

# Mobile animals and immobile protected areas: improving the coverage of nature reserves for Asian elephant conservation in China

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**Abstract** Many protected areas worldwide have been established to protect the last natural refuges of flagship animal species. However, long-established protected areas do not always match the current distributions of target species under changing environmental conditions. Here we present a case study of the Asian elephant *Elephas maximus* in Xishuangbanna, south-west China, to evaluate whether the established protected areas match the species' current distribution and to identify key habitat patches for Asian elephant conservation. Our results show that currently only 24.5% of the predicted Asian elephant distribution in Xishuangbanna is located within Xishuangbanna National Nature Reserve, which was established for elephant conservation. Based on the predicted Asian elephant distribution, we identified the most important habitat patches for elephant conservation in Xishuangbanna. The three most important patches were outside Xishuangbanna National Nature Reserve and together they contained 43.3% of the estimated food resources for Asian elephants in all patches in Xishuangbanna. Thus, we identified a spatial mismatch between immobile protected areas and mobile animals. We recommend the inclusion of the three identified key habitat patches in a new national park currently being planned by the Chinese authorities for the conservation of the Asian elephant.

**Keywords** Asian elephant, *Elephas maximus*, flagship species, human–elephant conflict, key habitat patches, national park, protected areas, Xishuangbanna

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## Introduction

Protected areas are currently the most important mechanism for preserving species and ecosystems (Pyke, 2007; Butchart et al., 2010). According to Aichi Biodiversity Strategic Goal C, parties to the United Nations Convention on Biological Diversity should improve their biodiversity status by safeguarding ecosystems, species and genetic diversity, with Target 11 setting a goal of 17% of land area being protected by 2020 and Target 12 setting a goal of improving the conservation status of threatened species by 2020 (Convention on Biological Diversity, 2010). By 2018, a total of 238,563 protected areas had been established worldwide, covering 14.9% of the total land area (UNEP-WCMC et al., 2018). However, few studies have assessed whether the established protected areas remain effective in supporting their original conservation target, given the environmental changes in recent decades (Song et al., 2018).

China supports an exceptional diversity of species and ecosystems, but human population growth and rapid economic development have resulted in conflict between development and environmental protection (Wu et al., 2014). China has been an active party to the Convention on Biological Diversity since 1993 and hosted Part 1 of the 15th Conference of the Parties (COP15) in Kunming in October 2021. China has many types of protected areas, including nature reserves, national parks, scenic zones, and world natural and cultural heritage sites (Cao et al., 2015). National parks aim to protect large natural ecosystems and are expected to eventually absorb smaller protected areas such as nature reserves within their expanding boundaries, bringing them under unified management (Zhou & Grumbine, 2011). Yet to date, the most important type of protected area is the nature reserve, which is under the strictest level of protection. By 2017, China had established 2,750 nature reserves. At that time, the total area covered by all types of protected areas in China was c. 20% (Xu et al., 2019). Many of these protected areas were established to protect iconic flagship species such as the giant panda *Ailuropoda melanoleuca* (Li & Pimm, 2016) and tiger *Panthera tigris* (Qin et al., 2015). The distribution range of some flagship species can change substantially over time, in response to changing environmental conditions or because of increasing population size. However, few nature reserves have had their effectiveness re-assessed or management

strategies adjusted in response to the changing distributions of these flagship species. Here we present a case study of Asian elephant *Elephas maximus* conservation in Xishuangbanna Dai Autonomous Prefecture (hereafter Xishuangbanna), south-west China, to illustrate the need for continuous reassessment of reserve effectiveness in meeting conservation goals and for consequent adjustment of conservation management strategies even outside nature reserves.

Xishuangbanna National Nature Reserve was established in 1958 and became part of the UNESCO Man and the Biosphere Reserve Network in 1993. One target for the Reserve has been to protect one of the region's iconic species, the Asian elephant (Yunnan Forestry and Grassland Administration, 2016). Combined with strict policies and laws to control poaching and the illegal trade in elephant products, the Reserve has successfully maintained a population of Asian elephants. The estimated number of Asian elephants in China has increased from 225 in 1983 to 313 in 2017, with 85% of them distributed in Xishuangbanna (Wang et al., 2017). Asian elephants can consume c. 10% of their body weight (170–200 kg) per day (Prajapati, 2008) and their varied diet comprises herbs, shrubs and trees (Campos-Arceiz et al., 2008). They prefer early successional plant species, particularly monocotyledons, to late successional plant species (Chen et al., 2006). As Asian elephants have large home ranges (Fernando et al., 2008; Alfred et al., 2012; Wilson et al., 2020), the increasing elephant population in the Reserve requires more food and habitat. However, the boundaries of the Reserve have remained unchanged for nearly half a century, whereas the land cover in Xishuangbanna has changed dramatically both inside and outside the Reserve over the same period (Chen et al., 2016a; Liu et al., 2017a; Zhang et al., 2019). In the past c. 25 years, there have been a number of dispersal events whereby elephants established new home ranges in the surrounding areas outside the Reserve, expanding the local elephant distribution range (Liu et al., 2017a; Wang et al., 2017). Elephant movements northwards to Kunming and southwards to Xishuangbanna Tropical Botanical Garden also indicate that the growing elephant population needs a larger habitat range (Campos-Arceiz et al., 2021). Recent incidences of severe human–elephant conflict (e.g. loss of crops, cash plantations and property, and human casualties caused by wild elephants) in Xishuangbanna (Chen et al., 2016b) reflect the elephants' tendency to move out of the Reserve to feed on crops, highlighting the need to manage the elephant population outside the Reserve. Immobile nature reserves are thus no longer sufficient for protecting this highly mobile flagship species.

