



CONTRIBUTED PAPER

Using elephant movements to assess landscape connectivity under Peninsular Malaysia's central forest spine land use policy

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Abstract

One of the most vital and urgent global conservation challenges is to deal with the loss and fragmentation of wildlife habitats, particularly for large-bodied and wide-ranging terrestrial megafauna. The Central Forest Spine Master Plan for Ecological Linkages (CFS) was developed by the Malaysian Federal Government in 2010 to protect biodiversity and ecosystem services by securing landscape connectivity between Peninsular Malaysia's main forest blocks. Here we present an evaluation of the effectiveness of the CFS master plan to promote functional connectivity for Asian elephants, one of its focal species. The specific objectives of our study were to identify the most critical forest patches to maintain connectivity for elephants in Peninsular Malaysia, assess functional connectivity within the CFS ecological linkages, and identify alternative corridors where appropriate to enhance CFS effectiveness. We used the largest animal movement dataset in Peninsular Malaysia (220,000 GPS locations from 53 elephants) to develop models of elephant movement probability and to estimate landscape resistance using step selection functions based on landscape characteristics. According to our evaluation of 28 linkages, 57% of them provided high functional connectivity, 28% provided acceptable connectivity, and 14% provided low to no connectivity. A very important and positive finding is that the CFS linkages with the highest centrality values (i.e., the most important to maintain overall connectivity in Peninsular Malaysia) also score highly in functional connectivity (i.e., they are actually effective corridors for elephant movement). This means that an adequate CFS implementation can lead to high levels of functional connectivity among Peninsular Malaysia's main forest blocks. Based on our assessment, we recommend to conduct some revisions on the CFS plan to ensure its effectiveness.

KEYWORDS

CFS, corridor, *Elephas maximus*, functional connectivity, habitat fragmentation, megafauna

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1 | INTRODUCTION

In the Anthropocene, humans continue expanding our global footprint and coopting resources away from other species (Barnosky, 2008). One of the most vital and urgent conservation challenges is to deal with the loss and fragmentation of wildlife habitats (e.g., Fahrig, 2003), particularly for large-bodied and wide-ranging terrestrial megafauna (Naidoo et al., 2018). Wildlife corridors represent a key element of landscape conservation planning and are one of the most popular solutions to deal with the deleterious effects of isolation and small population sizes. Wildlife corridors can be either fully protected areas or other areas managed to allow movements outside protected areas or between core habitat of the species of interest. A recent meta-analysis has confirmed the positive effect of corridors on wildlife by increasing the movement between habitat patches in several taxa (Gilbert-Norton, Wilson, Stevens, & Beard, 2010). Many plans have been proposed or are being implemented to use corridor networks to promote habitat connectivity for wildlife in conservation landscapes at continental, regional, and national scales (e.g., Jain, Chong, Chua, & Clements, 2014; Rabinowitz & Zeller, 2010). These are often ambitious and highly promising plans, but also costly with difficult implementation (Jain et al., 2014; Keeley et al., 2018) requiring careful consideration and critical evaluation.

The development of scientific tools to assess functional connectivity (i.e., how species move through a landscape) has improved our capacity to evaluate the effectiveness of wildlife corridors (Foltête, Clauzel, & Vuidel, 2012; Lechner, Doerr, Harris, Doerr, & Lefroy, 2015; McRae, Dickson, Keitt, & Shah, 2008; Wadey et al., 2018). Animal GPS telemetry, geospatial tools, and mathematical modeling can be combined to produce focal species functional connectivity models (e.g., Allen & Singh, 2016; Tucker et al., 2018), and then predict the effectiveness of proposed corridors, analyze how different factors affect corridor effectiveness, or redesign corridors when former alignments or locations become non-functional (Naidoo et al., 2018). Here we present an evaluation of an ambitious and complex country-scale wildlife corridor plan in Peninsular Malaysia.

