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Research article

Broad scale functional connectivity for Asian elephants in the Nepal-India transboundary region

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ABSTRACT

The Nepal-India transboundary region hosts one of Asia's most complex large mammal assemblages, including a small (but growing) population of Asian elephants (*Elephas maximus*). These elephants occur in four widespread and geographically disjunct subpopulations, and some of them undergo seasonal transboundary movements. We conducted a broad-scale evaluation of the amount and quality of elephant habitat available in the region and of functional landscape connectivity between and within subpopulations using Maxent, circuit theory, and least-cost path analysis. Habitat suitability was highly influenced by abiotic geographical factors (altitude and precipitation) and less by ecological factors (habitat heterogeneity, plant productivity) and human disturbance (distance to settlements). The region had a relatively small amount of high and optimal suitability habitat (12.6% out of 93,700 km^2) but all subpopulations seem to be far from carrying capacity, suggesting ample potential for further population growth. Landscape connectivity was higher between and within the west and far-west subpopulations, which should be considered a single subpopulation. The central and ea st subpopulations, however, had low to very low between-subpopulation connectivity. Conservation priorities include maintaining the current connectivity in the west subpopulation and across the border in the east, and protecting high-quality habitats in eastern Nepal. Restoring connectivity between the central and other subpopulations is possible if the number of elephants continues growing, and it should be a long-term conservation aspiration. Maintaining and enhancing landscape connectivity in this region requires transboundary cooperation and coordination between Nepali and Indian authorities. If successful, it will bring considerable benefits for the conservation of elephants and other wildlife.

1. Introduction

Human pressures have resulted in widespread loss and fragmentation of natural habitats (Venter et al., 2016), with dramatic consequences for wildlife conservation. The combined effects of reduced fragment area, increased fragment isolation, and increased edge habitat can result in reductions of animal abundance, movement between fragments, and ecological function (Haddad et al., 2015) and increases of human-wildlife conflicts (Acharya et al., 2017). Landscape functional connectivity is the ease of animal movement among points or resource patches (Taylor et al., 1993) and it depends on the characteristics of and distances between habitat patches and on the suitability and permeability of the matrix (Mimet et al., 2013). The impacts of habitat loss and fragmentation are particularly severe for megafauna, wide-ranging animals with large resource requirements that often come into conflict with people (Ripple et al., 2016).

The identification and protection of ecological corridors is important for wildlife conservation in fragmented landscapes (Phillips et al., 2021). The combined study of habitat suitability and ecological corridors has been used to identify spatial conservation priorities for threatened species (Zhang et al., 2021) and for groups of species sharing the same habitat (Liu et al., 2018). Circuit theory (McRae, 2006) and least-cost path modelling (Adriaensen et al., 2003) are two approaches commonly used for corridor planning. Circuit theory, analogous to an electric circuit, identifies multiple paths with low resistance and helps to understand the effects of landscape configuration on animal

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distribution, while least-cost path models identify a single path with the least resistance, assumed to be the single best possible route for movement between two patches. Both models use a resistance raster that measures the ease of movement between pixels and can be parameterized using a habitat suitability model (but see Scharf et al., 2018). Here we used Maximum Entropy (Maxent) to identify habitat suitability and both circuit theory and least-cost path modelling to evaluate broad scale landscape connectivity for an endangered megaherbivore, the Asian elephant (*Elephas maximus*), in the Nepal-India transboundary region (NITR).

Nepal's southern region of the Chure foothills and the Terai Arc (Fig. 1) is home to one of Asia's most complex and diverse assemblages of large mammals (MFSC, 2015), including a small and highly fragmented population of wild Asian elephants. Until the mid-20th century, the region was covered in dense and contiguous subtropical deciduous and riverine forests and probably hosted ~25 elephants/100 km^2 (Smith and Mishra, 1992). After large-scale malaria eradication and human settlement programs, there was a severe reduction of the region's forest cover (Sudhakar Reddy et al., 2018) and elephant numbers. Nepal's wild elephant population was on the verge of extinction in the 1990s but has increased since, largely due to immigration from India (Pradhan et al., 2011). For example, elephants were functionally extinct in Bardia National Park (NP) until 1994, when ~45 individuals recolonized the area, most likely coming from India (Pradhan et al., 2011). Bardia has now ~80 resident elephants (Flagstad et al., 2012).

Nepal's wild elephants occur in four geographically disjunct subpopulations (east, central, west, and far west; Fig. 1) and they can be classified in two types based on their seasonal movements: resident (those that stay year-round in Nepal) and itinerant (those that move seasonally between Nepal and northern India) (DNPWC, 2008). The number of Nepal's resident elephants is estimated in 227 individuals (45 in the east, 53 in the central, 113 in the west, and 26 in the far west subpopulation; Ram and Acharya, 2020). Three of these subpopulations (east, west, and far west) receive regular seasonal visits of itinerant elephants from India, while the central subpopulation is exclusively resident. The recent increase in elephant numbers has led to a rapid escalation of human-elephant conflicts (HEC; Pradhan et al., 2011; Neupane et al., 2014), especially in the east, where elephants occur almost entirely outside PAs.

The small, widespread, and fragmented elephant population in the NITR underscores the importance of broad-scale conservation planning and management strategies (Pradhan et al., 2011) and of transboundary collaboration (DNPWC, 2008). As the population continues growing, it is important to understand the amount and quality of habitat available for elephants, especially in areas that might soon be recolonized. Also, the long-term survival of this small and fragmented population is highly dependent on connectivity between subpopulations and their capacity to function as a metapopulation. Therefore, here we present a broad-scale spatial analysis to evaluate (a) factors that drive habitat suitability for elephants in the region, (b) amount and quality of suitable habitat available, and (c) functional landscape connectivity in the region, especially between the four elephant subpopulations and the key PAs within them.