The 19th National Congress of the Communist Party of China updated the protected areas system in the country such that national parks will now represent the principal protection category (Chen et al., 2019). In recent years, China has established 10 pilot national parks covering

> 220,000 km<sup>2</sup> (Zhou & Grumbine, 2011; He et al., 2018). A national park specifically for the conservation of the Asian elephant is currently under consideration (Chen et al., 2021). To support the planning for and establishment of this national park, our study aimed to determine the current potential distribution range of Asian elephants inside and outside Xishuangbanna National Nature Reserve. Based on their distribution range, we identified key habitat patches that are suitable for elephant conservation outside the Reserve.

Information on the food resource requirements of the target species is important for wildlife management but is often lacking. To fill this gap and evaluate the conservation priority of each key habitat patch, we calculated the biomass of the plant species comprising the natural diet of Asian elephants. Our study demonstrates the necessity of identifying key habitat patches according to the distribution of a flagship species and makes a first attempt to use dietary plant biomass to indicate the conservation priority of key habitat patches, which will provide useful information for the ongoing planning of the new Asian elephant national park.

## Study area

Our study area is located in Xishuangbanna, Yunnan Province, south-west China (Fig. 1). Xishuangbanna is one of the most biodiverse regions in China. It has two dry seasons (dry-cool season: November–February; dry-hot season: March–April) and a rainy/wet season (May–October; Zhang & Cao, 1995). Xishuangbanna National Nature Reserve was established with the aim of conserving elephants and the associated tropical ecosystem, and includes five geographically distinct sub-reserves: Mangao, Menglun, Mengyang, Mengla and Shangyong (Fig. 1). Economic development and the ensuing land transformation from traditional agriculture to rubber and tea plantations have led to severe deforestation and fragmentation of the landscape in Xishuangbanna since the 1980s (Liu et al., 2017b).

## Methods

To model the potential distribution of Asian elephants in Xishuangbanna, a research team led by one of the authors (Q-YW) from the Research Institute of the Nature Reserve first collected data on the presence of Asian elephants. The research team recorded dung piles and footprints along 21 randomly selected transect lines (of varying lengths as dictated by the survey area; range 2–20 km), both inside and outside the Reserve, during March–June 2017. Each transect line was surveyed only once. In addition, we also obtained presence data from publications documenting elephant location data collected during 2003–2017. We searched the Web of Science (Clarivate, Philadelphia, USA) using the