Malaysia is a megadiverse country (Mittermeier, Robles-Gil, & Mittermeier, 1997) and a hotspot for biodiversity (Myers, Mittermeier, Mittermeier, & da Fonseca, 2000) and threatened megafauna (Ripple et al., 2016). With an industry- and service-based economy and less than 0.5% of its population below the poverty line (Department of Statistics of Malaysia, 2017), Malaysia is considered an example of successful economic development. This development, however, has come with

environmental costs. Peninsular Malaysia's forest cover has declined from 80% in the 1940s (Aiken, 1994) to less than 40% in 2010 (Miettinen, Shi, & Liew, 2011), leading to loss and fragmentation of wildlife habitats and populations. To address the rapid decline of biodiversity and wildlife, Malaysia has developed a suite of policies that includes a National Policy on Biodiversity, species-specific conservation action plans, and a land-use master plan to promote landscape connectivity for wildlife (Regional Planning Division, 2009a, 2009b).

The Central Forest Spine Master Plan for Ecological Linkages (hereafter CFS) was developed by the Malaysian Federal Government in 2010 to protect biodiversity and ecosystem services by securing landscape connectivity between Peninsular Malaysia's main forest blocks (Regional Planning Division, 2009a, 2009b). The CFS covers ~53,000 km², representing over 40% of the terrestrial area and over 91% of the forest cover in Peninsular Malaysia. The CFS was designed with tigers *Panthera tigris*, Asian elephants *Elephas maximus*, and Malayan tapirs *Tapirus indicus* as focal species (Brodie et al., 2016). The plan identified and established 37 ecological linkages, including 17 primary and 20 secondary linkages. Primary linkages are linear corridors (i.e., unbroken stretches of forested habitats connecting larger forest patches), and secondary linkages are stepping-stones corridors (i.e., non-continuous patches of suitable habitat; Regional Planning Division, 2009a, 2009b). The principal aim of CFS linkages is to encourage and facilitate different types of wildlife movement by providing structural connectivity between Peninsular Malaysia's main forest blocks (Regional Planning Division, 2009a, 2009b), although none of these corridors were designed based on actual wildlife surveys on the ground (Jain et al., 2014). The CFS also provides sustainability guidelines for existing and new developments in the ecological linkages core and buffer areas. Importantly, the CFS provides a spatial template for other wildlife-related policies and plans to overlap with. The National Elephant Conservation Action Plan (NECAP), for example, includes three Managed Elephant Ranges (MERs), in which wild elephants are expected to roam in the foreseeable future. The MERs roughly overlap with the CFS landscapes (PMDWNP, 2013). The CFS is arguably the most important conservation initiative in Peninsular Malaysia. However, its implementation has been challenging so far (Jain et al., 2014; Maniam & Singaravelloo, 2015) and the adequacy of its linkages to promote functional connectivity has never been empirically evaluated.

Here we present an evaluation of the effectiveness of the CFS master plan to promote functional connectivity for Asian elephants, one of its focal species. The specific objectives of our study are to (a) identify the most critical

forest patches to maintain connectivity for elephants in Peninsular Malaysia, (b) assess functional connectivity within the CFS ecological linkages, and (c) identify alternative corridors where appropriate to enhance CFS effectiveness. We used the largest animal movement dataset in Peninsular Malaysia to develop models of elephant movement probability and to estimate landscape resistance using step selection functions (SSF) based on landscape characteristics. We then applied least-cost path and circuit theory models to evaluate the connectivity of CFS linkages. Finally, we synthesized our evaluation into practical recommendations for conservation decision-makers and other stakeholders to consider.

2 | METHODS

2.1 | Study area

Peninsular Malaysia extends 780 km from latitude 1°15' north of the Equator. Its terrain is hilly with several mountain ranges in a north–south alignment. Peninsular Malaysia is covered by approximately 57,900 km² of forest (PMDWNP, 2013), and the dominant forest types include lowland dipterocarp, hill dipterocarp, and montane forest with an altitudinal range from sea level to 2,187 m. Our study area included all the extension of NECAP's MERs, which roughly overlap with the CFS landscapes, and 17 primary and 11 secondary CFS linkages within them (Figure 1).

2.2 | Telemetry data

We used GPS telemetry data from “translocated” and “local” wild elephants. Translocated were elephants relocated from human–elephant conflict areas to protected areas by the Department of Wildlife and National Parks (DWNP) of Malaysia (Saaban et al., 2011). Local elephants were individuals sedated, collared, and released at the same location within a few hours. We used Inmarsat and Iridium satellite GPS collars (10D cells, Africa Wildlife Tracking, Pretoria, South Africa), programmed to record a location every 1, 2, or 5 hr.

