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Analysis of Landscape Connectivity among the Habitats of Asian Elephants in Keonjhar Forest Division, India

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Abstract: Land development has impacted natural landforms extensively, causing a decline in resources and negative consequences to elephant populations, habitats, and gene flow. Often, elephants seek to fulfill basic needs by wandering into nearby human communities, which leads to human–elephant conflict (HEC), a serious threat to conserving this endangered species. Understanding elephant space use and connectivity among their habitats can offset barriers to ecological flow among fragmented populations. We focused on the Keonjhar Forest Division in Eastern India, where HEC has resulted in the deaths of ~300 people and several hundred elephants, and damaged ~4100 houses and ~12,700 acres of cropland between 2001 and 2018. Our objectives were to (1) analyze elephant space use based on their occupancy; (2) map connectivity by considering the land structure and HEC occurrences; (3) assess the quality of mapped connectivity and identify potential bottlenecks. We found that (1) the study area has the potential to sustain a significant elephant population by providing safe connectivity; (2) variables like forests, precipitation, rural built-up areas, cropland, and transportation networks were responsible for predicting elephant presence (0.407, SE = 0.098); (3) five habitat cores, interconnected by seven corridors were identified, of which three habitat cores were vital for maintaining connectivity; (4) landscape features, such as cropland, rural built-up, mining, and transportation networks created bottlenecks that could funnel elephant movement. Our findings also indicate that overlooking HEC in connectivity assessments could lead to overestimation of functionality. The study outcomes can be utilized as a preliminary tool for decision making and early planning during development projects.

Keywords: landscape connectivity; least-resistant paths; habitat core; Asian elephant (*Elephas maximus*); human–elephant conflict; movement barrier; centrality

1. Introduction

Land cover transformations have profound consequences on species populations and habitats and are the main causes of the current biodiversity crisis [1]. Habitat fragmentation and loss mostly affect species in small and sometimes isolated populations. This increases their risk of extinction as they are exposed to demographic and environmental stochastic events, along with lack of gene flow or inbreeding depression [2–4]. The survival of a majority of species within expanding human-dominated landscapes is highly dependent upon the ecological connectivity among their spatially separated populations and habitats [5]. This is particularly true of wide-ranging mammals who are declining worldwide, as the connectivity among their habitat patches is being deteriorated due to conversion of the natural landscape into various land use patterns (e.g., transportation networks, patches of cropland, or other land use factors that hinder species movement) [6–9]. Thus, detecting

habitat patches and the linkages that establish connectivity among them is essential to facilitate effective spatial planning to conserve these habitat networks.

Umbrella species like elephants play a major role in the ecosystem and their loss would detrimentally affect the wellbeing of other species and communities sharing the same habitat [10–14]. The Asian elephant (*Elephas maximus*) is an endangered species that is threatened by habitat degradation, poaching for ivory, and especially by conflicts with people (such as house damage, crop raiding, and human death and injury caused by elephants), which makes it challenging to gather support from the local community to conserve this species [15–19]. They are scattered among 13 range countries in Asia and occupy only 5% of their original habitat range [20]. India harbors 60% of the current Asian elephant population, but 70% of elephant habitats in India have been disturbed by escalating anthropogenic pressures, such as rising human population, economic development, agriculture, logging, and livestock raising [21,22]. These activities have not only fragmented elephant habitats, but also hindered elephant movement pathways, allowing room for greater contact between elephants and people, especially in human-dominated landscapes [23]. Isolated elephant populations, thriving among ever-decreasing foraging resources, are being forced out of their native habitats into adjoining human communities, leading to human–elephant conflict (HEC) [24,25]. This has caused the death of ~2400 people and ~500 elephants in India during 2015–2018 [26] and between 2000 and 2010, and over 0.5 million households suffer from crop raiding by elephants annually [26,27]. More than US $19.2 million has been paid by the Indian government in compensation for the crops and property damaged in HEC, and around US $5 million has been paid for human casualties caused by HEC during 2014–2018 [26]. Wide-spread HEC can further deplete the already scattered and scarce population of Asian elephants and pose a serious threat to their survival [28,29].

The magnitude of threat to Asian elephants is directly linked to the consumption of resources by a rising human population [17,19]. Former elephant ranges and migratory pathways have been mostly altered into agricultural land, followed by human settlements and infrastructure [16,18], which has threatened the long-distance movement of elephants in search of food, water, and social interactions. Space use by elephants is influenced by vegetation type, distribution of available resources, land use change, and human interference to their habitation [30–33]; therefore, understanding their space use is a key factor that is necessary for conservation planning, identifying burdens that restrict their presence, and mitigating HEC [31,34–36]. Several methods have been employed for detecting space use by elephants, such as field methods (telemetry data, direct sighting, and scat observation) [31,34,35,37–40] and analytical methods (spatial regressions, habitat suitability, resource-selection functions, and presence-only modelling) [41,42]. However, these methods do not consider observation errors, such as imperfect detectability (sometimes animals might pass unobserved) and sampling biasness [31,43–46]. In addition, presence–absence surveys can underestimate species distribution [31,46,47] as they barely differentiate between the true absence of species and the non-detection of signs. Occupancy modelling, which is an unbiased estimate of the probability of species presence that explicitly accounts for imperfect detectability, can meet conservation needs because it also facilitates an assessment of the influence of anthropogenic and ecological variables on detection, as well as habitat occupancy [31,46–48].

Connectivity between resource patches and species populations, based on land structures (such as vegetation, transportation networks, human settlements, water bodies, industries, and cropland), is a crucial need for species conservation as it helps in maintaining ecosystem functioning, determining the ability of the species to adapt to the human dominant landscape [49,50] and gives insight into factors impeding or facilitating elephant movement [51–55]. Thus, assessing connectivity across heterogeneous landscapes will facilitate safe movement of elephants, which can help not only in preserving their sub-divided populations and reducing the risk of extinction by maintaining genetic flow [56–58], but also in managing conflict occurrence [59]. Many quantitative approaches, such as the least-resistant path [53,57,58,60–62] and the circuit theory [63–67], have been recently developed

to assess the connectivity and barriers associated with movement pathways. However, a majority of the studies on connectivity analysis are based on the characteristics of the landscape [59,63,64,68–76], while only few studies [69,70] have considered human–wildlife conflict occurrence when assessing connectivity. Conflict-prone regions act as a significant movement barrier, which forces the species to adapt accordingly by changing their use of resources [76–78]. Therefore, ignoring conflict occurrence can overestimate the effectiveness of connectivity, as it could lead researchers to overlook the probable effects of conflict along the estimated pathways that lead to the funneling of species into ecological traps in the conflict prone regions [69–78].