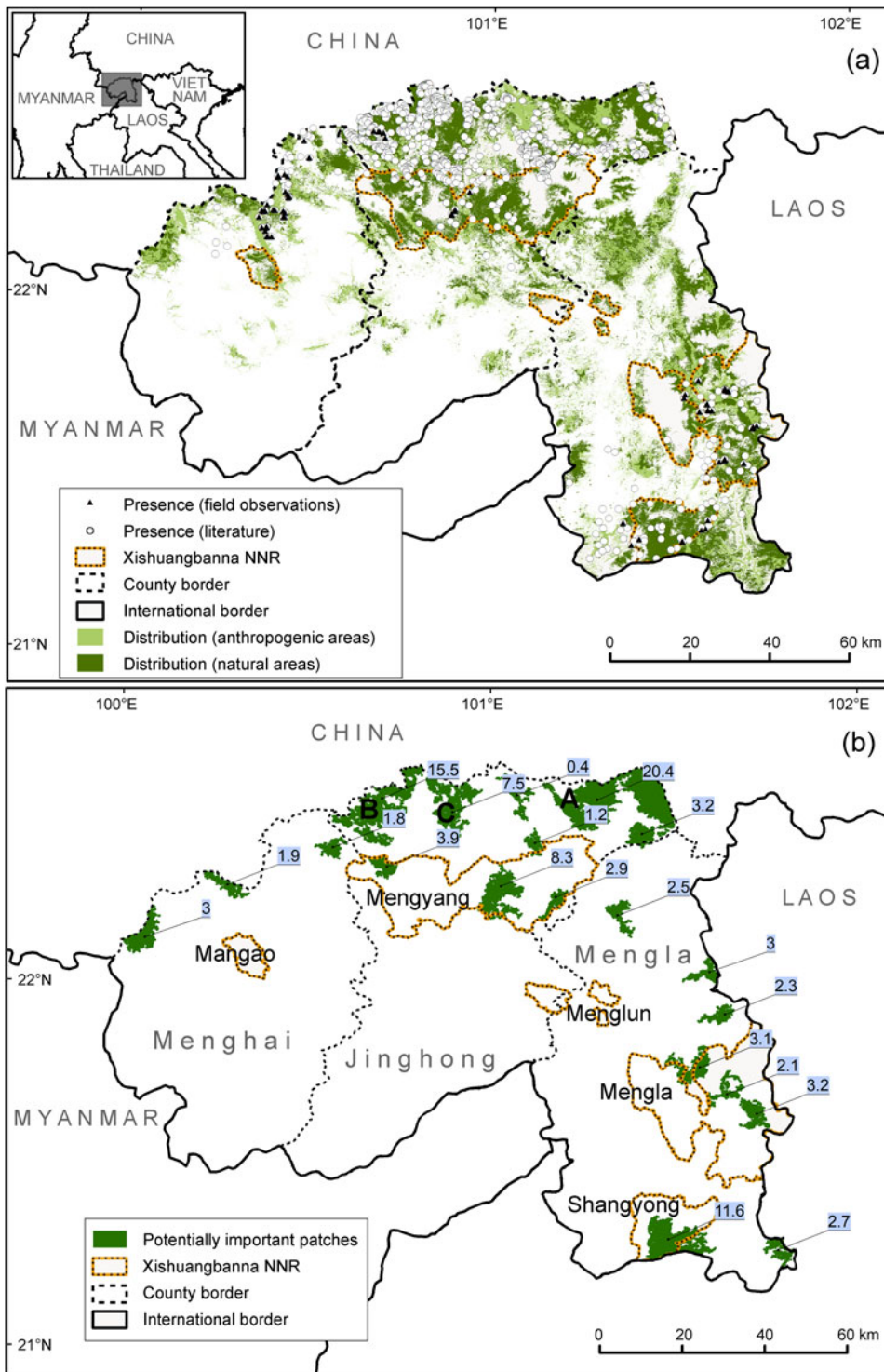


FIG. 1 (a) Presence points from field observations and the literature, and predicted distribution ranges of the Asian elephant *Elephas maximus* in Xishuangbanna Dai Autonomous Prefecture, south-west China. (b) Potentially important habitat patches for Asian elephants identified during this study. For each patch, the per cent of the total dietary plant biomass for Asian elephants in Xishuangbanna is shown. A, B and C represent the three key habitat patches. The names of the sub-reserves of Xishuangbanna National Nature Reserve (NNR) are given in black font on the map, and county names in grey font.

keywords ‘Asian elephant’, ‘Asian elephants’, ‘elephant’ or ‘elephants’ and ‘China’ in both English and Chinese and obtained eight references containing presence point data of Asian elephants in Xishuangbanna (Lin et al., 2011; Yang & Zhang, 2012; He et al., 2014; Chen et al., 2016b; Li et al., 2018; Wang et al., 2018; Huang et al., 2019a,b). However, because in two of these references (Chen et al., 2016b; Li et al., 2018) presence points were given as the location of the home

villages of people who had reported elephants, rather than actual presence points of elephants, we did not include these references in our analysis. We also removed duplicates of presence points (i.e. those included in more than one reference) from further analysis.

We used the maximum entropy model to predict the potential distribution of elephants in Xishuangbanna. To minimize spatial autocorrelation, we overlaid a 1 × 1 km



grid onto the study area and retained a single randomly selected presence point in cells that contained multiple points. The predictive variables included in the models were land cover, aspect, elevation, slope, distance to nearest water source, distance to nearest road, distance to the nearest Reserve boundary (for presence points outside the Reserve only; this was set to zero for presence points inside the Reserve), and kernel distribution of settlements. Land-cover data were provided by the Research Institute of the Reserve; they originated from Landsat 8 Operational Land Imager images from February 2014 and comprised 19 land-cover categories (Supplementary Table 1, Supplementary Fig. 1). The overall accuracy of the classification was 86.3%. Land cover changed less after 2014 than before that year; therefore, the 2014 classification is a fair representation of the land cover for 2010–2021 (Zhang et al., 2019). We tested for multi-collinearity using the *psych* package (Revelle, 2019) in *R* 3.4.1 (R Core Team, 2013) to determine whether the variables were highly correlated ( $|r| > 0.7$ ). We found no multi-collinearity between the variables. We used the K-fold of five groups to subset the data for model training and model testing. To minimize uneven sampling effort, we manipulated the sampling effort by adding a species bias file when running the maximum entropy model (Kramer-Schadt et al., 2013), where the bias file represented the record density and was created using the *ENMeval* package (Kass et al., 2021) in *R*. We then performed maximum entropy modelling in *R*, using the *dismo* package (Hijmans et al., 2017). We used the area under the receiver operating characteristics curve to assess model performance. In *dismo*, we applied *spec\_sens* as a threshold to define the potential distribution range of Asian elephants, at which the sum of sensitivity (true-positive rate) and specificity (true-negative rate) is the highest (Liu et al., 2013).

We then identified important habitat patches for Asian elephants in Xishuangbanna based on the predicted elephant distribution. We used the *FragPatch* algorithm (Kilheffer & Underwood, 2018) to delineate key patches, for which we set the spur (minimum width of habitat patch) and gap (maximum width of non-habitat between habitat patches) threshold at 100–300 m, with 50-m intervals. We selected 100 m as the minimum value according to the typical flight response distance of the Asian elephant (derived from the experience of Q-YW), and 300 m as the maximum value in case no patch was identified by the *FragPatch* algorithm. We retained those patches that scored 10 in the *FragPatch* analysis as important habitat patches and excluded patches  $< 25 \text{ km}^2$ .

