy G., van Weerd M., Vega Rivera J., Venkataraman M., Venn L., Vereá C., Volkmer de Castilho C., Waltert M., Wang B., Watts D., Weber W., West P., Whitacre D., Whitney K., Wilkie D., Williams S., Wright D.D., Wright P., Xiankai L., Yonzon P., Zamzani F. 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature* 489, 290.

Leutner, B., Horning, N., 2017. RStoolbox: Tools for remote sensing data analysis. R package version 0.1.7. <https://CRAN.R-project.org/package=RStoolbox>.

Lin, L., Jin, Y., Yang, H., Luo, A., Guo, X., Wang, L., Zhang, L., 2015. Evaluation of habitat for Asian elephants (*Elephas maximus*) in Xishuangbanna, Yunnan, China. *Acta Theriol. Sin.* 35, 2–13.

Liu, P., Hui, W., Liu, L., Jing, L., Li, Z., 2016. Habitat evaluation for Asian elephants (*Elephas maximus*) in Lincang: Conservation planning for an extremely small population of elephants in China. *Biol. Conserv.* 198, 113–121.

Liu, P., Wen, H., Harich, F.K., He, C., Wang, L., Guo, X., Zhao, J., Luo, A., Yang, H., Sun, X., Yu, Y., Zheng, S., Guo, J., Li, L., Zhang, L., 2017. Conflict between conservation and development: cash forest encroachment in Asian elephant distributions. *Sci. Rep.* 7, 6404.

Liu, S., Yin, Y., Li, J., Cheng, F., Dong, S., Zhang, Y., 2018. Using cross-scale landscape connectivity indices to identify key habitat resource patches for Asian elephants in Xishuangbanna, China. *Landsc. Urban Plan.* 171, 80–87.

McDonald, R.I., Boucher, T.M., 2011. Global development and the future of the protected area strategy. *Biol. Conserv.* 144, 383–392.

Mcrae, B.H., Dickson, B.G., Keitt, T.H., Shah, V.B., Mcrae, B.H., Dickson, B.G., Keitt, T.H., Shah, V.B., 2008. Using circuit theory to model connectivity in Ecology, Evolution, and Conservation. *ECOLOGY* 89, 2712–2724.

McRae, B.H., Shah, V.B., 2009. Circuitscape user's guide. Univ. California, St. Barbar.

Mishra, C., Allen, P., McCarthy, T., Madhusudan, M.D., Bayarjargal, A., Prins H.H.T., 2003. The role of incentive programs in conserving the snow leopard. *Conserv. Biol.* 17, 1512-1520.

475 Mudappa, D., Noon, B.R., Kumar, A., Chellam, R., 2007. Responses of small carnivores to
476 rainforest fragmentation in the southern Western Ghats, India. *Small Carniv. Conserv.* 36,
477 18–26.

478 Munshi-South, J., Tchignoumba, L., Brown, J., Abbondanza, N., Maldonado, J.E., Henderson,
479 A., Alonso, A., 2008. Physiological indicators of stress in African forest elephants
480 (*Loxodonta africana cyclotis*) in relation to petroleum operations in Gabon, Central Africa.
481 *Divers. Distrib.* 14, 995–1003.

482 Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson,
483 R.P., 2014. ENMeval: An R package for conducting spatially independent evaluations and
484 estimating optimal model complexity for ecological niche models. *Methods Ecol. Evol.* 5,
485 1198–1205.

486 Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da, F.G., Kent, J., 2000. Biodiversity hotspots
487 for conservation priorities. *Nature* 403, 853.

488 Palei, N.C., Palei, H.S., Rath, B.P., Kar, C.S., 2014. Mortality of the endangered Asian elephant
489 *Elephas maximus* by electrocution in Odisha, India. *Oryx* 48,

490 Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black
491 box: an open-source release of Maxent. *Ecography* 40, 887–893

492 Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species
493 geographic distributions. *Ecol. Modell.* 190, 231–259.

494 R Development Core Team, 2013. R: A language and environment for statistical computing.
495 Vienna: R Foundation for Statistical Computing.

496 Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity
497 conservation. *Ecol. Lett.* 12, 982–998.