Our study focused on the Keonjhar Forest Division in Eastern India (Figure 1), home to a population of 70–75 elephants. This area is also famous for tuskers and hosting elephants that are migrating from adjoining areas [26]. HEC in this region has escalated to an extreme level, taking more than 300 human lives, and damaging 4100 houses and 12,700 acres of cropland between 2001 and 2018. Several elephants were also killed as a result of electrocution, road-train mishaps, falling from hills, HEC, and very few were lost due to poaching [26,79]. Therefore, analyzing elephant space use and delineating safe dispersal pathways in this human-dominated landscape can help to mitigate HEC [26]. We used three years of elephant location data collected by the forest staff, based on direct and indirect (tracks, scats, and feeding sign) observations on a daily basis to (1) analyze the intensity of elephant space use through occupancy modelling; (2) map potential connectivity pathways among elephant habitat patches based on landscape structure and HEC occurrence; (3) assess the major bottlenecks along the estimated pathways.
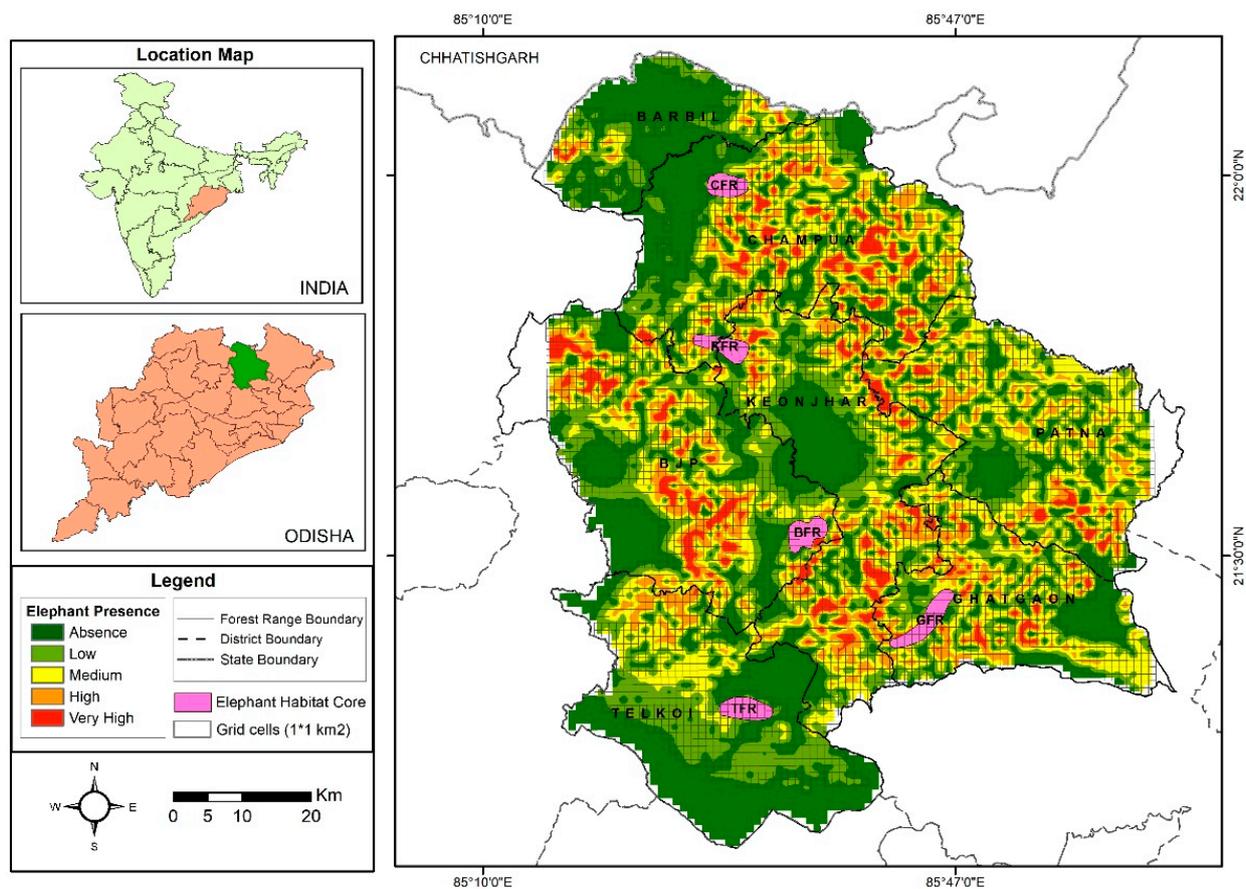

Figure 1. Map of the study landscape showing the pattern of the estimated probability of elephant occupancy with the red region showing a very high probability of elephant presence. Five elephant habitat cores (pink color polygon) were identified and named as CFR, KFR, BFR, GFR, and TFR. Keonjhar Forest Division has seven forest ranges (Barbil, Bhuiyan-Juang Pihra (BJP), Champua, Ghatgaon, Keonjhar, Patna, and Telkoi).

2. Materials and Methods

2.1. Study Area

Keonjhar Forest Division (Figure 1) was selected for this study, which is aimed at identifying connectivity pathways for Asian elephants that would limit potential contact with human communities. The division is situated between latitudes 21°1′ N–22°10′ N and 85°11′ E–86°22′ E, in the eastern part of India and covers an area of nearly 6038 km², with approximately 3400 km² of forest cover that provides suitable habitat for many species. Keonjhar Forest Division is rich in biodiversity and is a stronghold for Asian elephants [78–80]. The study area has seven forest ranges, namely Champua, Barbil, Keonjhar, BJP, Patna, Ghatgaon, and Telkoi. The majority of the tree species found in this district are dry deciduous and semi-evergreen, where the Sal tree (*Shorea robusta*) is the dominant species. More than 85% of the total human population lives rurally [70] and 80% of the residents earn their livelihoods from agriculture.

2.2. Data Collection and Analysis

Beginning in 2017, information on elephant sightings was recorded on a daily basis through direct observations by the Divisional Forest Office of Keonjhar District. There are seven forest ranges, where 45 forest beats (smallest administrative unit of a forest division, usually 50–60 km² in expansion) cover the whole study area. A forest guard, patrolling staff, and a para staff or protection squad are assigned to each beat and are responsible for controlling human wildlife conflict, especially HEC, in their respective regions. The staff collects locational data of elephants through direct sightings as well as indirect observations such as foot marks, fresh dung, feeding signs, broken branches, and conflict incidences, on a daily basis. This data contains GPS readings (latitude-longitude), village name, number and characteristics of elephants (male or female), direction of their movement, and their distance from railway track, etc. In order to assess the patterns of elephant space use, we collected around 10,300 elephant locations from July 2017 to August 2020.