To determine the available food biomass for Asian elephants, we first compiled an inventory of the species' dietary plants (Supplementary Table 2) from the literature (45 plant species; Chen et al., 2006) and field observations (110 plant species). We applied random sampling to survey the dietary plant biomass of Asian elephants in 10 land-cover types,

excluding six anthropogenic land-cover types (urbanized area, cropland, tea plantation, rubber plantation, orchard and other tree plantation) and three land-cover types that were not suitable for Asian elephants or were too small (limestone monsoon forest, mossy evergreen broad-leaved forest and savannah shrub grassland; Supplementary Table 1). We also excluded water as a land-cover type. We combined warm bamboo forest with hot bamboo forest in the dietary plant biomass survey, as bamboo forest. For non-tree dietary plant species, we chose 900 m<sup>2</sup> quadrats (30 × 30 m), within which we established five 9 m<sup>2</sup> sample plots (3 × 3 m) at each corner and at the centre of each quadrat (95 samples in total; see Supplementary Table 3 for sample size details). We weighed the edible portions of fresh dietary plants in the sample plots. When weighing the edible portions of tree species, we eliminated trees with a height  $> 10 \text{ m}$  or diameter at breast height  $> 15 \text{ cm}$ , because elephants usually do not select such large trees when foraging (Feng & Zhang, 2005). Based on field observations and the experience of one of the authors (Q-YW), we weighed all edible parts of these tree species, such as the roots or leaves. We took all measurements during February 2016–November 2017.

As the amount of food available in the dry season limits the Asian elephant population in Xishuangbanna (Zhang et al., 2003), we used dry season biomass when estimating the dietary plant biomass for elephants in the study area. However, we collected some of our samples in the wet season. Because the activity range of Asian elephants in search of food can be twice as large in the dry compared to the wet season (Zhang et al., 2003), we divided the dietary plant biomass obtained in the wet season by two to represent the food biomass in dry season. For tree species, we applied linear regression in *R* using paired diameter at breast height and weight data collected in the dry season to estimate the dietary plant biomass of the tree species sampled in each quadrat. To calculate the food biomass of each land-cover type, we added the total weight of both non-tree and tree species and then averaged this value across the number of samples of each land-cover type. We then calculated the total dietary plant biomass in the proposed protected areas by multiplying the area of each land-cover type in each proposed protected area by our estimate of the food plant biomass in that land-cover type. We then calculated the per cent of dietary plant biomass in each potential protected area to determine its conservation priority.

## Results

In total we obtained 1,004 presence points of Asian elephants inside and outside the Reserve (Fig. 1a). Our model generated a reliable predicted potential distribution range of Asian elephants, with the area under the receiver operating characteristics curve equal to 0.795. The *spec\_sens* threshold value was 0.521; we defined cells with a value higher than this

as part of the potential Asian elephant distribution range. The Xishuangbanna National Nature Reserve included 24.5% of the potential Asian elephant distribution range, and 75.5% of the potential distribution range was outside the Reserve (Table 1).

Distance to the Reserve contributed the most to our model (33.3%), followed by land-cover type (22.6%), distance to the nearest road (12.7%) and elevation (11.9%). Kernel distribution of settlements contributed 8.5%, slope 7.1%, distance to nearest water source 3.0% and aspect 0.8% to the model. Of the 19 land-cover types in Xishuangbanna, monsoon evergreen broad-leaved forest occupied the largest area (6,996 km<sup>2</sup>, 36.6% of Xishuangbanna), followed by rubber plantation (4,834 km<sup>2</sup>, 25.3%) and cropland (2,215 km<sup>2</sup>, 11.6%). Amongst natural habitats, the distribution probability of Asian elephants was the highest in warm-hot coniferous forest and shrub; in anthropogenic landscapes, it was highest in cropland, tea plantations and other tree plantations.

During our fieldwork, we recorded 110 plant species that Asian elephants consume in Xishuangbanna (Supplementary Table 2). These belong to 42 families, amongst which Gramineae (21 species), Moraceae (11 species) and Zingiberaceae (10 species) comprised 38% of the dietary plant species. Shrub, which represents secondary regrowth after clearance, had the highest biomass of dietary plants per area (0.63 kg/m<sup>2</sup>), followed by montane rainforest (0.29 kg/m<sup>2</sup>), seasonal rainforest (0.15 kg/m<sup>2</sup>), monsoon evergreen broad-leaved forest (0.15 kg/m<sup>2</sup>), deciduous monsoon forest (0.15 kg/m<sup>2</sup>) and warm deciduous broad-leaved forest (0.14 kg/m<sup>2</sup>).