The GPS dataset used in this analysis includes the movements of 53 Asian elephants monitored between 2011 and 2018, including 21 local (13 female and eight male) and 32 translocated (six female and 26 male) individuals (Table S1). This dataset presents one of the largest collections of Asian elephant movements to date with 220,325 localizations. Elephants were tracked an average of 340 ± 277 (range = 10–1,016) days. See Appendix S1, Figure S1 and Table S1 for details on the telemetry data treatment.

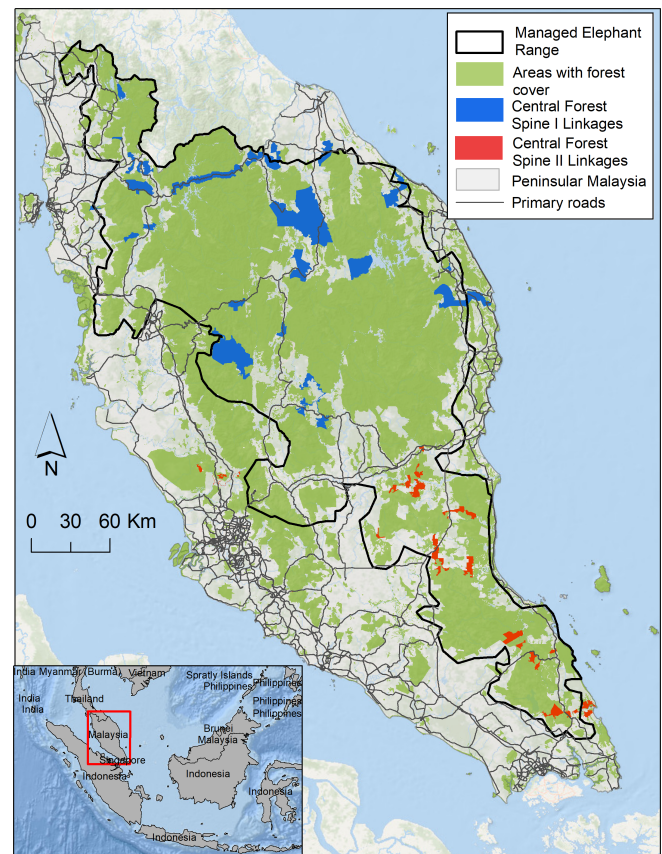


FIGURE 1 Study area in Peninsular Malaysia which included the complete extension of the Managed Elephant Ranges and 28 Central Forest Spine ecological linkages (17 primary and 11 secondary) occurring within them

2.3 | Landscape covariates

We compiled a geospatial dataset representing environmental and anthropogenic landscape covariates for Peninsular Malaysia (Table S2). This dataset included variables associated with the land use, such as forest cover, regrowth to secondary forest, open areas, mosaic, water (main rivers and lakes), and large-scale monocultures, as well as distance to forest edge and distance to plantations (oil palm and rubber). To evaluate the influence of anthropogenic activities we tested mean of nightlight and distance to main roads covariates. We also included terrain related variables such as elevation and slope. Detailed explanation of each one of variables used in this analysis is included in Table S2.

We included a range of optical remote sensing products processed in Google Earth Engine. We derived a multivariate cloud free mosaic surface reflectance product from Landsat images, and from this mosaic we calculated the Enhanced Vegetation Index (EVI), the Normalized Difference Vegetation Index (NDVI), the Normalized Difference Water Index (NDWI), and the Tasseled Cap

Wetness Index (hereafter “wetness”; Table S2). These covariates capture important information about the vegetation such as forest structure or moisture content. For all these explanatory variables, we generated raster layers of 30 m of resolution (Table S2).

We calculated some of the above-mentioned covariates (Table S2) at five spatial scales using different circular moving windows with radii of 197, 762, 1,167, 4,016, and 7,567 m, which represent the mean distance traveled by the tracked elephants in 5 h, 10 h, 24 h, 1 week, and 1 month, respectively.

2.4 | Focal habitat patches

To develop our functional connectivity analysis, we defined as focal habitat patches all the isolated, that is, completely broken off, forest patches within the MERs (Figure 1), which we did by extracting all the forest areas from Miettinen, Shi, and Liew (2016) land use layer. We then calculated the area, perimeter, perimeter ratios, and the center of each focal habitat patch. We assumed that these forest patches were occupied by elephants or could potentially sustain an elephant population in the future.