The landscape level variables used in the study were divided into two categories: (i) environmental variables—open forest (%), dense forest (%), bush (%), enhanced vegetation index (EVI), terrain roughness index (TRI), annual average precipitation, land surface temperature (LST), Euclidian distance (ECD) from waterbodies; (ii) anthropogenic variables—ECD to mining, ECD to cropland, ECD to rural built-up, ECD to urban areas, road–railway density and population density. The datasets used in this study are provided in Supplementary Table S1.

Although the normalized difference vegetation index (NDVI) is an effective substitute for forage availability that can increase the elephant occurrence [81,82] we used EVI, which has shown better saturation in high biomass regions, apart from being modified for aerosol effect and controlled for noise from soil background [19,83–85]. Elephants face difficulties in thermoregulation when temperatures exceed their core body temperature [86], so their occupancy will be lesser in the regions with high temperatures. Studies have shown that foraging, movement rate, and habitat preferences of Asian elephants increase in the open forest and bush habitat [16,63] compared with dense forests. Thus, we categorized the forest cover into open forest (%), dense forest (%), and bush (%). Although the presence of water sources enhances the space use by elephants, linear water bodies like rivers or drainage canals can act as barriers [32,87]. Nevertheless, overall, we assumed that the farther the distance from waterbody, the lesser the detectability of elephants would be. Moreover, in this study, we considered all water bodies, comprising proximal rivers, non-proximal rivers, canals, dams, and ponds.

Dense human settlements, mining areas, and road–railway networks are associated with higher risks to elephants, which, in turn, create a hindrance for their movement [30,31]. It was observed that houses, farmlands, and water sources located within 1 km of the elephant range are frequently raided by elephants [88–91] because of their easy accessibility and higher food availability (e.g., stored grains, fruits. and kitchen food). According to Tripathy et al. [26], since house damage occurred frequently in the villages of the study

area, we assumed that elephant detection might be higher near rural built-up, especially in the forest fringe zone, while there will be lesser detection closer to urban areas. Although elephants prefer to forage in croplands, which are an easily accessible food source, crop raiding is a source of HEC [53,92–94], which poses a serious threat to elephants. We used a Sentinel-2 Level-1C product of 10 m resolution to extract settlements, croplands, water bodies, and mining, which was later improved for classification accuracy using Google Earth products. The ECD for these variables, along with that of waterbodies, was calculated using the straight line function in the Spatial Analyst module in ArcMap 10.5, which calculates the distance from every cell to the adjoining source. Roads and railways act as major barriers and are associated with high risk due to road–railway accidents [95–97], which eventually can reduce elephant detectability near dense transportation networks. Thus, we calculated the density of road–railway networks using the Line Density tool in ArcGIS 10.5 and categorized the results into four classes (high, medium, low, and absent). The population density was also assumed to have a negative influence on elephant detection, as it is a measure of direct human alteration of natural landscape based on the intensity of development activities [19] that affect elephant movement.

All the covariates were projected again onto the WGS 84/UTM zone 45N and resampled to 1 km resolution using cubic convolution. Prior to further analysis, collinearity for all the covariates was examined using stepwise variance inflation factors (VIF). We created a linear model using these explanatory variables, with less collinearity (VIF < 10), to evaluate the significance ($p < 0.01$) of variables that are related to the response variable.

2.3. Occupancy Modelling and Habitat Core Estimation

We fitted a single-season, single-species standard occupancy framework to evaluate elephant space use along with the factors affecting their presence in the study area. Elephant occupancy (Ψ = Pr (site is occupied by elephants)) was estimated using elephant locational data, while accounting for detectability (ρ = Pr (detection at a grid cell | elephants present in the grid cell and site)) in the "unmarked" package in R [98]. Detection probability was modelled using 3 years of elephant presence data, based on the pattern of the presence–absence matrix [99,100]. We considered the effect of spatial autocorrelation on the accuracy of elephant space use detection and followed a spatial thinning processes [101,102] for daily locational data, where all the observed locations within each 1×1 km grid cell were aggregated. Then, we categorized each cell to make a daily presence–absence matrix, where "1" (presence) was assigned if the grid cell has aggregated observed locations, otherwise "0" (absence) was assigned. Moreover, we ensured that the size of each grid cell was appropriate enough and less than the minimum home range ($\sim$100 km^2) of Asian elephants [20,103]. The number of repeated observations per grid cell ranged from 4–71.

The modelling process was broken down into two stages, where occupancy probability (Ψ) was modelled after detection probability (ρ) [69]. In the first stage, single covariate models were built while keeping the occupancy constant at 1, in order to limit the possible number of potential covariates for effective modelling of detection probability. All these models were ranked using Akaike's information criterion (ΔAIC) [48,69] and the covariates of models with ΔAIC values less than 2 (ΔAIC < 2) were denoted as the plausible covariates for detection modelling. The additive effect of these plausible covariates, along with the global model (additive effect of all the covariates), were used for detection model preparation. The covariate structure of Ψ was kept constant following Karanth et al. [69], as we assessed the role of covariates for ρ by conditioning the covariate structures of Ψ (Ψ as 1) before modelling occupancy. Then, the structure of ρ in the model with the lowest ΔAIC value was retained to build elephant occupancy models by combining all the covariates for Ψ in all possible ways [103]. The models with ΔAIC values less than 2 were considered to be the best-fitting elephant occupancy models [69,103]. Then, we applied a model-averaging technique for these best-fitting models to create weight-averaged values for estimating elephant occupancy probability within each grid cell across the landscape. From among

the few goodness-of-fit tests for occupancy models, we used MacKenzie and Bailey's (2004) goodness-of-fit test. It calculated the chi-square fit statistics from the observed and expected frequencies of detection histories for the average of plausible occupancy models using "mb.gof.test" function in the AICcmodavg package. This process simulated a large number of bootstrap samples (nsim = 100). We also estimated the over dispersion (c-hat) for the average of plausible occupancy by dividing the observed chi-square statistic by the mean of the statistics obtained from 100 simulations.

The time local convex hull (T-LoCoH) method was used to generate habitat cores using the "tlocoh" package, based on the hulls, which is a prerequisite step for connectivity analysis. Hulls are the building blocks of T-LoCoH analyses and are minimum convex polygons constructed around each point from a set of nearest neighbors. We used the "lxy.nn.add" function to determine the nearest neighbors (k), which was found to be 17 in number, and thus created a hull set with up to 17 nearest neighbors for each location. And the "tlocoh::lxy.lhs" function was used to create hull sets, by setting the parameter s = 0, because we did not consider the temporal component (re-visitation), which represented the hulls of heavily used areas that did not cut across unused areas [104]. Finally, isopleths were created using the "lhs.iso.add" function by aggregating the hulls that were sorted according to density, reflecting the intensity of use [104]. Thereafter, we extracted a 50% isopleth [105,106] and overlaid it on the occupancy map to clip the core regions of elephant space use.