The results of the *FragPatch* analysis showed that three key habitat patches with high proportions of estimated dietary plant biomass fell outside the Nature Reserve (Fig. 1b). Patch A (320.1 km<sup>2</sup>) contained 20.4% of the total dietary plant biomass for elephants in Xishuangbanna, Patch B (199.7 km<sup>2</sup>) contained 15.5% and Patch C (121.9 km<sup>2</sup>) contained 7.5%. Mengyang sub-reserve had a large predicted elephant distribution range (618.2 km<sup>2</sup>) but the patches in this sub-reserve only contained 15.0% of the dietary plant biomass for Asian elephants in Xishuangbanna. Shangyong sub-reserve had a predicted elephant distribution range of 246.2 km<sup>2</sup> and the habitat patches in this sub-reserve contained 11.6% of the dietary plant biomass (Table 1, Fig. 1b).

## Discussion

Our results demonstrate the dynamic nature of socio-ecological systems and the importance of updating knowledge for effective conservation. We evaluated ongoing changes in the geographical distribution of a flagship species in relation to the boundaries of a protected area established half a century ago. According to our distribution model, 75.5% of the potential distribution range of Asian elephants in Xishuangbanna fell outside Xishuangbanna National

TABLE 1 Predicted distribution ranges of the Asian elephant *Elephas maximus* inside the sub-reserves of Xishuangbanna National Nature Reserve, south-west China (Fig. 1).

Sub-reserve	Distribution area (km <sup>2</sup> )	Per cent of the total distribution area
Mangao	42.1	0.72
Menglun	25.3	0.43
Mengyang	618.2	10.51
Mengla	507.5	8.63
Shangyong	246.2	4.19
<i>Total</i>	1,439.3	24.48

Nature Reserve, and the available dietary plant biomass inside the Reserve was considerably less than outside. As one of the primary aims of the Reserve was to protect Asian elephants (Yunnan Forestry and Grassland Administration, 2016), the mismatch between the location of the Reserve and the Asian elephant distribution range illustrates that the current protected area is no longer sufficient to support the Asian elephant population in Xishuangbanna, as is the case for other protected areas throughout the species' range (Leimgruber et al., 2003; de la Torre et al., 2021; Fernando et al., 2021).

Some research suggests that landscape changes inside the Reserve could be driving elephants to areas outside its boundaries (Wang et al., 2017). However, our findings demonstrate that distance to the Reserve contributed the most (having a negative effect) to the species distribution model, with a higher distribution probability of Asian elephants nearer the Reserve. This suggests that the current Reserve still functions as a refuge for Asian elephants. The Reserve has played an important role in protecting Asian elephants since its establishment, which could be one of the reasons for the increasing Asian elephant population in China. However, given the increasing population of Asian elephants (Wang et al., 2017), their range expansion outside the Reserve (Campos-Arceiz et al., 2021) and the highly fragmented habitats in Xishuangbanna (Liu et al., 2017a,b), it is time to consider expanding the current protected area coverage to connect the currently separated sub-populations of Asian elephants.

The three key habitat patches identified in this study are vital for preserving the habitat and natural food resources for Asian elephants. These habitat patches are food-rich, containing 43.3% of the total dietary plant biomass in the important habitat patches in Xishuangbanna. Overall, our study is consistent with previous research on the habitat preferences of Asian elephants in China (Zhang et al., 2015; Huang et al., 2019a,b), and we detected key habitat patches based not only on habitat suitability modelling but also on the availability of dietary plants. Integrating suitable habitats outside the Reserve into a protected areas network could reduce the intensity of intraspecific competition amongst Asian elephants. As a new Asian elephant national

park is now under consideration, we hope that this study can contribute to the design and management of this future park, with the key habitat patches being protected through their incorporation into the national park as core areas. Shangyong sub-reserve contained 11.6% of the total dietary plant biomass in the important habitat patches identified in Xishuangbanna, and this area is adjacent to Laos, supporting the transboundary movements of Asian elephants (Lv et al., 2019). We therefore suggest that Sino–Laos cooperation should be promoted to achieve effective transboundary conservation of Asian elephants (Wang et al., 2021).

There are several limitations to our study. Firstly, it is challenging to estimate dietary plant biomass for species with a diverse diet, such as the Asian elephant. Taking into consideration the relative food preferences of Asian elephants could make such an estimate more robust, but such information is not available. Our study included as many local dietary plant species of Asian elephants as possible, to improve the accuracy of the estimated availability of natural food resources for the species in the region. Secondly, given that dietary plant weight can change considerably between the dry and rainy seasons, simply dividing the weight of samples obtained in the rainy season by two (as described in the Methods section) is not ideal for estimating dietary plant biomass. Future research should obtain data on the weight of dietary plants in the dry season, to accurately calculate dietary plant biomass for Asian elephants. Finally, because of time limitations, the samples of dietary plant biomass for each land-cover type in our study may have been insufficient to generate robust results, which must be considered when interpreting our results. However, based on our findings, protecting the areas identified as important habitat patches could help save the last refuges for Asian elephants in Xishuangbanna, mitigating the effects of the rapid land conversion that has occurred over the last decade (Liu et al., 2017a,b).

Our distribution model predicted Asian elephants to occur in both natural and human-made land-cover types, reflecting the fact that Asian elephants in Xishuangbanna are able to occupy highly human-dominated landscapes and consume crops as part of their food resources, which has caused damage to local communities (Chen et al., 2016b). With the increasing population of Asian elephants and expansion of their range, it is predicted that conflict between people and elephants will escalate unless effective management strategies are implemented that keep people safe from Asian elephants (Campos-Arceiz et al., 2021). Expanding protected areas plays an important role in preserving habitat for this growing Asian elephant population. Simultaneously, human–elephant conflict mitigation (e.g. insurance compensation, elephant-proof fences, early-warning systems) needs to be improved to help ensure the safety and protect the livelihoods of local communities (Chen et al., 2013, 2016b).