2.5 | Functional connectivity model

We used a SSF model to evaluate how the landscape variables described above affect elephant movements and to calculate resistance to movement surfaces. SSF uses a case-control design, where each habitat covariate used during the observed movement steps is contrasted to the habitat available to an animal using a conditional logistic regression (Thurfjell, Ciuti, & Boyce, 2014). We first calculated the distance of each step between consecutive GPS fixes and filtered the data, retaining only steps that measured 500 m or more. This distance threshold was chosen to ensure that steps represent actual “movement” behavior of elephants through the landscape rather than resource use (Zeller et al., 2016). We simulated nine “available” steps for each “used” step. Step lengths were simulated from the empirical movement data using the gamma distribution with a maximum likelihood, and turning angles were drawn from a uniform distribution between $-\pi$ and π (Signer, Fieberg, & Avgar, 2017).

For each observed and control step, we calculated the values of the predictor landscape covariates at the end point of the steps. We constructed several SSF models using different combinations of explanatory variables, and then we used the Akaike Information Criterion (AIC) to identify the best SFF (Burnham & Anderson, 2002). To implement the SSFs, our first step was to

evaluate the most informative scale (197, 762, 1,167, 4,016, or 7,567 m) for each variable using univariate models and compared them contrasting their likelihood explained and AIC values. Later, we ran multivariate models using the most informative scale of the variables assessed. We tested all explanatory variables for multicollinearity using the Pearson's correlation matrix, and we did not include variables in the same candidate model that were correlated at $>.5$.

We used the best SSF model to predict elephant probability of movement in a 250-m resolution grid across our entire study area. The resulting probability of movement layer characterizes each cell with continuous values between 0 and 1, representing the permeability of the landscape to elephant movements. We used the inverse of the probability of movement to represent the landscape resistance, which denotes the difficulty of elephants to move across the landscape.

On the basis of resistance surfaces, we modeled potential connectivity using two approaches: least cost path (LCP) and circuit theory methods. LCP allowed us to estimate cost-effective distances between the focal habitat patches and estimate the shortest distance between two focal patches while considering the resistance to movement (Adriaensen et al., 2003). Circuit theory allowed us to estimate the current density which is a proxy for the probability of a random walker (i.e., a stochastic process describing a path conformed by a succession of random steps on some mathematical space) moving between patches found within any pixel (McRae et al., 2008). We calculated and mosaicked the cost-weighted distance surfaces to build a single network of links across the focal habitat patches. We then estimated the current density, effective resistances, and current flow centrality for focal habitat patches and links. Current flow centrality analysis evaluates the importance of patches and links using a graph theoretic approach by ranking their contribution to facilitating ecological connectivity across a network of patches in a landscape (Carroll, Mcrae, & Brookes, 2012). Connectivity analyses were conducted in Linkage Mapper and Circuitscape 4.0.

To evaluate the functional connectivity model performance, we retained 10% of the GPS fixes from every elephant tracked before the implementation of any analysis (Zeller et al., 2018). We buffered each GPS evaluation fix with a radius equal to the maximum distance step length (4,513 m) and generated nine random points within each buffer. We extracted the resistance and current density values for the GPS evaluation fixes and the simulated random points, and we compared them using a resampling procedure randomly selecting 500 samples from each population and contrasting them by their 95% Confidence Intervals. Our expectation was that, if our

elephant movement probability model had high predictive power, resistance should be lower, and current density higher, at actual movement points than at random points.

2.6 | Assessment of the functionality of the central forest spine corridors

We used two approaches based on the LCP and circuit theory analyses to evaluate the effectiveness of CFS linkages, restricting our analysis to the 28 CFS linkages (17 primary and 11 secondary) within the MERs (Figure 1). For the first assessment, we calculated the mean current density values within the CFS linkages and used our LCP analysis to assess the most efficient, or least-costly, way to move between two focal patches connected by CFS linkages. The LCP represents the best connectivity scenario against which the CFS linkages were compared. We calculated the mean current density of the LCP links using the polygons of the LCP calculated using the threshold value of 200,000 at the cost-weighted distance surface.