498 Robert, S., Wanlop, C., Naret, S., 2006. Collaborating to conserve large mammals in southeast
499 Asia. *Conserv. Biol.* 20, 1391–1401.

500 Rodrigues, T.F., Chiarello, A.G., 2018. Native forests within and outside protected areas are key
501 for nine-banded armadillo (*Dasypus novemcinctus*) occupancy in agricultural landscapes.
502 *Agric. Ecosyst. Environ.* 266, 133–141.

503 Rodrigues, T.F., Kays, R., Parsons, A., Versiani, N.F., Paolino, R.M., Pasqualotto, N., Krepschi,
504 V.G., Chiarello, A.G., 2017. Managed forest as habitat for gray brocket deer (*Mazama*
505 *gouazoubira*) in agricultural landscapes of southeastern Brazil. *J. Mammal.* 98, 1301–1309.

506 Ruiz-González, A., Gurrutxaga, M., Cushman, S.A., Madeira, M.J., Randi, E., Gómez-Moliner,
507 B.J., 2014. Landscape genetics for the empirical assessment of resistance surfaces: The
508 European pine marten (*Martes martes*) as a target-species of a regional ecological network.
509 *PLoS One* 9, e110552.

510 Sitompul, A.F., Griffin, C.R., Rayl, N.D., Fuller, T.K., 2013. Spatial and temporal habitat use of
511 an Asian Elephant in Sumatra. *Anim. an open access J. from MDPI* 3, 670–679.

512 Verissimo, D., Macmillan, D.C., Smith, R.J., 2011. Toward a systematic approach for identifying
513 conservation flagships. *Conserv. Lett.* 4, 1–8.

- Wadey, J., Beyer, H.L., Saaban, S., Othman, N., Leimgruber, P., Campos-Arceiz, A., 2018. Why did the elephant cross the road? The complex response of wild elephants to a major road in Peninsular Malaysia. *Biol. Conserv.* 218, 91–98.
- Wang, F., McShea, W.J., Wang, D., Li, S., Zhao, Q., Wang, H., Lu, Z., 2014. Evaluating landscape options for corridor restoration between Giant Panda Reserves. *PLoS One* 9, e105086.
- Wegmann, M., Leutner, B., Dech, S., 2016. Remote sensing and GIS for ecologists: using open source software. Pelagic Publishing: Exeter, UK.
- Wharton, C.H., 1968. Man, fire and wild cattle in Southeast Asia, in: *Proceedings of the Annual Tall Timbers Fire Ecology Conference*. pp. 7–167.
- Wilson, E.O., MacArthur, R.H., 1967. The theory of island biogeography. Princeton, NJ.
- Wilson, S., Davies, T.E., Hazarika, N., Zimmermann, A., 2013. Understanding spatial and temporal patterns of human-elephant conflict in Assam, India. *Oryx* 49, 140–149.
- Zhang, L., Dong, L., Lin, L., Feng, L., Yan, F., Wang, L., Guo, X., Luo, A., 2015. Asian elephants in China: Estimating population size and evaluating habitat suitability. *PLoS One* 10, e0124834.
- Zhang, L., Lichao, M.A., Feng, L., 2006. New challenges facing traditional nature reserves: Asian elephant (*Elephas maximus*) conservation in China. *Integr. Zool.* 1, 179–187.
- Zhang, L., Wang, N., Wang, Y., Ma, L., 2003. A preliminary study on the habitat and behaviors of Asian elephant (*Elephas maximus*) in Simao, Yunnan, China. *Acta Theriol. Sin.* 23, 185–192.

Figure 1

The study area and distribution range of Asian elephants in China

The populations are represented by the tags of orange (Xishuangbanna-Pu'er population), blue (Cangyuan population), green (Menghai-Lancang population), and purple (Mengla-Shangyong population).