2. Materials and methods

2.1. Study area

The study area (27°06′-26°05′N, 88°43′-79°50′E) covers 93,722 km^2, encompassing the southern belt of Nepal (Terai and Chure foothills; 37,336 km^2), and parts of northern India (55,129 km^2) and Bangladesh (1257 km^2) within 50 km from Nepal's border (Fig. 1). The area comprises three ecoregions (Himalayan subtropical broadleaf forest, Gangetic plains moist deciduous forest, and Terai-Duar savannas and grasslands) and nine forest types (Chaudhary and Subedi, 2019). The study area includes 28.7% of forest, 3.8% of grassland, and 2.0% of waterbodies, plus 51.5% of croplands, 12.8% of built-up area, and 1.3% of bare land (see details in Table S1). It also includes six PAs in Nepal, six

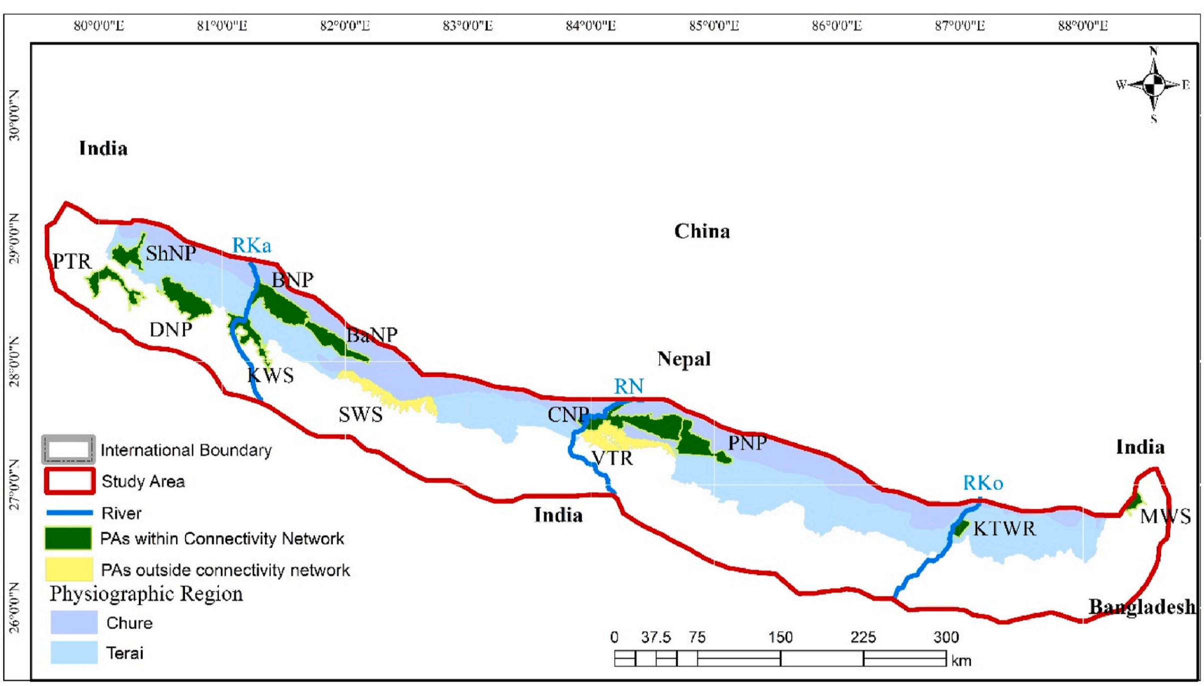

Fig. 1. Extent of the study area showing the Terai (blue) and Chure (purple) regions in Nepal, 12 protected areas (in green), and major rivers (blue lines) demarcating the four sectors: eastern sector right to the River Koshi (RKa), central between River Koshi (RKa) and River Narayani (RN), western between River Narayani (RN) and River Karnali (RKa), and far-western, left to River Karnali (RKa) Protected Areas: PTR: Pilibhit Tiger Reserve; ShNP: Shuklaphanta National Park; DNP: Dudhwa National Park; BNP: Bardia National Park; KWS: Katarniaghat Wildlife Sanctuary; BaNP: Banke National Park; SWS: Suhelwa Wildlife Sanctuary; VTR: Valmiki Tiger Reserve; CNP: Chitwan National Park; PNP: Parsa National Park; KTWR: KoshiTappu Wildlife Reserve; MWS: Mahananda Wildlife Sanctuary. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

in India, and none in Bangladesh. We divided the study area into four sectors based on the current elephant subpopulations: i.e., the eastern, central, western, and far-western sectors. These sectors are naturally divided by rivers (Fig. 1). Since Bangladesh represents a small part (1.3%) of the study area, where elephants currently do not occur, we will generally refer to the study area as the 'Nepal-India transboundary region' (NITR).

2.2. Field surveys

We conducted surveys in Nepal, in areas of known elephant activity based on interviews with local people, forest officials, and park officials. Accordingly, we surveyed inside PAs, in PAs' buffer zones, and in national and community forests.

Elephant presence locations were collected from 2011 to 2015 by walking in a center-line transect ($n = 168$; with dimension of approximately 10 km long and 100 m wide) in a grid of 10×10 km^2 (Fig. S1). Within each transect, a survey team walked along trails, fire breaks, roads, or creek beds in search of elephant signs. Each transect was sampled twice, once during September/October and later during November/December. We chose this sampling period because the rainy season has ended by then (facilitating field logistics) and HEC incidence is higher than average (Neupane et al., 2014). Tracks and signs of elephant damage were used to help locate dung samples; however, only fresh dung piles (estimated to be less than 48 h old) were considered for presence data. Locations were recorded using GPS (model: GPSMAP®64ST, accuracy$\pm$10 m) based on the GCS WGS 1984 reference system.

2.3. Presence points and environmental variables

We initially used a total of 525 elephant presence points. To reduce spatial autocorrelation and sampling bias, presence points were spatially filtered, and we used only one point when multiple points were within 1 km from each other (Boria et al., 2014). After filtering, we retained 231 points for the final model. We used topographic, vegetation, and disturbance-based environmental variables that have been previously described to influence Asian elephant habitat use (de la Torre et al., 2021; Neupane et al., 2019; Rood et al., 2010) plus variables such as soil bulk density, clay content, or soil coarse fragment that we speculated might be correlated with vegetation and food availability, and hence influence elephant movements. We considered a total of 22 variables, however, three of them (solar radiation, annual temperature, and pH) were excluded from the final model, as they were correlated ($r \geq |0.8|$) with other variables (Table S2). See Appendix S1 and Table S3 for details on the environmental variables, their sources, and how we processed them. All presence data, as well as the environmental variables, were converted to South Asia Albers equal-area conic projection.