2.4. Landscape Connectivity Analysis

2.4.1. Resistance Surface

Resistance surface is a significant factor in estimating the suitable least-resistant movement pathways [61,106], where each grid cell value indicates the cost of, or difficulty of, a hypothetical elephant movement through that cell. The higher the estimated resistance for a grid cell, the lower the chance of an elephant moving through it. The resistance score for each landscape factor was assigned based on the literature [62,64,71,72,107] along with expert consultation. We included land use land cover (LULC), slope, road, railway, human population density, and HEC density factors and categorized them to develop a resistance surface (Supplementary Figure S1). As HEC is a serious threat that can act as a movement barrier for elephants [18,21,22,77,78], a higher resistance value was assigned for areas with higher HEC density in order to estimate pathways that will have lesser interaction with human society.

Overall, we assigned a resistance score between 1 and 100 (where 1 = least resistance level and 100 = highest resistance level, Table 1) to every category for each specific factor and then assigned a weight between 1 and 5 (1 = least impact, 5 = highest impact, Table 1). Here, the weight of a factor quantitatively indicates its probability level of impact on elephant movement. The resistance surface was produced by using the weights of each layer and scores of each variable that consisted of environmental and anthropogenic variables in ArcGIS 10.5. The resistance surface (Figure 2a) was classified into five classes (0–25 = very low; 25–40 = low; 40–65 = medium; 65–85 = high; 85–100 = very high).

2.4.2. Mapping Elephant Movement Pathways

The Linkage Mapper tool [108] was used to delineate potential elephant movement pathways, based on circuit theory, graph theory, and cost distance assessment (resistive distance) [65,66]. Circuit theory evaluates the path of electrical current flow (i.e., elephant movement) through the least-resistant path in a circuit having multiple paths [65]. Graph theory elucidates the landscape as a set of nodes (habitat cores), where movement between these nodes is possible through the connecting edges (connecting paths) [109,110]. Resistive distance represents the distance to the nearest nodes for each grid cell, based on the least-cumulative resistance. Therefore, the possibility of a trade-off between resistive distance and travel distance among the nodes assesses the significance of linkages in the landscape, by offering the shortest least-accumulative resistive distance [66,74,111].

Table 1. Variables used to create the elephant movement resistance surfaces. Resistance score represents the resistance to elephant movement posed by each category (e.g., open forest, agriculture, or barren land) for each variable (e.g., LULC, slope or HEC density), which was scored on a scale of 1–100 (where 1 = least resistance level and 100 = highest resistance level). Score denotes the probable impact of each layer on connectivity among elephant habitats on a weight of 1–5 (1 = least impact and 5 = highest impact).

Variable	Category		Resistance Score	Weightage
LULC		Bush/Scrub	5	2
		Open Forest	1	
		Dense Forest	20	
		Rural built-up	80	
		Urban development	100	
		Agriculture	75	
		Barren	15	
	Water bodies	River	20	3
		Canal/Drain	40	
		Reservoir/Tank	5	
		Lake/Pond	5	
	Mining	Active Mining and Quarry	90	2
		Industrial Areas	100	
		Waste and abandoned area	80	
Railway	Absent		1	1
	Present		100	
Road	Absent		1	2
	Present (Major)		100	
	Present (Minor)		60	
Slope	High		85	3
	Medium		50	
	Low		1	
Population Density	Absent		1	1
	Low		30	
	Medium		60	
	High		100	
HEC Density	High		90	3
	Medium		60	
	Low		20	

The tool identifies habitat cores and connects them to one another by edges using a one-to-many condition. The grid cells were treated as a network of nodes and abstracted as a graph to quantify the distance via the graph–theoretic metric [74,112]. The shortest, least-resistant pathways for each pair of habitat cores were then mosaicked to plot connectivity maps [65,67,108] where the movement flow densities were high. We used a cutoff width of 1.5 km to denote the potential extent of elephant movement pathways that may comprise at least 30–40% forest cover. Moreover, connectivity of this width would be more practical and it would accommodate the uncertainty in the underlying GIS layers, estimated resistance surfaces, and connectivity modelling.

2.4.3. Assessing the Characteristics of Least-Resistant Paths

The Centrality Mapper function was used to quantify the importance of habitat cores and least-resistant pathways in maintaining connectivity in the entire habitat network [65,108,113]. It calculated the current flow centrality (elephant movement flow) by deducing the cumulative flow through all pairs of habitat cores and estimated the pathway

networks. Furthermore, two ratios are calculated to determine the characteristics of potential pathways. Firstly, the ratio between the resistance-accumulated distance and the Euclidean distance (Ra:Ed) was used to measure the quality of the connectivity pathways, by assessing the elephant movement difficulty between a pair of habitat cores with respect to their surroundings. The second ratio, between the resistance-accumulated distance and the length of the least-resistant path (Ra:Lr), calculates the resistance per unit length for elephant dispersal along the estimated pathways [113].
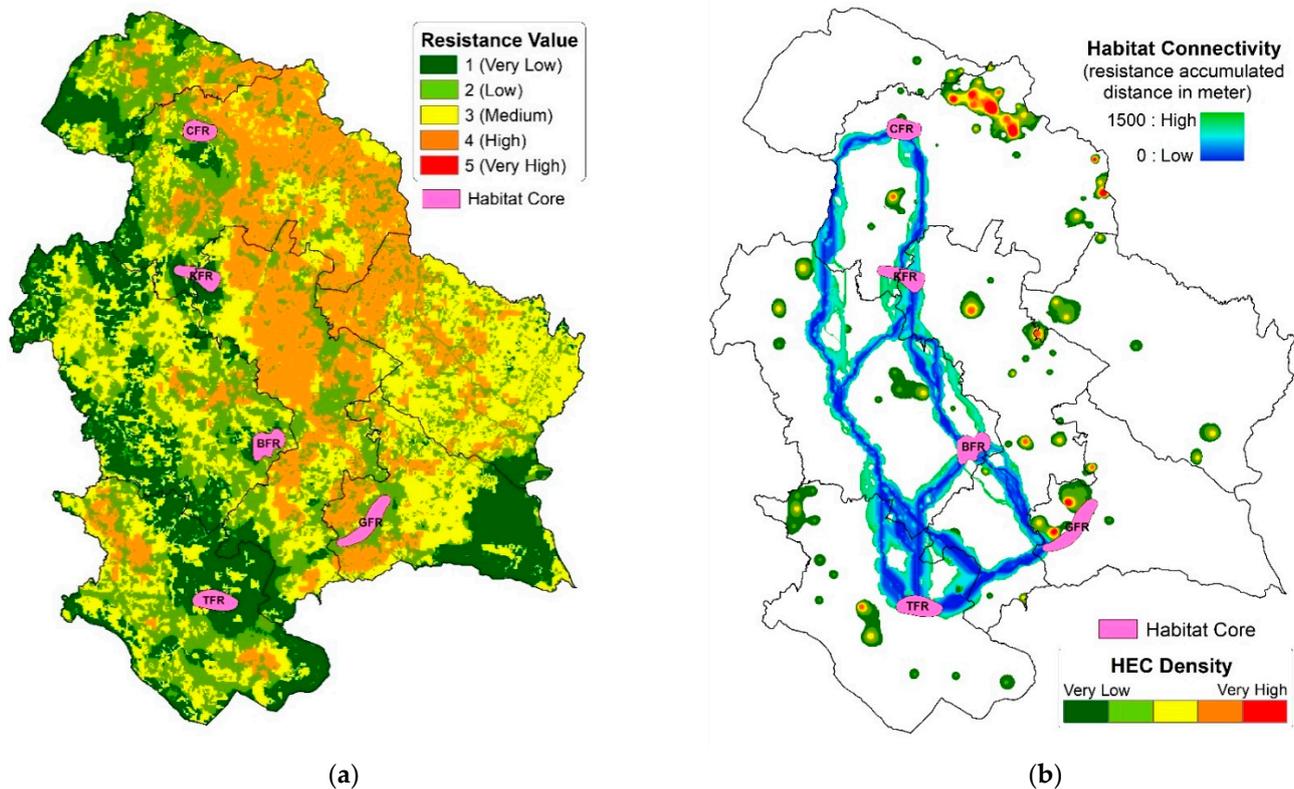