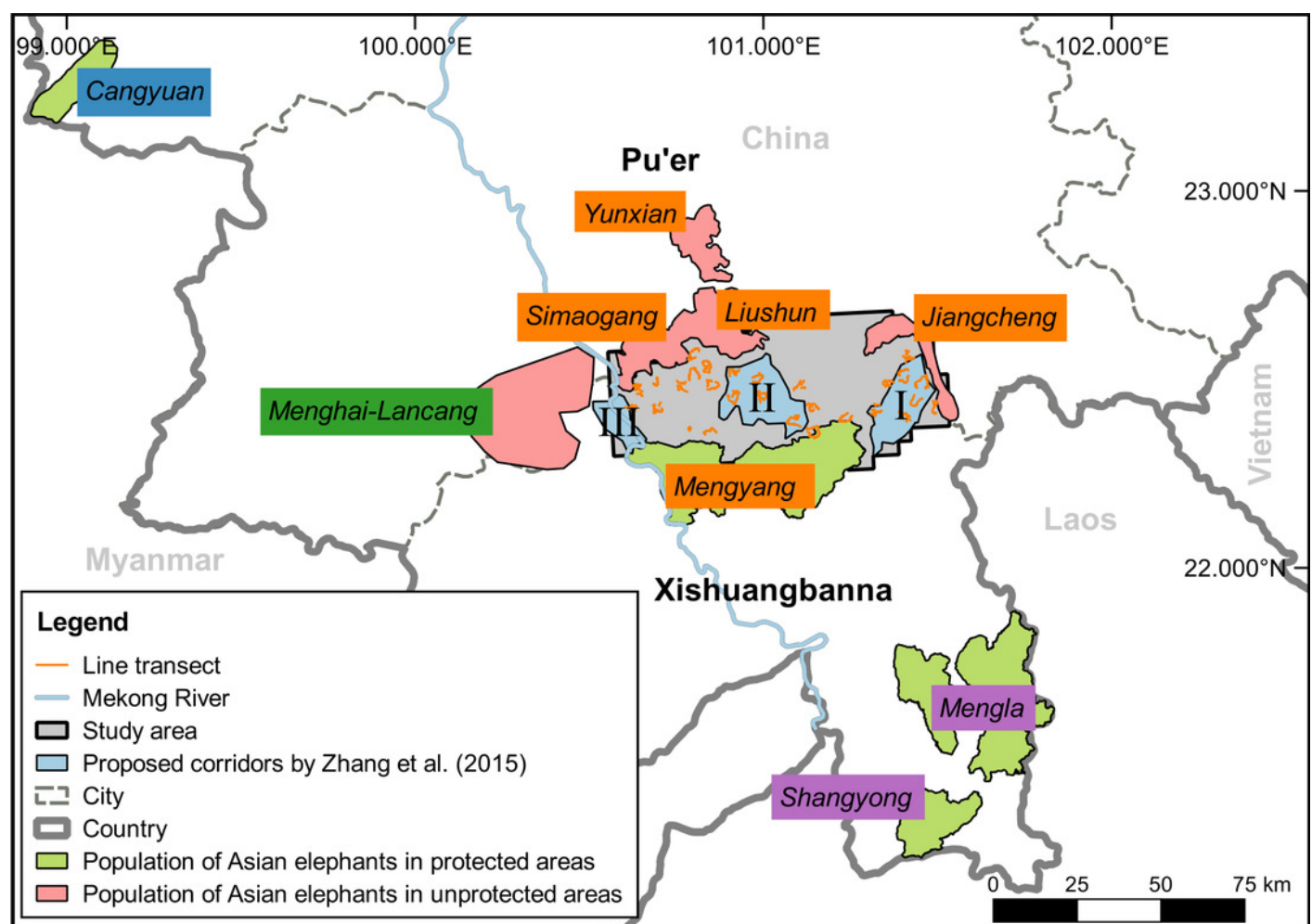


Figure 2

Habitat suitability map for Asian elephants in the study area.

The suitable habitat of Asian elephants was mainly distributed in the areas of forest matrix with multiple land-use, away from towns, and near community settlements.