2.4. Maxent modelling and variable importance

We used Maxent (Phillips et al., 2006) to model Asian elephant habitat suitability in the study area. Maxent has the advantages of not requiring absence data (i.e., it operates with presence-only data) and having a superior ability than other models to predict species' distribution (Elith et al., 2006), even with a small number of data points (Støa et al., 2019). To run the model, the presence points were divided in training and testing datasets in a ratio of 60:40 (Heumann et al., 2013). Because presence-only data is prone to sampling bias where much sampling occurs in a place convenient to the surveyor, Phillips and Dudík (2008) recommend the use of a bias file which helps to select background points with a similar bias and reduce model over-fitting. Known presence points can then be contrasted against these unmeasured background points to predict habitat suitability (Merow et al., 2013). Accordingly, we created a bias file using Gaussian Kernel density and extracted 1000 background points in the *dismo* package (Hijmans et al., 2017) of R (R Core Team, 2021). To reduce potential over-fitting, we compared models fitted with different options of Maxent's regularization multiplier (RM) and 'features' and retained the options that produced the most parsimonious model. Altering the regularization multiplier reduces the risk of precise fitting of the data (Phillips and Dudík, 2008) by penalizing complex models (Merow et al., 2013), while the use of different features allows the comparison of different relationships between variables and suitability, from simple to more complex. We used regularization multipliers 1 to 5 (RM_1-RM_5) and features linear, quadratic, hinge, and their combination. We performed model fine-tuning and selection (considering only models with ΔAICc <2) in R environment using *ENMEval2.0* (Kass et al., 2021). We ran the final model with 20 replicates using both presence and background points and the most parsimonious regularization multiplier and feature estimates. We used R's package *sdm* (Naimi and Araújo, 2016) to calculate the relative importance of each variable (correlation tests) and to run the Maxent model. This test randomly permutes variables to be studied and then calculates the correlation between predicted and permuted values, giving higher correlation for variables with lower importance (Naimi and Araújo, 2016). Model accuracy was evaluated using area under the receiver operating characteristic curve (AUC) and True Skilled Statistics (TSS; Allouche et al., 2006) using test data. We converted the predicted probability to four categories of habitat suitability, which we defined combining approaches from Liu et al. (2005) and Convertino et al. (2014). First, we identified unsuitable areas using sensitivity-specificity sum maximization (Liu et al., 2005), which in our case resulted in habitat suitability values of [0–0.11]. Then, we used thresholds consistent with Convertino et al. (2014) to classify habitat suitability in the remaining areas as: low-medium (0.11–0.4], high (0.4–0.6], and optimal (0.6–1.0] habitat suitability. Unsuitable habitats are those not used by elephants; while low-medium, high, and optimal suitability areas can be described as habitats rarely, regularly, and frequently used by elephants. We considered optimal and high suitability area as elephants' 'potential habitat'.

2.5. Analysis of habitat patches and connectivity

Elephant ease of movement was analyzed using two methods (Acharya et al., 2017): current flow and (Adriaensen et al., 2003) least cost path. First, we obtained the habitat suitability model using Maxent from the species distribution model, which we used to prepare a model of resistance by the landscape. Then, we applied a linear transformation of the obtained habitat suitability model using the function (1- habitat suitability index) to parameterize the landscape resistance (Huang et al., 2019). The resistance model thus extended between 0 and 1, with 0 representing the least and 1 the maximum resistance. Being complementary in nature, we used both LCP length (Adriaensen et al., 2003) and current flow (McRae et al., 2008) to identify corridors to connect key PAs and different elephant subpopulations in the study area. We used the ten PAs (excluding Suhelwa Wildlife Sanctuary and Valmiki Tiger Reserve) in the study area where elephants are known to occur as nodes to model the corridors. We ran an algorithm that calculated the cumulative sum of the resistance of the initial step, and the average of the resistance between the initial and the next step, later the LCP length was derived after all possible paths were evaluated (Adriaensen et al., 2003). Current flow derives its origin from circuit theory, where the total current flowing in a landscape is equal to the cumulative sum of conductance on the landscape (McRae, 2006). Least-cost path modelling was done in ArcGIS toolbox "Linkage Mapper" (McRae and Kavanagh, 2011) and the current flow modelling was done using the *Circuitscape* software (McRae et al., 2008). We elaborated a current flow map following Koen et al. (2014), adding nodes outside the study area. Specifically, we buffered 20% of the longest width of the study area, placed 50 nodes at equal distances along the outer edge of the buffer, calculated the pairwise current between all nodes, and then averaged for a final composite score in each pixel.

2.6. Analysis of importance of corridor and patches

We assessed the relative importance of corridors and patches for overall network connectivity using the software *Conefor2.6* (Saura and Torné, 2009) to calculate the integral index of connectivity (IIC) and probability of connectivity (PC) values for nodes (PAs) and links (corridors). The relative importance of the corridor or patch is calculated as the change in the metric (dIIC and dPC) after removal of the patch or corridor (Saura and Pascual-Hortal, 2007). We calculated the distance between PAs using LCP length from the border of the PAs. Based on a recently recorded long-distance Asian elephant dispersal event (Campos-Arceiz et al., 2021), we used 300 km as the connectivity threshold to calculate IIC (Pascual-Hortal and Saura, 2006). We converted the distance into a probability value using the 'distance to probability' conversion inbuilt in Conefor software, which computes the internode dispersal probability as a decreasing negative exponential function of distance. For this, we gave a probability of 0.05 for the dispersal distance (300 km) used as connectivity threshold in this study (Saura and Pascual-Hortal, 2007). Additionally, we evaluated the effect of the chosen threshold on dPC values by conducting the analyses using shorter (100 and 200 km) and longer (400 km) distances. Since patterns were generally consistent across threshold distances, here we report results for the 300 km threshold, while the additional results are presented in the online supplement. Thus, LCP length was used to identify the shortest appropriate (suitable) corridor to connect the elephant habitat patches, while current flow analysis contributed to evaluate the corridors permeability for elephants to move from one patch to another in a random walk. We used Jenks natural breaks optimization to break down dPC and dIIC values of nodes and links into five categories ranging from very low to very high importance.