(**a**) (**b**)

Figure 2. Landscape resistance and connectivity for elephant movement. (**a**) Surface map representing the landscape resistance to elephant dispersal, where each grid cell indicates the struggle for hypothetical elephant movement through that grid cell. (**b**) Map showing the least-resistant passage for elephant dispersal, which was clipped at a 1.5 km resistance-accumulated distance. The blue regions represent the lowest resistance-accumulated path, while the green regions represent the highest. The estimated pathways are safer as they avoid the dense HEC (shown in the background)-occurrence regions.

Finally, the Pinchpoint Mapper tool was used, to calculate the cumulative movement flow for each grid (amp/grid), which identified the bottlenecks for movement within the pair of estimated pathways and for the entire connectivity network. The current study evaluated the bottlenecks with respect to the entire network, as we were interested in finding the regions for prioritizing conservation efforts, where elephant movement may get funneled, or connectivity might be disproportionately interrupted by even minimal obstruction around the pinch points [75]. It identified the regions where the low-resistance cover types were narrowed due to factors such as transportation networks, high density of HEC occurrence, and developed areas.

3. Results

3.1. Elephant Occupancy

Environmental variables, such as terrain roughness index, land surface temperature, and dense forest (%), as well as anthropogenic variables, such as ECD mining, ECD urban, and population density were removed because of collinearity, and the AICs of significant variables were used for occupancy prediction, as listed in Table 2. In the first stage of

occupancy analysis, additive effects of variables such as open forest (%), precipitation, ECD cropland, and ECD rural received the lowest AIC to model ρ (Table 2). By retaining this covariate structure of ρ, occupancy models were built using the additive function of various covariates for Ψ. We found three plausible models (ΔAIC < 2) that fit the data very well and determined the probability of elephant occupancy in our study landscape. Subsequently, we averaged these plausible models to derive the final parameter estimates.

Table 2. List of top models for probability of elephant detection (ρ) and occupancy (ψ), ranked based on Akaike's information criterion (AIC). The first part of the table lists best-fit covariates, while the second part lists the top ρ models built using the best-fit covariates. The last part lists the best ψ models built using the top ρ model's structure. ECD—Euclidean distance; EVI—enhanced vegetation index.

Scheme	Model	AIC	ΔAIC
	Covariates selection		
1	ρ (Open forest %) ~ Ψ (1)	882.31	0
2	ρ (Precipitation) ~ Ψ (1)	882.66	0.35
3	ρ (ECD_cropland) ~ Ψ (1)	883.04	0.73
4	ρ (ECD_rural) ~ Ψ (1)	883.79	1.48
5	ρ (Road–railway density) ~ Ψ (1)	883.86	1.55
6	ρ (Bush %) ~ Ψ (1)	884.02	1.71
7	ρ (ECD_waterbodies) ~ Ψ (1)	884.31	2.00
8	ρ (EVI) ~ Ψ (1)	884.62	2.03
	Detection model		
1	ρ (Open forest % + Precipitation + ECD_cropland + ECD_rural) ~ Ψ (1)	1123.86	0
2	ρ (Open forest % + Precipitation + ECD_cropland + ECD_rural + Road–railway density + Bush %) ~ Ψ (1)	894.04	0.18
3	ρ (Open forest % + Precipitation + ECD_cropland + Road–railway density) ~ Ψ (1)	894.57	0.71
4	ρ (Open forest % + ECD_cropland + Road–railway density + ECD_rural) ~ Ψ (1)	895.24	1.38
5	ρ (Open forest % + ECD_cropland + ECD_rural + Bush % + ECD_waterbodies) ~ Ψ (1)	895.95	2.09
	Occupancy model		
1	ρ (Open forest % + Precipitation + ECD_cropland + ECD_rural) ~ Ψ (Open forest % + Precipitation + ECD_cropland + ECD_rural + Road–railway density)	894.63	0
2	ρ (Open forest % + Precipitation + ECD_cropland + ECD_rural) ~ Ψ (ECD_cropland + Precipitation + Road–railway density + Bush %)	895.12	0.49
3	ρ (Open forest % + Precipitation + ECD_cropland + ECD_rural) ~ Ψ (Open forest % + Precipitation + ECD_cropland + ECD_rural + Road–railway density + Bush %)	895.96	1.33
4	ρ (Open forest % + Precipitation + ECD_cropland + ECD_rural) ~ Ψ (Open forest % + ECD_rural + Road–railway density + Bush % + ECD_waterbodies)	896.54	1.91
5	ρ (Open forest % + Precipitation + ECD_cropland + ECD_rural) ~ Ψ (Open forest % + ECD_cropland + ECD_rural + ECD_road–railway + ECD_waterbodies)	896.87	2.24

The overall probability of elephant occupancy was 0.407 (SE = 0.098), based on the averaged model, while it was only 0.372 as per the naive occupancy of the study area. We estimated that elephants were distributed over 43% (about 2710 km^2) of the study area and BJP, Ghatgaon, and Champua forest ranges represented a higher potential of elephant occupancy. The probability of elephant occupancy within each grid cell across the study area is shown in Figure 1. The *p*-value (the probability of obtaining the calculated

chi-square statistic) was found to be 0.621, which proves that there is no evidence of lack of fit (as *p*-value > 0.1) [48]; additionally, the estimate of the over-dispersion parameter for the averaged elephant occupancy model (c-hat) was 0.703, indicating that there is no evidence for over dispersion as the variance is not greater than the mean (c-hat is close to 1) [48]. We found five elephant habitat cores in the study area, Champua, Keonjhar, BJP, Ghatgaon, and Telkoi forest ranges, which were named as CFR, KFR, BFR, GFR, and TFR, respectively.