Similar attention needs to be paid to the nature reserves established for other flagship species in China. There are 428 national nature reserves in China, of which 299 were established before 2000 and 67 have a particular focus on wild fauna conservation (Zhu et al., 2018). Some of these nature reserves serve as refuges for protected animal species. These animal populations could thus increase and some are likely to reach the carrying capacity of the reserves, leading to their geographical expansion outside protected areas. However, some of the established nature reserves are affected by human disturbance or climate change (Liu et al., 2001). In response to the changing environment, some flagship animals could move outside of the nature reserves; this applies especially to mammals and birds, which are often highly sensitive to habitat quality and deterioration (Xu et al., 2017). In such cases, immobile protected areas may no longer be sufficient to maintain the populations of the target animals. Animal movements away from protected areas demonstrate the need to adjust management strategies to ensure efficient conservation.

In conclusion, as most of the protected areas in China were established more than 20 years ago, our study highlights the importance of assessing the conservation effectiveness of protected areas over time and adjusting management policies as necessary, particularly if target animals move away from protected areas. This is applicable not only to the Asian elephant but also to the conservation of other flagship species whose distributions are sensitive to environmental changes and whose habitats are being transformed rapidly under pressures from social and economic development.

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**Author contributions** Study design: L-LL, Q-YW, R-CQ; fieldwork: Q-YW, H-PY, Y-XT, L-XW, Z-BY; data analysis and writing: L-LL, AC-A, R-CQ.

**Conflicts of interest** None.

**Ethical standards** This research abided by the *Oryx* guidelines on ethical standards.

## References

- ALFRED, R., AHMAD, A.H., PAYNE, J., WILLIAMS, C., AMBU, L.N., HOW, P.M. & GOOSSENS, B. (2012) Home range and ranging