3. Results

3.1. Model performance and variable importance

The final Maxent model had a weighted AICc of 80.5% and AUC and TSS values of 0.76 ± 0.019 and 0.43 ± 0.03, respectively, indicating a moderate discrimination ability.

The model included linear, quadratic, hinge, and RM_2 parameters (see Table S4 for the results of the model selection procedure). All 19 variables considered were included in the final model, although their relative importance differed considerably (Fig. 2). Altitude (relative importance = 26.7%) was the most important variable, followed by annual precipitation (16.4%), heterogeneity index (13.5%), NDWI (11.9%), and distance to settlements (10.3%). Other, less important variables were distance to grassland (5.7%), proportion of forest (5.5%), and slope (5.2%). Additionally, nightlight illumination (0.9%), proportion of grass (0.5%), and sand (0.4%) barely contributed to the model.

The response curve analysis (Fig. S2) suggests that elephants in our study area preferred areas with low altitude (preferably below 200 m asl), annual accumulated precipitation between 2000 and 2700 mm, greater landscape heterogeneity, intermediate values of NDWI, low NDVI values, low slopes, and bulk density below 140 kg/m^3. Additionally, elephants preferred areas near forest, grass, water, and road networks; and far from human settlements.

3.2. Habitat suitability

The study area presented relatively low overall habitat suitability for elephants, with just 1.5% of the study area presenting optimal suitability, 11.1% high suitability, 45.5% low-medium suitability, and 42.2% being classified as unsuitable (Fig. 3 and Table 1). The percentage of potential habitat was higher in Nepal (24.4% of the area) than in India (4.5%). By sectors, the largest amount of potential habitat was found in the central sector (overall: 3468 km^2; Nepal: 3068 km^2), followed by the far-western sector (overall: 3293 km^2; Nepal: 1997 km^2), western (overall: 2626 km^2; Nepal: 2408 km^2), and eastern sector (overall: 2387 km^2; Nepal: 1643 km^2; Table 1).

Habitat suitability was much higher within PAs. Nepal's PAs provided 1962 km^2 of potential habitat (54.8% of PAs total area) while India's provided 1084 km^2 (44.6% of PAs total area). Koshi Tappu Wildlife Reserve (WR), in eastern Nepal, lacked optimal suitability habitat and had only a small portion (2.3%) of high suitability area. Community forests in the east of Koshi Tappu WR, however, showed greater suitability for elephant conservation (Fig. 3d). In India, only Dudhwa NP (825 km^2, 65% of its area) and Pilibhit Tiger Reserve (TR; 202 km^2, 33.5% of its area), both in the far-west sector, provided abundant potential habitat for elephants.

3.3. Patch importance, functional connectivity, and potential corridors

Our model identified the relative importance of the different PAs for functional connectivity within the study area, with dPC and dIIC results showing high consistency (Table 1). Dudhwa and Bardia NPs had very

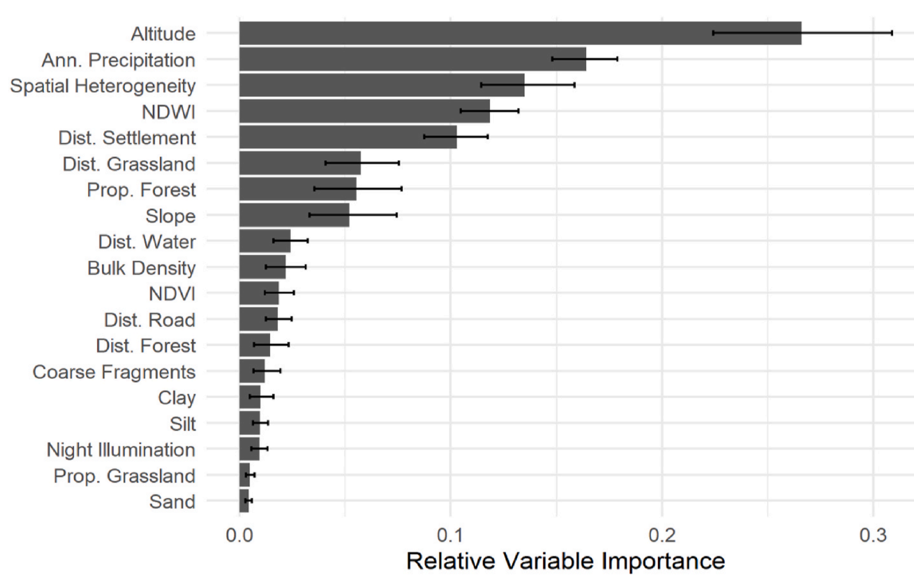

Fig. 2. Relative variable importance (with SE) for the distribution of Asian elephants in the trans-boundary region of Nepal, India, and Bangladesh, based on correlation metrics.