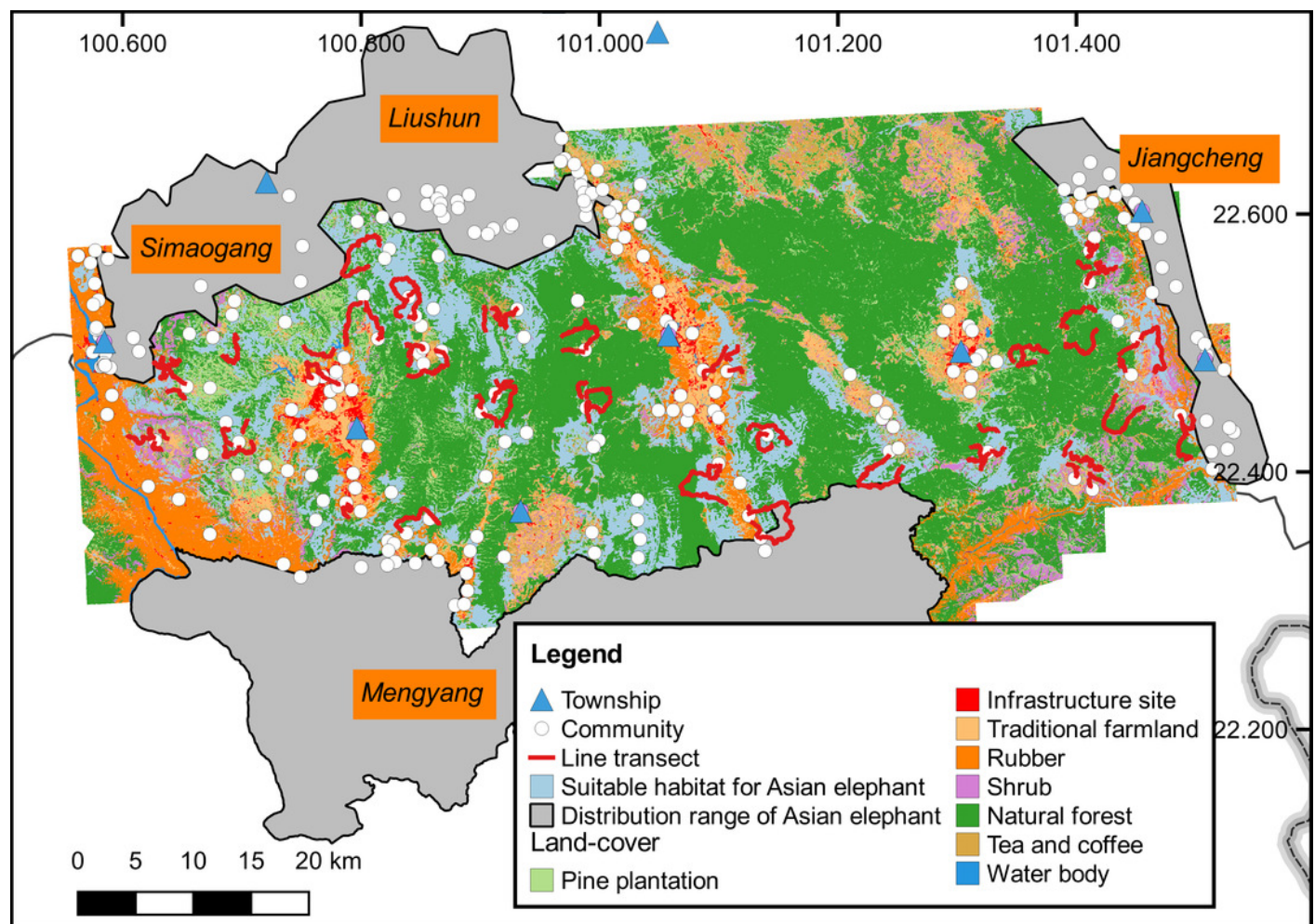


Figure 3

Habitat connectivity for Asian elephants calculated by the circuit model and the least-cost path in the study area.