The probability of elephant occupancy varied asymmetrically with each variable, as shown in Supplementary Figure S2. The magnitude of coefficient estimates for the averaged model, shown in Table 3, indicated the strength of their expected influence, while the (+)/(−) signs demonstrate the relationship. In our study area, open forest (%), precipitation, and ECD_rural were the key covariates that positively influence elephant presence, while ECD_cropland, bush (%), and road–railway density were shown to negatively influence elephant presence (Table 3). We found that elephant occupancy was high when the open forest % in the study area was above 40%. Occupancy was also high when the bush % increased up to 50% but then reduced with further increments of bush %. Although Euclidian distance to water bodies has been identified as a potential factor in estimating elephant distribution in India, Indonesia, China, and Thailand [35,64,114,115], it did not become a prominent predictor in this study, due to difficulties in identifying water bodies using coarse resolution satellite images; however, it showed a positive association with the annual average precipitation in the study area. A relatively higher elephant presence was observed farther away from rural built-up because of the cumulative effect of a variety of anthropogenic pressures on elephants [37,103,116]. Road–railway mishaps of elephants have been mentioned as one of the major causes of elephant mortality [95–97] and consequently, we evidenced lower elephant occupancy in the regions with denser transportation networks. Moreover, we observed higher elephant detectability near croplands because they prefer grazing crops over natural forage due to higher accessibility, palatability, and nutrition [10,58].

Table 3. Coefficient estimates of the Asian elephant occupancy model, averaged from 3 occupancy models with ΔAIC < 2 (ECD—Euclidean distance; EVI—enhanced vegetation index; SE—standard error).

Model	Estimate	SE
Detectability		
Intercept	2.21	0.11
Open forest %	1.68	0.51
Precipitation	0.20	0.35
ECD_cropland	−0.74	0.09
ECD_rural	0.13	0.89
Occupancy		
Intercept	0.96	0.04
Open forest %	2.17	0.16
Precipitation	0.32	0.22
ECD_cropland	−1.17	0.07
Bush %	−0.09	1.08
ECD_rural	0.03	0.61
Road–railway density	−2.32	0.13

3.2. Elephant Habitat Connectivity

The central and northeast regions of the study area demonstrated a higher resistance (Figure 2a) to elephant movement. When assessing the elephant habitat connectivity (Figure 2b), each cell of the resulting map represented a relative value of landscape connectivity that allowed us to outline the pathways that have the highest potential to facilitate elephant movement among habitat cores. Seven potential linkages were identified—which varied with respect to their importance in the overall network—where the pathway between GFR and TFR (19.76 km) was the shortest least-resistant distance, while the pathway

between GFR and CFR was the longest least-resistant pathway (103.12 km). Several pairs of habitat cores appeared to have more than one connecting linkage, for instance, the linkage between GFR and BFR has two alternative pathways available for elephants. One is a direct connection having shorter distance with a higher resistance, while the other linkage, via TFR, has a lower resistance. A similar case was also observed for the remaining pairs of habitat cores, which had more than two linkages. A major insight from our analysis was that most of the connectivity networks were through the BJP forest range and hardly any least-resistant routes were identified from the central and western parts of the study area, which are areas that were generally assumed to lack connectivity for elephants.

According to the measure of centrality (Figure 3a), KFR was the most important habitat core, followed by GFR and TFR (core centrality values 6.57, 6.02, and 5.44, respectively, from Table 4A), due to their relatively larger area and their significance in connecting habitat cores in the study area. Similarly, the centrality of elephant movement was highest around KFR–CFR, BFR–KFR, and GFR–TFR linkages (linkage centrality values 3.34, 2.83, and 2.48, respectively, from Table 4B). Considering the GFR–BFR and GFR–TFR pathways, despite being nearly equidistant least-resistant paths (19.7 km), the difficulty of elephant dispersal along the GFR–TFR pathway was found to be the lowest (Ra:Ed ratio 1.33, Table 4B). Meanwhile, the resistance per unit length for the GFR–TFR pathway (Ra:Lr = 1.24) was less than that of GFR–BFR (Ra:Lr = 2.11), which resulted in a higher movement flow (value of 2.83) between GFR and TFR. Thus, another major insight would be that, even with equidistant least-resistant pathways, their quality in terms of difficulty in movement varied, which was also true for the TFR–BFR (length = 24.5 km, Ra:Ed = 1.35, Ra:Lr = 1.21) and BFR–KFR (length = 26.5 km, Ra:Ed = 1.84, Ra:Lr = 1.65) pathways.
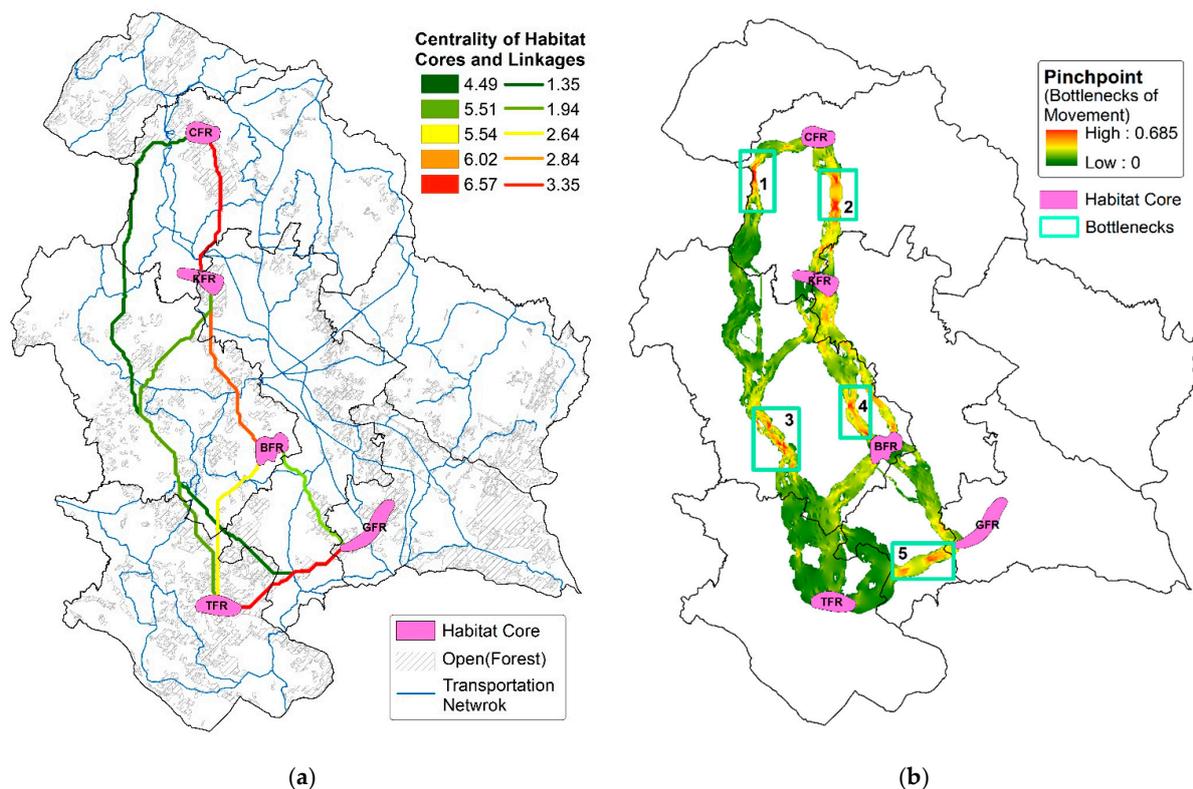