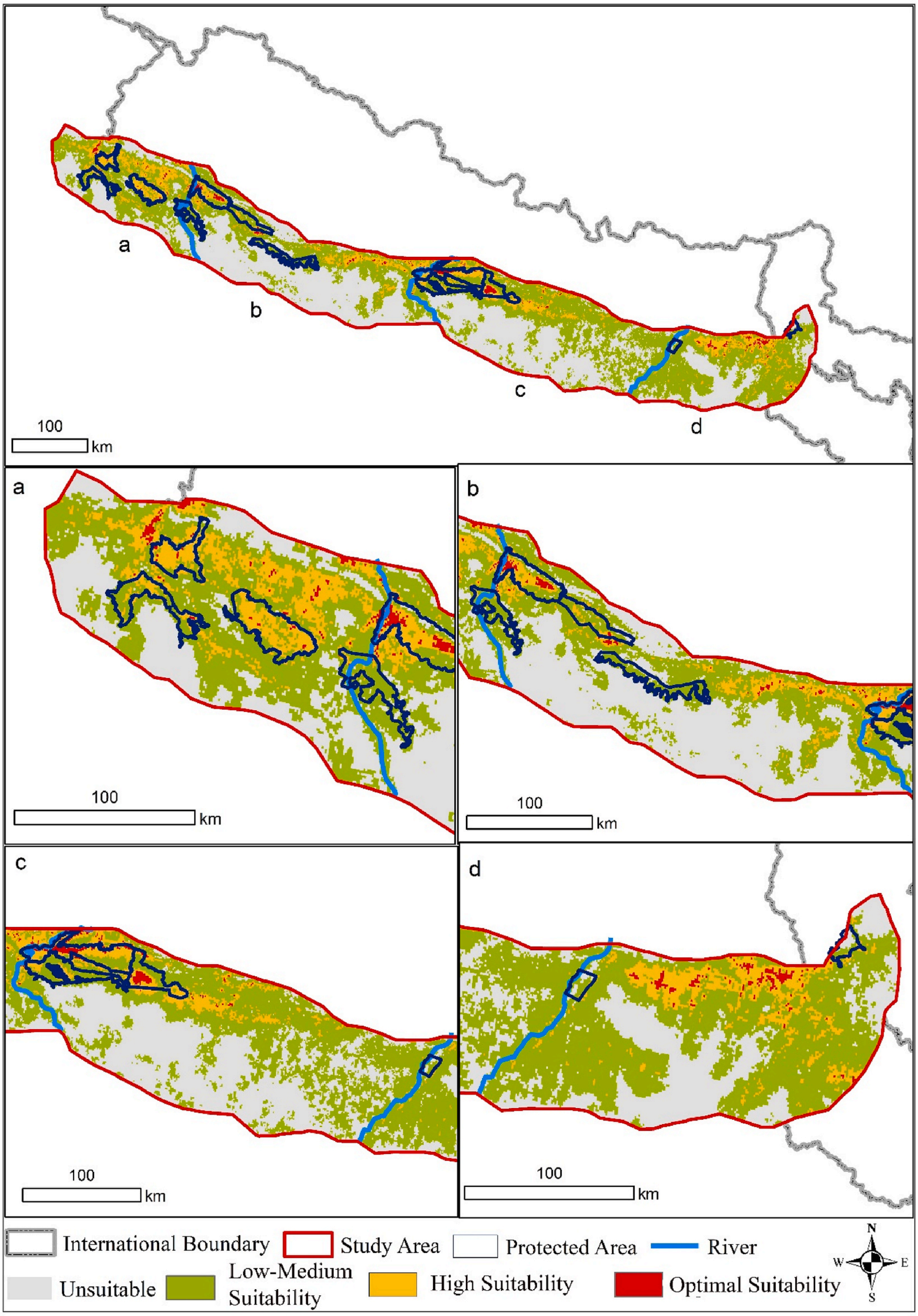

Fig. 3. Habitat suitability for Asian elephants in the Nepal-India transboundary region with details for the (a) far-western, (b) west, (c) central, and (d) eastern sectors.

high importance, and their exclusion resulted in over 30% loss of overall connectivity; Pilibhit TR had high importance, while Banke and Chitwan NPs scored either high or medium in importance for different metrics; Parsa and Shuklaphanta NPs had low importance; and Koshi Tappu WR and Mahananda Wildlife Sanctuary (WS) had very low importance, with their exclusion resulting in less than 3.5% loss of overall connectivity in the study area (Table 1). The results of the sensitivity analysis were also consistent across dispersal thresholds (i.e., 100, 200, and 400 km; Table S5). The only remarkable difference between thresholds was that Banke NP's dPC had low importance with the 100 km threshold but its dIIC had very high importance with the 400 km threshold.

The western sector presented the greatest current flow, indicating higher permeability to elephant movement, especially along the Chure foothills, but also across the international border (Fig. 4a). Additionally,

Table 1
Habitat suitability values for Asian elephants in the Nepal-India transboundary region. Areas are expressed in km^2. Numbers under parentheses represent the percentage of area. dPC = change in probability of connectivity; dIIC = change in connectivity integral index. PAs = protected areas. BNP: Bardia National Park; CNP: Chitwan National Park; BaNP: Banke National Park; PNP: Parsa National Park; ShNP: Shuklaphanta National Park; KTWR: Koshi Tappu Wildlife Reserve; DNP: Dudhwa National Park; KWS: Katarniaghat Wildlife Sanctuary; PTR: Pilibhit Tiger Reserve; MWS: Mahananda Wildlife Sanctuary. VL = very low importance; L = low importance; M = medium importance; H = high importance; VH = very high importance of PAs.

PAs	Total Area	Unsuitable	Low-medium suitability	High suitability	Optimal suitability	dPC (LC)	dIIC (LC)
Nepal							
BNP	968	93 (9.7)	334 (34.5)	369 (38.1)	172 (17.7)	30.43 (VH)	31.80 (VH)
CNP	953	1	238 (25.0)	495 (51.9)	219 (23.0)	**16.96 (H)**	**13.57 (M)**
BaNP	550	54 (10.0)	386 (70.1)	102 (18.5)	8 (1.4)	**12.97 (M)**	**18.07 (H)**
PNP	627	2 (0.3)	251 (40.1)	267 (42.5)	107 (17.0)	11.53 (L)	10.86 (L)
ShNP	305	4 (1.2)	82 (26.9)	208 (68.3)	11 (3.6)	9.11 (L)	10.02 (L)
KTWR	175	53 (30.2)	118 (67.4)	4 (2.3)	0	0.64 (VL)	3.37 (VL)
Subtotal Nepal PAs	3578	207 (5.8)	1409 (39.4)	1445 (40.4)	517 (14.4)		
Nepal Outside PAs	33,758	8150 (24.1)	18,460 (54.7)	6414 (19)	734 (2.2)		
Subtotal Nepal	**37,336**	**8357 (22.4)**	**19,869 (53.2)**	**7859 (21.0)**	**1251 (3.4)**		
India							
DNP	1270	8 (0.6)	437 (34.4)	801 (63.1)	24 (1.9)	40.98 (VH)	41.72 (VH)
KWS	401	31 (7.7)	329 (82.0)	39 (9.8)	2 (0.5)	14.41 (M)	13.16 (M)
PTR	603	5 (0.8)	396 (65.7)	197 (32.7)	5 (0.8)	16.69 (H)	19.80 (H)
MWS	158	65 (41.3)	77 (48.8)	16 (9.9)	0	0.36 (VL)	1.56 (VL)
Subtotal India PAs	2431	109 (4.5)	1239 (50.9)	1053 (43.3)	31 (1.3)		
India outside PAs	52,698	30,940 (58.7)	20,338 (38.6)	1326 (2.5)	93 (0.2)		
Subtotal India	**55,129**	**31,049 (56.3)**	**21,577 (39.2)**	**2379 (4.3)**	**124 (0.2)**		
Bangladesh	1257	146 (11.6)	950 (75.6)	152 (12.1)	9 (0.7)		
Sectors	16,032	4913 (30.7)	7826 (48.8)	3064 (19.1)	229 (1.4)		
Far west							
West	28,532	15,356 (53.8)	10,550 (37.0)	2316 (8.1)	310 (1.1)		
Central	31,285	13,942 (44.6)	13,875 (44.3)	2874 (9.2)	594 (1.9)		
East	17,873	5341 (29.9)	10,145 (56.8)	2136 (11.9)	251 (1.4)		
Total Study Area	**93,722**	**39,552 (42.2)**	**42,396 (45.2)**	**10,390 (11.1)**	**1384 (1.5)**		