- behaviour of Bornean elephant (*Elephas maximus borneensis*) females. *PLOS ONE*, 7, e31400.
- BUTCHART, S.H., WALPOLE, M., COLLEN, B., VAN STRIEN, A., SCHARLEMANN, J.P., ALMOND, R.E. et al. (2010) Global biodiversity: indicators of recent declines. *Science*, 328, 1164–1168.
- CAMPOS-ARCEIZ, A., DE LA TORRE, J.A., WEI, K., WU, X.O., ZHU, Y., ZHAO, M. et al. (2021) The return of the elephants: how two groups of dispersing elephants attracted the attention of billions and what can we learn from their behavior. *Conservation Letters*, 14, e12836.
- CAMPOS-ARCEIZ, A., LIN, T.Z., HTUN, W., TAKATSUKI, S. & LEIMGRUBER, P. (2008) Working with mahouts to explore the diet of work elephants in Myanmar (Burma). *Ecological Research*, 23, 1057–1064.
- CAO, M., PENG, L. & LIU, S. (2015) Analysis of the network of protected areas in China based on a geographic perspective: current status, issues and integration. *Sustainability*, 7, 15617–15631.
- CHEN, F., TANG, F.L., WANG, D.T., WANG, M.J., SUN, H.Y., SUN, G.Z. et al. (2019) Research on Asian elephant national park. *Forestry Construction*, 6, 23–29. [In Chinese]
- CHEN, H., YI, Z.F., DIETRICH, S.V., ANTJE, A., PHILIP, B., CHRISTOPH, K. et al. (2016a) Pushing the limits: the pattern and dynamics of rubber monoculture expansion in Xishuangbanna, SW China. *PLOS ONE*, 11, e0150062.
- CHEN, J., DENG, X., ZHANG, L. & BAI Z. (2006) Diet composition and foraging ecology of Asian elephants in Shangyong, Xishuangbanna, China. *Acta Ecologica Sinica*, 26, 309–316.
- CHEN, S., SUN, G.-Z., WANG, Y., HUANG, C., CHEN, Y., LIU, P. et al. (2021) A multistakeholder exercise to identify research and conservation priorities for Asian elephants in China. *Global Ecology and Conservation*, 27, e01561.
- CHEN, S., YI, Z.-F., CAMPOS-ARCEIZ, A., CHEN, M.-Y. & WEBB, E.L. (2013) Developing a spatially-explicit, sustainable and risk-based insurance scheme to mitigate human–wildlife conflict. *Biological Conservation*, 168, 31–39.
- CHEN, Y., MARINO, J., CHEN, Y., TAO, Q., SULLIVAN, C.D., SHI, K. & MACDONALD, D.W. (2016b) Predicting hotspots of human–elephant conflict to inform mitigation strategies in Xishuangbanna, southwest China. *PLOS ONE*, 11, e0162035.
- CONVENTION ON BIOLOGICAL DIVERSITY (2010) *COP 10 Decision X/2. Strategic Plan for Biodiversity 2011–2020*. United Nations, New York, USA. [cbd.int/decision/cop/?id=12268](http://cbd.int/decision/cop/?id=12268) [accessed November 2022].
- DE LA TORRE, J.A., WONG, E.P., LECHNER, A.M., ZULAIKHA, N., ZAWAWI, A., ABDUL-PATAH, P. et al. (2021) There will be conflict – agricultural landscapes are prime, rather than marginal, habitats for Asian elephants. *Animal Conservation*, 24, 720–732.
- FENG, L. & ZHANG, L. (2005) Habitat selection by Asian elephant (*Elephas maximus*) in Xishuangbanna, Yunnan, China. *Acta Theriologica Sinica*, 25, 229–236. [In Chinese]
- FERNANDO, P., DE SILVA, M., JAYASINGHE, L., JANAKA, H. & PASTORINI, J. (2021) First country-wide survey of the Endangered Asian elephant: towards better conservation and management in Sri Lanka. *Oryx*, 55, 46–55.
- FERNANDO, P., WIKRAMANAYAKE, E.D., JANAKA, H.K., JAYASINGHE, L.K.A., GUNAWARDENA, M., KOTAGAMA, S.W. et al. (2008) Ranging behavior of the Asian elephant in Sri Lanka. *Mammalian Biology*, 73, 2–13.
- HE, Q., WU, Z., XU, F., GUO, X. & ZHU, Z. (2014) Human–elephant relations becoming crisis in Xishuangbanna, southwest China. In *Biocultural Landscapes: Diversity, Functions and Values* (eds S.-K. Hong, J. Bogaert & Q. Min), pp. 69–80. Springer, New York, USA.
- HE, S., GALLAGHER, L., SU, Y., WANG, L. & CHENG, H. (2018) Identification and assessment of ecosystem services for protected area planning: a case in rural communities of Wuyishan National Park pilot. *Ecosystem Services*, 31, 169–180.
- HIJMANS, R.J., PHILLIPS, S., LEATHWICK, J. & ELITH, J. (2017) *Species Distribution Modeling*. [rspatial.org/sdm](https://rspatial.org/sdm) [accessed 1 January 2019].
- HUANG, C., LI, X., HU, W. & JIANG, X. (2019a) Predicting indirect effects of transportation network expansion on Asian elephants: implications for environmental impact assessments. *Biotropica*, 52, 196–202.
- HUANG, C., LI, X., KHANAL, L. & JIANG, X. (2019b) Habitat suitability and connectivity inform a co-management policy of protected area network for Asian elephants in China. *PeerJ*, 7, e6791.
- KASS, J.M., MUSCARELLA, R., GALANTE, P.J., BOHL, C.L., PINILLA-BUITRAGO, G.E., BORJA, R.A. et al. (2021) ENMeval 2.0: redesigned for customizable and reproducible modeling of species' niches and distributions. *Methods in Ecology and Evolution*, 12, 1602–1608.
- KILHEFFER, C. & UNDERWOOD, H.B. (2018) Hierarchical patch delineation in fragmented landscapes. *Landscape Ecology*, 33, 1533–1541.
- KRAMER-SCHADT, S., NIEDBALLA, J., PILGRIM, J.D., SCHRÖDER, B., LINDENBORN, J., REINFELDER, V. et al. (2013) The importance of correcting for sampling bias in *MaxEnt* species distribution models. *Diversity and Distributions*, 19, 1366–1379.
- LEIMGRUBER, P., GAGNON, J.B., WEMMER, C., KELLY, D.S., SONGER, M.A. & SELIG, E.R. (2003) Fragmentation of Asia's remaining wildlands: implications for Asian elephant conservation. *Animal Conservation*, 6, 347–359.
- LI, B.V. & PIMM, S.L. (2016) China's endemic vertebrates sheltering under the protective umbrella of the giant panda. *Conservation Biology*, 30, 329–339.
- LI, W., LIU, P., GUO, X., WANG, L., WANG, Q., YU, Y. et al. (2018) Human–elephant conflict in Xishuangbanna prefecture, China: distribution, diffusion, and mitigation. *Global Ecology and Conservation*, 16, e00462.
- LIN, L., ZHANG, L., LUO, A., WANG, L. & ZHANG, L. (2011) Population dynamics, structure and seasonal distribution pattern of Asian elephant (*Elephas maximus*) in Shangyong Protected Area, Yunnan, China. *Acta Theriologica Sinica*, 31, 226–234. [In Chinese]
- LIU, C., WHITE, M. & NEWELL, G. (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, 40, 778–789.
- LIU, J., LINDERMAN, M., OUYANG, Z., AN, L., YANG, J. & ZHANG, H. (2001) Ecological degradation in protected areas: the case of Wolong Nature Reserve for giant pandas. *Science*, 292, 98–101.
- LIU, P., WEN, H., HARICH, F.K., HE, C., WANG, L., GUO, X. et al. (2017a) Conflict between conservation and development: cash forest encroachment in Asian elephant distributions. *Scientific Reports*, 7, 6404.
- LIU, S., YIN, Y., LIU, X., CHENG, F., YANG, J., LI, J. et al. (2017b) Ecosystem services and landscape change associated with plantation expansion in a tropical rainforest region of southwest China. *Ecological Modelling*, 353, 129–138.
- LV, T., ZHENG, X., ZHU, G., TANG, Y., JIANG, G., LI, Z. & CHEN, M. (2019) Dynamics analysis of Xishuangbanna Mengla Asian elephant population. *Forestry Construction*, 6, 91–96. [In Chinese]
- PRAJAPATI, A. (2008) *Nutrient analysis of important food tree species of Asian elephant (Elephas maximus) in hot-dry season in Bardia National Park, Nepal*. MSc thesis. Kathmandu University, Dhulikhel, Nepal.
- PYKE, C.R. (2007) The implications of global priorities for biodiversity and ecosystem services associated with protected areas. *Ecology and Society*, 12, 4.
- QIN, Y., NYHUS, P.J., LARSON, C.L., CARROLL, C.J., MUNTIFERING, J., DAHMER, T.D. et al. (2015) An assessment of south China tiger