As a second evaluation, we calculated the mean current density values within the buffer boundaries of the CFS corridors. Our assumption was that corridors should have higher current density values than the more diffuse buffer areas. To calculate the buffer size of each linkage, we estimated the minimum bounding geometry rectangle for each link and then added a buffer, the width of which was the minimum bounding geometry rectangle/2. Because, the number of grid cells along the LCP between the focal nodes was always lower than the number of grid cells within the CFS linkages and the buffers, we randomly sampled grid cells within these polygons to evaluate an identical number of grid cells for CFS linkages, their buffer boundaries, and their associated LCP. To evaluate if current density values were different between CFS linkages and their associated buffer boundaries and LCP, we contrasted them using their 95% confidence intervals of their mean current values.

We then used these two comparisons to assign a score of effectiveness to each CFS linkage. First, if the CFS linkage had equivalent (i.e., not significantly different) current density values than the LCP, we assigned it a score of “1”; if it had lower, then we assigned the score “0.” Second, if the CFS linkage had higher current density than its buffer boundaries, we assigned the score of “2”; for equivalent values, we assigned the score of “1,” and for lower mean values we assigned a score “0.” Therefore, each CFS link could get the maximum score of “3” and a minimum score of “0.” Effectiveness of the

CFS links were categorized according their scores values as: very good (3), good (2), acceptable (1), poor (0).

2.7 | Animal subjects

Elephant immobilization process was carried out by the Department of Wildlife and National Parks Peninsular Malaysia, and all the procedures fulfilled the research and ethics requirements by the Malaysian government (permit #JPHL%TN(IP):80-4/2).

3 | RESULTS

3.1 | Focal habitat patches

We identified 34 polygons of forest within Peninsular Malaysia's MERs and the CFS master plan (Figure 2, Table 1). The mean area of the polygons was $1,041.7 \pm 2,170.8$ km², with a range of 1–11,750 km², together encompassing a total area of 35,448 km². The mean Euclidian distance between the closest-neighbor polygons was 2.7 ± 3.3 km (range: ~100 m to 13 km). These 34 polygons were the focal habitat patches in our connectivity analysis.

3.2 | Probability of movement

Our SSF models revealed important insights regarding Asian elephant movements in Peninsular Malaysia. Our best SSF model included 13 landscape variables (Table 2) and had a Δ AIC value of 1.51 for the second-best ranked model ($w_i = 0.44$; Table S4).

The most influential variables to explain elephant probability of movement were forest-related (“wetness,” “wetness²,” and “distance to forest at the 197 m scale”; Table 2). Overall, elephant movements were more likely in areas of disturbed vegetation such as forest gaps, secondary forests, and areas of regrowth and new plantations (positive effect of “wetness” and “percentage of regrown and new plantations at the 1,961 m scale”). “Wetness²” shows that elephants actually preferred intermediate values of forest openness, while the positive effect of “distance to forest” shows that elephants preferred open vegetation but always close to mature forest (Table 2). Elephants clearly avoided high elevations and areas with steep and rugged terrain and were attracted to sources of permanent water (197 m scale) such as lakes and large rivers (Table 2). The relationship of elephant movements with plantations was also complex. Elephants were attracted to the proximity of plantations (“distance to plantations at the 30 m scale”) and to areas of new