current flow was generally lower at the tip of the far western and eastern sectors. The current flow model suggested that elephants would find higher permeability to move from Parsa NP, in the central sector, to Bardia NP in the west, and also eastward towards the eastern sector. The LCP analysis was consistent and suggested that elephants could move efficiently within Nepal through the Chure foothills' forest-agriculture mosaics (Fig. 4b). In the eastern sector, however, the LCP traversed areas of settlements and farmlands near forests.

In terms of LCP between elephant subpopulations, the west and far west sectors had the best inter-population connectivity with three corridors connecting Bardia NP (west) with Katarniaghat WS and Dudhwa NP (far west; Fig. 4c and Table S6). The ~300-km corridor connecting the central (Chitwan NP) with the western sector (Banke NP) had a low importance (dPC = 0.21), despite its central location in the study area; while the corridor connecting the east (Koshi Tappu WR) with the central sector (Parsa NP) had very low importance (dPC = 0.08) for maintaining connectivity.

Within subpopulations, there was higher probability of transboundary connectivity in the west sector (corridor connecting Bardia NP with Katarniaghat WS; dPC = 3.8), and high connectivity in the far west sector (two paths with dPCs = 2.15 and 1.24), while the link between Mahananda WS and Koshi Tappu WR, in the eastern sector, had very low (dPC = 0.08) to medium (dIIC = 1.36) importance.

4. Discussion

This is the first broad-scale evaluation of habitat suitability and landscape connectivity for any wildlife species in the NITR. Asian elephants' habitat suitability and range shifts, however, had been previously studied in South Asia, in the context of climatic change (Kanagaraj et al., 2019). Overall, we found that a relatively small proportion of the region is suitable for Asian elephants and that landscape connectivity is better in the western half of the study area.

4.1. Environmental variables

Elephants in our study area preferred lowlands (<200 masl) with accumulated annual precipitation up to ~2700 mm, intermediate levels of plant productivity (NDVI: 0.1–0.3), high habitat heterogeneity (heterogeneity index >1.5), and far (>2 km) away from human settlements. Abiotic geographical factors had a high influence on our model of habitat suitability, with altitude and accumulated annual precipitation alone accounting for over 40% of the relative importance in the model, similar to previous findings in Indonesia (Rood et al., 2010) and Nepal's Western Terai (Sharma et al., 2020; Neupane et al., 2019). We attribute this high influence of geography to the broad scale of our analysis and to the location of our study area at the northern edge of the species range, in a region with high topographic variability between the Terai Arc lowlands and the Himalayas' foothills. Ecological habitat factors were also important, particularly land cover heterogeneity and NDWI (values: −0.25–0), reinforcing the idea of Asian elephants' preference for forest edges, rather than cores (de la Torre et al., 2021). Further, human disturbance was also important in determining habitat suitability, with elephants showing a strong avoidance of people (distance to settlements). Despite this negative preference for settlements, the intense conflict in the study area (Neupane et al., 2014; Ram et al., 2021) shows the complexity of human-elephant spatial interactions, suggesting that elephants come into closer contact with people in some circumstances, perhaps during crop ripening seasons or when moving through highly fragmented parts of their home ranges.

Eleven of the 19 covariates included in our habitat suitability model had relatively low importance (<2.5%). Among these, it is worth noting soil-related variables such as bulk density, coarse fragment, clay, silt, and sand content, which may influence land use patterns (e.g., agriculture) and vegetation (e.g., Sanaei et al., 2019), and indirectly influence elephants' habitat preferences and movements.