(**a**)   (**b**)

Figure 3. Characteristics of the estimated habitat cores and linkages. (**a**) Map representing the centrality of elephant habitat cores and linkages in maintaining connectivity within the entire habitat network. The red polygon or line has high centrality while the green has the lowest centrality. The pathways with the highest linkage centrality (KFR–CFR, KFR–BFR, and GFR–TFR) are supported by open forests with fewer transportation barriers (shown in the background). (**b**) Map illustrating the bottlenecks for elephant dispersal along the estimated linkages. The regions in shades of red have higher restrictions for elephant movement between the adjacent pairs of habitat cores. Five bottlenecks were identified and are highlighted with blue boxes.

Table 4. Characteristics of habitat cores and elephant movement pathways, where centrality signifies the importance of each pathway in maintaining the connectivity. The centrality of (**A**) 5 estimated habitat cores and (**B**) 7 least-resistant pathways evaluated by the Centrality Mapper tool. Ra:Ed represents the movement difficulty between habitat cores, relative to the whole connectivity network, while Ra:Lr represents the resistance per unit length along least-resistant pathways.

(A)							
Habitat Core	**Area (m^2)**	**Habitat Core Centrality**					
CFR	1,55,57,714.91	4.49561					
BFR	1,85,89,494.01	5.51905					
TFR	1,90,63,388.80	5.54219					
GFR	2,35,76,210.22	6.02567					
KFR	1,78,06,542.70	6.57972					
(B)							
From_Core	**To_Core**	**Ed (meter)**	**Ra (meter)**	**Lr (meter)**	**Ra:Ed**	**Ra:Lr**	**Movement Flow Centrality**
GFR	TFR	18,360	24,576	19,769	1.33856	1.24372	2.8322
TFR	BFR	21,943	29,728	24,519	1.35478	1.21261	2.4845
TFR	KFR	48,458	71,124	59,573	1.46772	1.1939	1.7817
KFR	CFR	20,295	35,989	22,765	1.77325	1.58085	3.3494
GFR	CFR	64,157	11,831	10,314	1.84427	1.14769	1.6431
BFR	KFR	24,118	44,516	26,566	1.84575	1.65803	2.6478
GFR	KFR	42,811	89,507	73,149	2.09076	1.22627	1.3545
GFR	BFR	17,150	41,882	19,772	2.44219	2.11857	1.9408

The matrices of the two ratios (Ra:Ed and Ra:Lr) were calculated for characterizing the linkage among habitat cores (Table 4B). The ratio of Ra:Ed (mean 1.76) is lowest for GFR–TFR and TFR–BFR pathways, with a value of 1.33 and 1.35, respectively, which indicates the highest quality along the least-resistant pathways. The movement resistance per unit length (Ra:Lr) for these pathways was 1.24 and 1.21, respectively, which was the lowest when compared with the rest of the connectivity network.

The grid cells of the bottlenecks map represent the cumulative elephant movement, while the higher values highlight the significance of priority conservation. We identified five major pinch points (Figure 3b) in almost every linkage, where elephant movement may get funneled, or the connectivity may be interrupted by even the least obstruction. The landscape characteristics of the regions that have the highest possibility of being constricted are shown in Supplementary Figure S3. In bottleneck_1, which was found in the Champua forest range, the major landscape feature hindering elephant movement was identified as mining. Whereas croplands were a common key feature of this landscape that contributed to bottlenecks to elephant movement. The KFR–CFR (bottleneck_2) and BFR–KFR (bottleneck_4) pinch points were along the shortest pathways where the bottlenecks between the connectivity networks were extremely narrow, while bottleneck_3 and bottleneck_1 were observed on the longer pathways of TFR–KFR and TFR–CFR. Moreover, the TFR–GFR pathway had bottlenecks to some extent.

4. Discussion

4.1. Variables Influencing Elephant Detection

Forest covers with multiple land-use activities are usually preferred by elephants over relatively intact forests [35,38,39,64]. Bushes, which are the primary forage of elephants, can grow easily in open forests as they receive better space and light conditions [57,58,117]. Our study indicated that open forests, along with bush cover, strongly influenced elephant occupancy in the study area, as they provide food and shelter and also help in their thermoregulation [35,37,40]. We found a positive influence of precipitation on elephant detection, contrary to a study [31] conducted in Southern India in an extremely wet landscape,

which found that precipitation was the least influential covariate. But it is noteworthy that extreme wet conditions (such as dense and evergreen-canopied regions) can lead to an underestimation in the prediction of elephant occupancy. However, favorable rainfall conditions improved water availability, while increasing the productivity of deciduous forests with an abundance of palatable trees [26,40,103,118], which attracted more elephants to these regions in the study area.

Elephants struggle to live in human-populated areas, due to the negative impacts of linear infrastructure (road and railway networks, drains, canals, and wells), mining, settlements, and electrocution, along with retaliatory killing [92,94–97]. Elephants were present even in areas with a human density of ~2300 persons/km^2 in the central region of the study area; whereas, a previous study [103] had stated that elephants did not coexist with humans when the density reached ~15.6 persons/km^2. Roever et al. [33] indicated that elephants can penetrate areas with dense human populations, but their sustainable existence in these areas was questionable, particularly in areas with lower forest cover. Hence, in determining elephant occupancy, anthropogenic factors predominated over environmental factors, with the exception of open forest and precipitation. Despite this, elephants were present in the rural areas, probably because of easier access to food (stored grains, kitchen food, and local brew) from houses within the range from 200 m to 1 km of an elephant habitat range near the forest fringes [88–90].