The area of the white triangle is located among the subpopulations of Mengyang, Liushun, and Simaogang

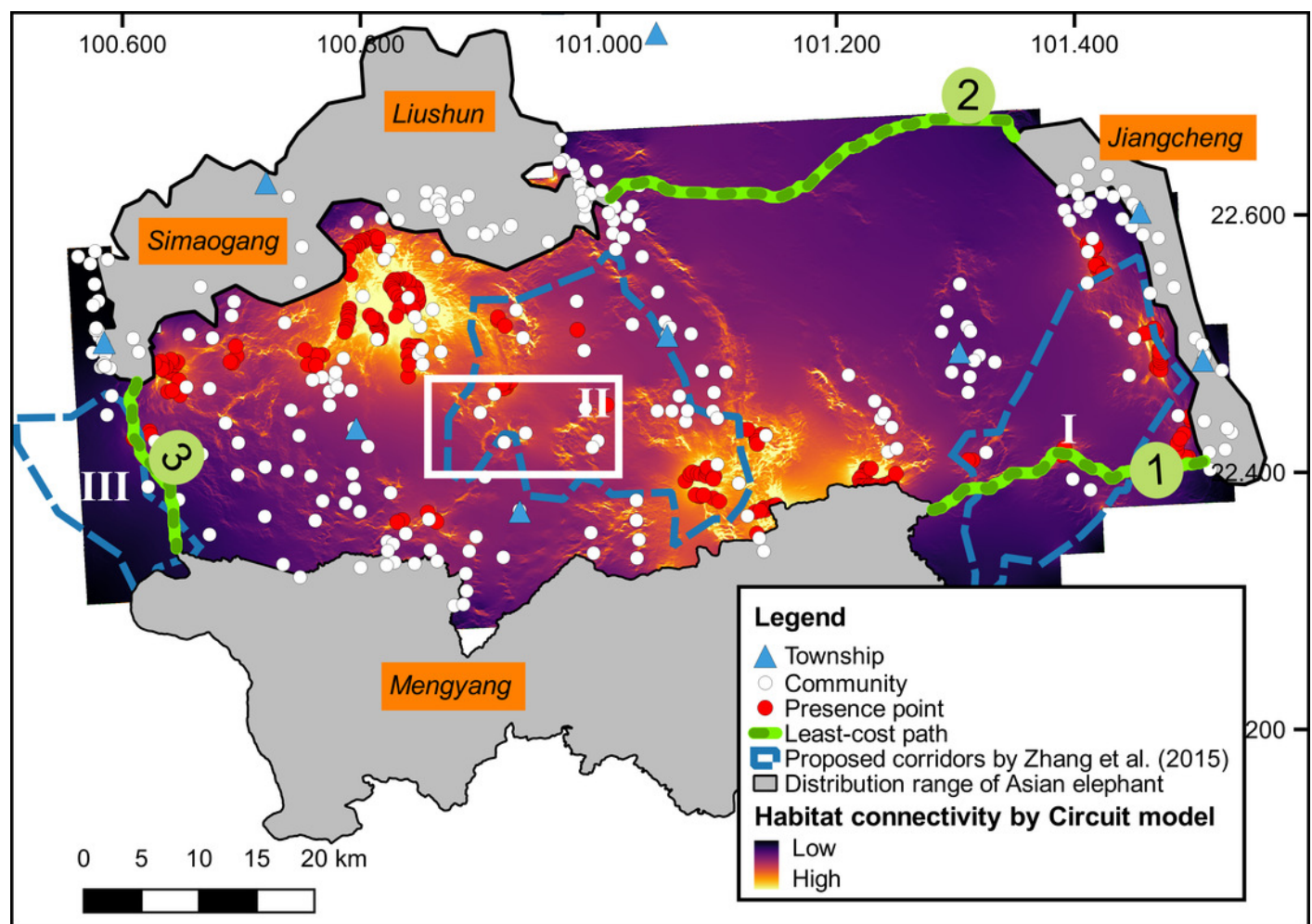


Table 1 (on next page)

Environmental variables selected in habitat suitability models for Asian elephants

1

Category	Variable	Data and calculation
Geographic and topographic	Altitude	ASTER GDEM
	Terrain roughness index	Calculated from ASTER GDEM in R
Land-cover	Distance to: natural forest pine plantation traditional farmland	Calculated by “distance” function in R
	Percentage of: natural forest pine plantation traditional farmland	Calculated in Fragstats by 1.5 km radius from land-cover map
	Edge density of: natural forest pine plantation traditional farmland	Calculated in Fragstats by 1.5 km radius from land-cover map
Human disturbance	Distance to: town community	Calculated by “distance” function in R

2

3