4.2. Habitat suitability

The NITR had a relatively small area of potential elephant habitat

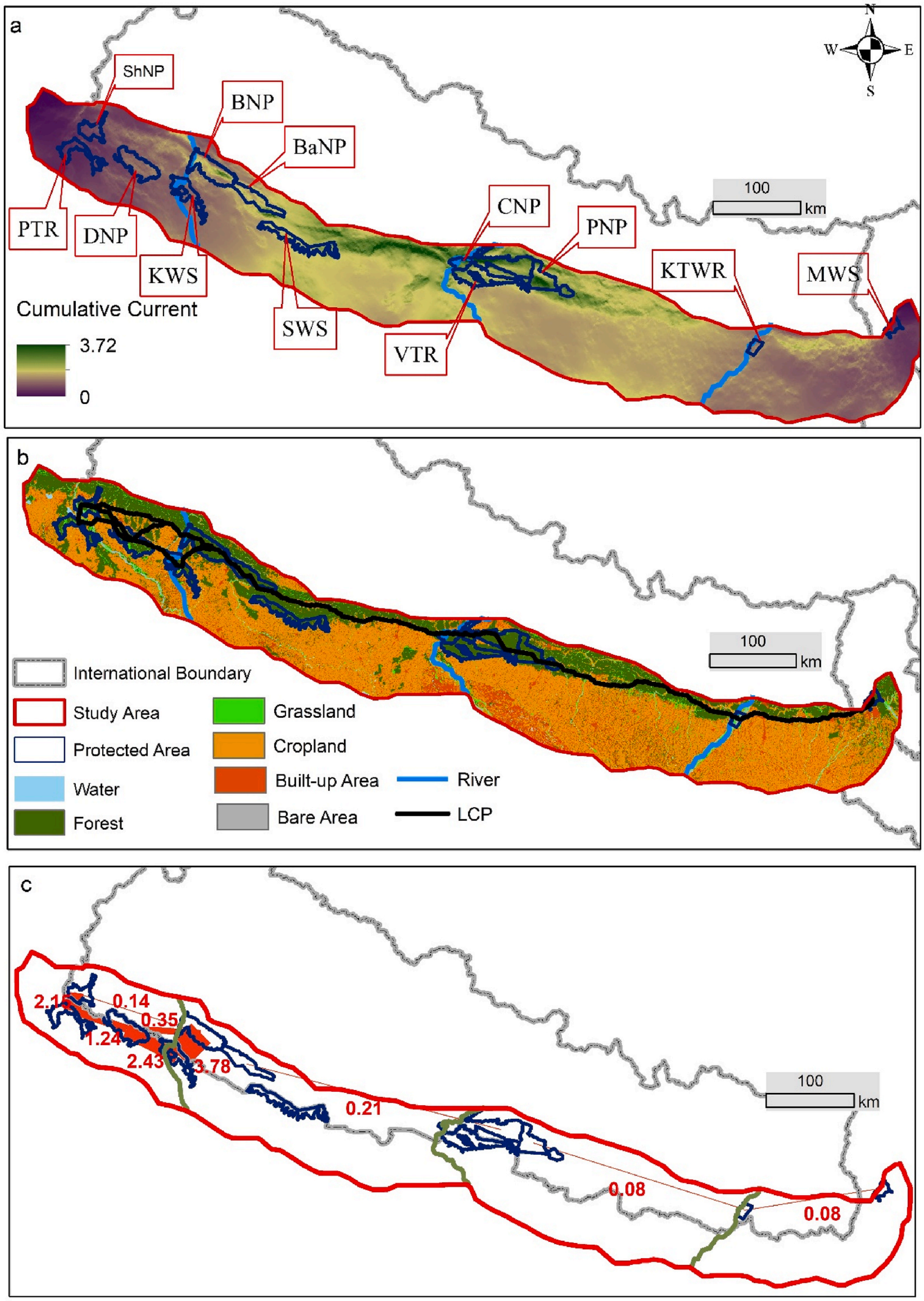

Fig. 4. Functional connectivity for Asian elephants in the Nepal-India transboundary region. a. current flow diagram indicating ease of elephant movement in the study area, b. Least cost path analysis for Asian elephant movement in Nepal and its trans-border region, c. dPC values for links between protected areas in the study area.

(12.6% out of ~93,700 km^2), with just 1.5% of the total presenting optimal suitability. The general scarcity of optimal habitat might be pushing elephants to use high and low-medium suitability areas (Neupane et al., 2020; Pradhan et al., 2011) and leading to the escalation of HEC in the region (Ram et al., 2021; Neupane et al., 2014).

Habitat suitability was higher in Nepal than in the Indian side, in the central and western sectors, and within PAs. If we consider the elephant population size in relation to the potential habitat available, the western sector holds the highest elephant density (4.7 ind./100 km^2 of potential habitat), followed by the eastern sector (2.7), and the central (1.7) and far western (1.3) sectors. Such densities are low for Asian elephants in South Asia. For example, Kaziranga NP, located at a similar latitude in the Indian state of Assam and with ecologically similar habitats, has an estimated density of >130 elephants per 100 km^2 (including all age and sex classes; Goswami et al., 2019). This suggests that elephant subpopulations in the NITR are far from ecological carrying capacity and have ample potential for growth, especially in the central sector where Chitwan and Parsa NPs offer suitable habitat with low risk of conflict with people.

Habitat suitability in PAs was considerably higher than outside them, with 39.6% of the optimal suitability habitat being inside PAs (despite PAs comprising just 6.4% of the study area), especially in Nepal (14.4% of PAs in Nepal presented optimal suitability, compared to just 1.3% in India). The lower adequacy of habitats inside and around Indian PAs might have influenced elephants' dispersal movements to Nepal (Neupane et al., 2014; Pradhan et al., 2011). Habitat quality inside PAs could be improved by promoting landscape heterogeneity inside Banke NP, Katarniaghat WS, Pilibhit TR, and Mahananda WS.

The remaining 60.4% of the optimal suitability habitat was located outside PAs, pointing out to the importance of elephant conservation outside PAs, e.g., in buffer zones and community forests (Neupane et al., 2020). This result is particularly relevant in the eastern sector, where the only PA is Koshi Tappu NP, with just 2.3% of potential elephant habitat, and where elephants occur largely outside PAs under intense conflict with local communities (Neupane et al., 2014). Thus, promoting human-elephant coexistence outside PAs requires careful mitigation of human-elephant conflict (Fernando et al., 2021).

4.3. Functional connectivity between and within populations

Functional connectivity is essential for the conservation of wide-ranging wildlife since isolated habitats restrict movement, limiting gene flow and access to key ecological resources (Zhang et al., 2021). In the NITR, functional connectivity between and within subpopulations is key for the survival of this highly fragmented elephant population. We found connectivity to be relatively high between the west and far west subpopulations (with three functional corridors), low between the west and central, and very low between the central and east subpopulations.

Based on our connectivity results, the west and far west sectors should be considered as a single subpopulation. This subpopulation has some substantial resident numbers (e.g., >80 elephants in Bardia) and regular movements of itinerant elephants through highly functional corridors between India and Nepal. Importantly, Shuklaphanta NP might be connected with a much larger (>1500 individuals) elephant population in the Indian states of Uttarakhand and Uttar Pradesh (Rangarajan et al., 2010). In Bardia NP there is genetic evidence of out-mating (ca. 60% heterozygosity) with high kinship coefficients between calves and adult females (Flagstad et al., 2012) because of itinerant elephants visiting from India (Neupane et al., 2014; Pradhan et al., 2011). The main barrier between these two sectors is the Karnali River, which is difficult for elephants to cross during the monsoon season. Protecting the existing connectivity in this west-far west subpopulation should be the top conservation priority in terms of connectivity in the region, which requires international cooperation since much of the connectivity occurs across the India-Nepal border. Habitat suitability in the corridors can be improved by promoting landscape heterogeneity by restoring grassland, forest, and waterholes.