- reintroduction potential in Hupingshan and Houhe National Nature Reserves, China. *Biological Conservation*, 182, 72–86.
- R CORE TEAM (2013) *R: A Language and Environment for Statistical Computing*. R Core Team, Vienna, Austria.
- REVELLE, W. (2019) *Procedures for psychological, psychometric, and personality*. [personality-project.org/r/psych](https://personality-project.org/r/psych) [accessed 1 February 2019].
- SONG, X.P., HANSEN, M.C., STEHMAN, S.V., POTAPOV, P.V., TYUKAVINA, A., VERMOTE, E.F. & TOWNSHEND, J.R. (2018) Global land change 1982–2016. *Nature*, 560, 639–643.
- UNEP-WCMC, IUCN & NGS (2018) *Protected Planet Report 2018*. UNEP-WCMC, IUCN and NGS, Cambridge, UK, Gland, Switzerland, and Washington, DC, USA.
- WANG, L., YANG, B., BAI, Y., LU, X., CORLETT, R.T., TAN, Y. et al. (2021) Conservation planning on China's borders with Myanmar, Laos, and Vietnam. *Conservation Biology*, 35, 1797–1808.
- WANG, Q.Y., CHEN, Y. & SHI, K. (2018) Prediction of potential distribution area of *Elephas maximus* in Menghai County based on MaxEnt model. *Forest Inventory and Planning*, 43, 36–41. [In Chinese]
- WANG, Q.Y., TAO, Y.X., LI, J.S., DONG, Z., YAN, B. & YANG, H.P. (2017) Factors on transition of distribution of the wild Asian elephant in Xishuangbanna. *Forest Inventory and Planning*, 42, 113–118. [In Chinese]
- WILSON, G., GRAY, R.J. & SOFYAN, H. (2020) Identifying the variation in utilization density estimators and home ranges of elephant clans in Aceh, Sumatra, Indonesia. *European Journal of Wildlife Research*, 66, 88.
- WU, R., LONG, Y., MALANSON, G.P., GARBER, P.A., ZHANG, S., LI, D. et al. (2014) Optimized spatial priorities for biodiversity conservation in China: a systematic conservation planning perspective. *PLOS ONE*, 9, e103783.
- XU, W., PIMM, S.L., DU, A., SU, Y., FAN, X.Y., AN, L. et al. (2019) Transforming protected area management in China. *Trends in Ecology and Evolution*, 34, 762–766.
- XU, W., XIAO Y., ZHANG J., YANG, W., ZHANG, L., HULL, V. et al. (2017) Strengthening protected areas for biodiversity and ecosystem services in China. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 1601–1606.
- YANG, F. & ZHANG, L. (2012) Population genetic structure and population genetic diversity analysis based on mitochondrial DNA of Asian elephant (*Elephas maximus*) in China. *Acta Theriologica Sinica*, 32, 90–100. [In Chinese]
- YUNNAN FORESTRY AND GRASSLAND ADMINISTRATION (2016) *Annual Report of the Nature Reserve of Yunnan Province*. Yunnan Forestry and Grassland Administration, Kunming, China. [In Chinese]
- ZHANG, J. & CAO, M. (1995) Tropical forest vegetation of Xishuangbanna, SW China and its secondary changes, with special reference to some problems in local nature conservation. *Biological Conservation*, 73, 229–238.
- ZHANG, J., CORLETT, R.T. & ZHAI, D. (2019) After the rubber boom: good news and bad news for biodiversity in Xishuangbanna, Yunnan, China. *Regional Environmental Change*, 19, 1713–1724.
- ZHANG, L., DONG, L., LIN, L., FENG, L., YAN, F., WANG, L. et al. (2015) Asian elephants in China: estimating population size and evaluating habitat suitability. *PLOS ONE*, 10, e0124834.
- 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 Theriologica Sinica*, 23, 185–192. [In Chinese]
- ZHOU, D. & GRUMBINE, R.E. (2011) National parks in China: experiments with protecting nature and human livelihoods in Yunnan Province, Peoples' Republic of China (PRC). *Biological Conservation*, 144, 1314–1321.
- ZHU, P., HUANG, L., XIAO, T. & WANG, J. (2018) Dynamic changes of habitats in China's typical nature reserves on spatial and temporal scales. *Journal of Geographical Sciences*, 73, 92–103.