4.2. Interpretation of the Characteristics of Estimated Connectivity

Our results suggested that this landscape provides potential connectivity among habitat cores, as a number of alternative pathways are available for species to move, which provide flexibility for planning and proposed infrastructure development in the landscape [113]. KFR–CFR, BFR–KFR, and GFR–TFR linkages can offer better functionality due to their higher centrality. Also, the highest centrality habitat cores have a significant role in maintaining the suitable least-resistant network, which was also consistent with the conclusions of previous literature [107]. The GFR–CFR pathway was observed to have the least resistance (value of 1.14) in the study area, but its movement flow centrality was found to be very low (value of 1.64) because of the greater distance (nearly 103.12 km) between the GFR and CFR habitat cores. Although the KFR–CFR pathway had the highest movement flow (value of 3.34), its quality was considerably lowered due to the presence of several bottlenecks along the pathway, such as from mining and rural development [58]. Our results could not find least-resistant movement pathways for elephants in the western region of the area, where one of the major factors limiting connectivity was the existence of a river pattern which acts as a barrier to elephant movement. However, in the central part, the relatively lower forest cover with high human density, dense road–railway network, and high HEC occurrence [18,26,52,58] also created hurdles for elephant movement.

Rural development, mining or industry, and transportation networks were the common key features that contributed to bottlenecks (Supplementary Figure S3), while cropland was indirectly influential. Although elephants are adaptable and prefer to forage on crops, they face a high mortality risk when crossing patches of cropland because of farmer retaliation due to crop raiding or other damages caused by their movement. As a result of the funneling effect of these kinds of landscapes, they tend to act as ecological traps for elephants [119–121]. Hence, another major insight drawn from this study was that overlooking HEC in connectivity assessment could lead to overestimating the functionality, because HEC is a major factor challenging elephant movement in these zones. Apart from that, we observed that the mining activities, particularly in bottleneck_2, can significantly affect the connectivity between KFR and CFR, as there were no alternative pathways for elephant dispersal. Yet, sufficient knowledge is still lacking on elephant movement in a human-dominated landscape in which suitable pathway selection may vary due to changes in environmental aspects and responsive behavior [107].

4.3. Implications and Recommendations

Connectivity, along with the spatial distribution of elephants, can be effective for assessing the influence of landscape configuration on population level processes. It can assist in improving the information on the factors influencing elephant conservation and developing management plans to protect them by recognizing the threats present in the habitat range [29,107]. Overall occupancy of elephants can be treated as a useful baseline against which future changes in elephant distribution can be assessed [29]. In order to maintain the connectivity network, major landscape barriers (mining, transportation networks, and dense HEC regions) along the estimated bottleneck regions should be kept intact and protected from further degradation through necessary adaptive planning [107]. During landscape planning, these regions should be given spatial prioritization for conservation and restoration because they are narrow routes which lack alternative connectivity and low resistance landscapes. Therefore, in order to facilitate effective planning, provision of land and infrastructure development, the connectivity, bottlenecks, and region-based connectivity characteristics could be useful and informative for authorities in allocating conservation resources to areas with high conservation value. However, these passages will also be helpful in connecting other species to their sub populations in the study area [18,68], while minimizing interactions with human society.

The outcomes of this study endorse conservation and landscape planning recommendations, based on the habitat use of elephants and landscape permeability by considering resistances to elephant movement accompanied by HEC risk. First, we recommend improving protection strategies in forest reserves that comprise habitat cores by enabling appropriate expansion of the forests dimensions to control further degradation of these habitats. Incorporation of neighboring forests is also recommended to restore connectivity and facilitate dispersal among fragmented elephant populations outside our study area, which can help to increase the functionality and genetic diversity [57,122]. Second, the potential linkages with low resistance and HEC risk require strict law enforcement, so that these areas are protected from future unregulated land cover alterations, poaching for ivory, and retaliations that occur subsequent to damages caused during HEC. Additionally, individual development projects should be considered as case studies and the consequences of land cover changes on elephant pathways and their movement behavior should be carefully discussed with multiple stakeholders. Third, as an effort to control the conflict risk, regions with more dispersal bottlenecks due to high HEC (in Keonjhar and Ghatgaon forest ranges) require urgent conflict mitigation intervention, such as streamlined compensation policies, community-based initiatives, and awareness programs to change people's attitudes towards co-existence [26,79]. As potential higher connectivity regions allow frequent movement of elephants, leading to a higher possibility of conflict [122], in order to predict HEC, the estimated connectivity values across the landscape should be tested for their correlation with conflict occurrence.

The establishment of the proposed pathways should be considered as sustainable conservation goals, since elephant movement across the estimated pathways will not be evidenced in the immediate future. The effectiveness of the estimated pathways could be sensitive to errors in the base data, collected through remote sensing, potential biases in the expert opinions used in assessing resistance surfaces and uncertainty of the required width for proposed corridors [59]. Actual connectivity could be more restricted than the estimated connectivity, since elephants may opt for routes other than the ones indicated in the study, depending on their behavior and adaptability to the landscape. Therefore, we suggest using radio telemetry data, accompanied by data on elephant behavioral states, to assess the effectiveness and utilization of the estimated pathways, and to reveal unaccounted site-specific resistance for elephant dispersal. Careful interpretation of the estimated centrality on a wider scale is recommended, as regions outside the study area may also have the potential for maintaining connectivity among elephant populations of neighboring habitats. Considering the negative perception towards elephants and the socio-economic status of local communities, an inclusive ecotourism program with a focus on involving and

benefitting these communities could increase the sustainability of the proposed elephant pathways.

5. Conclusions

The central Indian landscape is a priority zone for elephant conservation but it is highly fragmented and dominated by anthropogenic activities. While maintaining elephant movement pathways in such a human-dominated landscape is challenging, a connectivity study such as this can provide useful guidance for improving management and present a low-cost alternative approach to improving connectivity quantification, while accounting for HEC incidence. The connectivity characteristics related to HEC occurrence delivered valuable insights on the spatial prioritization of research efforts. Estimated multiple pathways between pairs of habitat cores indicated the potential of the study area to sustain a significant elephant population by providing them safe connectivity, even in a human-dominated landscape. Hence, connectivity analysis is a useful preliminary tool for planning and land use decisions, while providing a degree of flexibility for managers in designing ways to conserve the essential connectivity regions.

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