The situation in the central subpopulation is more challenging, since the population is small (~50 elephants), it includes only two PAs (Chitwan and Parsa NP, both in Nepal), and it is largely isolated from other subpopulations. The main barrier to connect the central and western subpopulations is the relatively long distance (~300 km) between Chitwan and Banke NPs. Habitat conditions along the Chure foothills, however, are favorable and allow for optimism about connectivity between subpopulations in the mid to long term, especially if there is a considerable growth of the population numbers. Some districts in this gap area (West Nawalparasi and Rupandehi) have not experienced elephant presence in many decades, probably since the 1950s. Sporadic elephant presence, however, has been observed east of Banke NP (e.g., Dang and Kapilbastu districts) and west of Chitwan NP (East Nawalparasi; Ram et al., 2021). Habitat quality could be improved by restoring habitat in the foothills of Rupandehi District and promoting grassland management in the forests between Banke and Chitwan NPs. Maintaining habitat connectivity and mitigating HEC between Chitwan and Banke NPs are the main priorities in terms of connectivity for the central subpopulation.

The eastern subpopulation is also isolated due to the long distance to the central subpopulation (~260 km) and the scarcity of suitable habitats between them. Within the eastern sector, there is relatively high connectivity between India's Mahananda WS and Nepal's resident elephants, as evidenced by a large number of elephants (over 100 individuals) that cross the border seasonally in this sector (DNPWC, 2008; Pradhan et al., 2011) . Importantly, the eastern population seems connected with the very large elephant population in the Indian state of Assam (DNPWC, 2008). Elephants and their potential habitat, including some optimal suitability areas, in the eastern sector occur in community forests, not in PAs. Protecting transboundary connectivity and the available high and optimal suitability habitat should, therefore, be the conservation priorities for the eastern subpopulation. Connecting the eastern and central elephant subpopulations would require abundant habitat restoration to improve habitat suitability and should be considered as a longer-term aspiration.

4.4. Limitations and further studies

This study has several caveats worth discussing. First, we used a habitat suitability model to parameterize the resistance map later used for the connectivity analyses. While this approach is common in the literature (e.g., Huang et al., 2019; Liu et al., 2018; Zhang et al., 2021), animal preferences for habitat selection and dispersal are not necessarily the same (e.g., Dickson et al., 2013; Scharf et al., 2018; Vasudev et al., 2015) and dispersal may take place in sub-optimal permeable habitats that are unlikely to be suitable for the establishment of permanent home ranges (Mateo-Sánchez et al., 2015). Second, we collected elephant presence data exclusively in natural habitats and avoided using elephant presence from HEC incidents in highly disturbed environments, although these areas could also be used by elephants to disperse. For these two reasons, our results can be considered conservative and likely to underestimate the actual connectivity in the study area. A more accurate landscape resistance could be obtained from satellite telemetry data, which allows to distinguish between foraging and dispersal movement patterns (e.g., de la Torre et al., 2019). Third, Maxent might overestimate the probability of elephant occurrence (Gomes et al., 2018). In future studies, an ensemble model should be considered as a more robust way to handle uncertainties, particularly while predicting the responses to future conditions (Latif et al., 2013). Fourth, we used LCP's dPC and dIIC to evaluate connectivity, but several other metrics are available and could have added value to our analyses; e.g., LCP cumulative cost (Etherington and Penelope Holland, 2013), current score (Petsas et al., 2020), reachability attribute (Petsas et al., 2021), betweenness centrality (Bodin and Saura, 2010), steppingstone betweenness centrality (Petsas et al., 2021) and others that should be considered in future studies. Finally, the subjective choice of a connectivity dispersal distance (300 km in our case) could be another source of bias. To mitigate this risk, we conducted a sensitivity analysis that showed that the results did not vary much when using dispersal thresholds in the range of 100–400 km (Tables S4 and S5).

For future studies we recommend focusing on elephant ranging behavior, especially the seasonal movements between PAs across the India-Nepal border and the ecological drivers of such movements. Additionally, it would be important to better understand the ecological consequences of the elephant range expansion, especially in the context of complex large mammal assemblages as in Chitwan and Bardia NPs.

5. Conclusions

The NITR is home to a highly fragmented, widespread, and small but growing population of Asian elephants, some of which undergo seasonal movements between PAs in both countries. Although we found a relatively small (~13%) amount of potential elephant habitat in the region, the population is still very far from carrying capacity and there is, therefore, ample potential for population growth. This growth will often involve elephants expanding outside PAs, where they will come into conflict with people. Predicting and preparing to mitigate these future conflicts is key for elephant conservation and people's well-being in the region.

Our results demonstrate that the elephant population in the NITR is divided into three, rather than four, subpopulations with low to very low connectivity among them. The western subpopulation (including west and far west sectors) presents high internal connectivity. This subpopulation is the stronghold for Asian elephant conservation in the region; protecting its existing connectivity, especially across the international border, should be a top conservation priority. The central subpopulation is small and isolated from the other two subpopulations. The availability of high-quality habitats (Chitwan and Parsa NPs) should allow for the central subpopulation to continue growing with relatively few conflicts with people. Elephant translocation from other subpopulations should be considered as an option to increase genetic diversity. The eastern subpopulation, although isolated from other subpopulations, presents effective transboundary connectivity. The priority here is to protect this transboundary connectivity and to consider the establishment of a new PA in Nepal, where there are relatively large patches of high-quality habitat in community forests. On the bright side, both the western and the eastern subpopulations seem to be part of the much larger north-western and north-eastern Indian elephant populations, and our results show that the Chure foothills and the NITR could one day restore connectivity across the study area, linking these two larger populations. This would be a significant positive outcome for Asian elephant conservation and should be a long-term conservation aspiration.

The Asian elephant population in the NITR is located at the extreme of the species range and is likely to suffer especially severe consequences due to climate change (Kanagaraj et al., 2019). Protecting and enhancing functional landscape connectivity in the region will require cooperation and coordination between Nepalese and Indian authorities and will be important for the complex mammal assemblages in the region, particularly Asian elephants.

Author contributions

DN: Conceptualization, data gathering and analysis, manuscript drafting, reviewing. SB: Data analysis, manuscript drafting and reviewing. TSR: Supervision, manuscript reviewing, obtaining funding for data collection. ACA: Conceptualization, manuscript drafting and reviewing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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