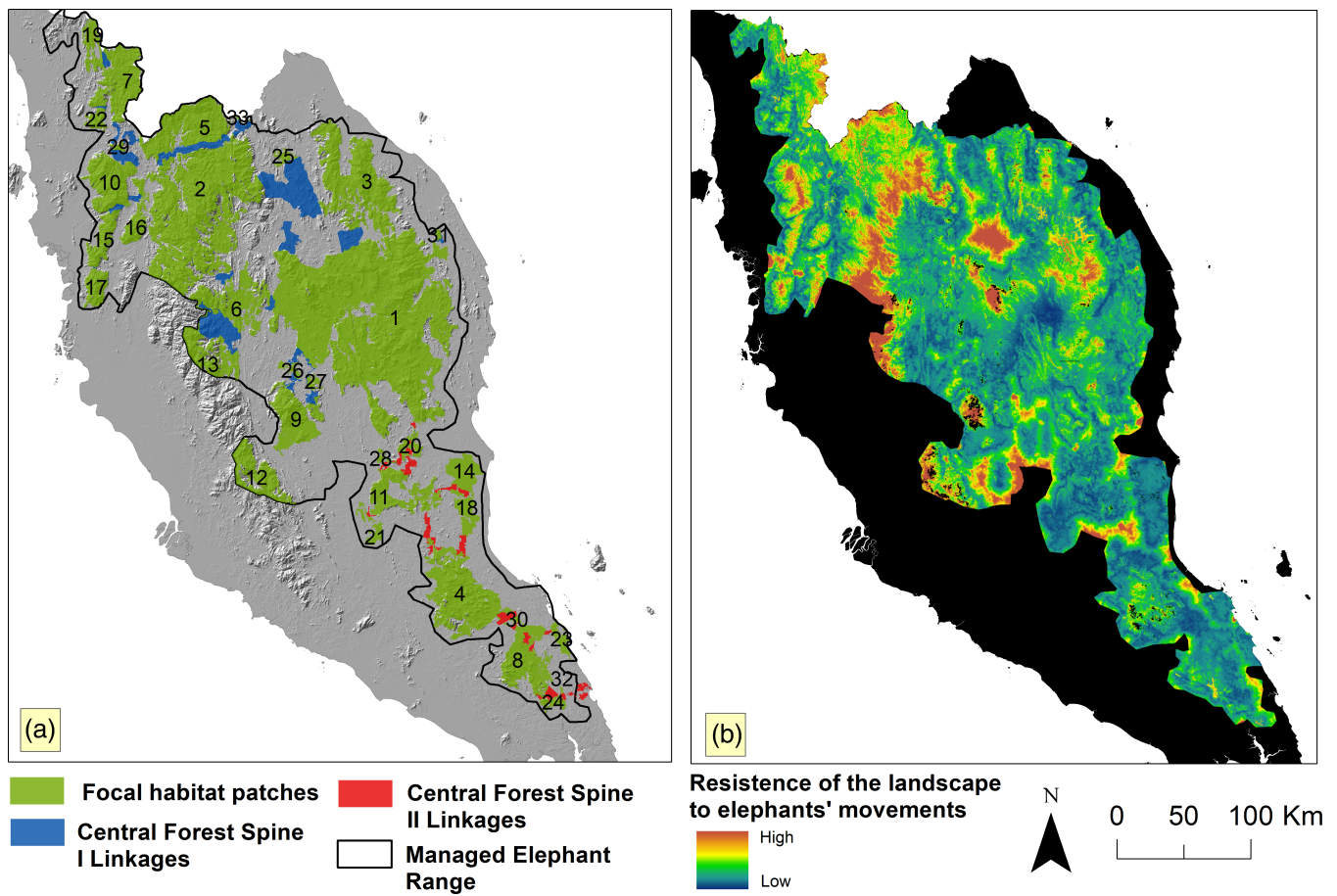


FIGURE 2 (a) Habitat patches (1, Taman Negara; 2, Temengor; 3, Tembat; 4, Endau; 5, Royal Belum; 6, Uu Jelai 1; 7, Ula Muda; 8, Lenggong Tengah; 9, Krau; 10, Gunung Inas; 11, Ibam; 12, Ulu Jelai 3; 13, Ulu Jelai 2; 14, Pekan; 15, Bukit Larut; 16, Papulut; 17, Bubu; 18, Nenasi; 19, Pedu; 20, Lepar; 21, Tasik Bera; 22, Rimba Telui; 23, Tenggaroh; 24, Panti; 25, Sokortaku; 26, Bencah; 27, Som; 28, Temiang; 29, Belukar Semang; 30, Mersing; 31, Jerangau; 32, Ulu Sungai; 33, Jeli 1; 34, Jeli), and Central Forest Spine Linkages evaluated in this study; (b) resistance surface to Asian elephants' movements in Peninsular Malaysia used in the connectivity analysis

TABLE 1 Top 10 ranked habitat patches of primary forest within Peninsular Malaysia's MERs and the CFS master plan according to their values of core centrality (see Table S3 for the complete list)

Focal patch ID	Name	Area (km ²)	Euclidian distance to nearest focal patch (m)	ID of the nearest focal patch	Core centrality	Rank
1	Taman Negara	11,723.1	453.6	3	364.6	1
2	Temengor	5,648.6	488.3	16	294.1	2
11	Ibam	867.4	6,641.0	20	264.5	3
6	Uu Jelai 1	1,215.4	1,629.7	1	246.4	4
18	Nenasi	344.5	250.0	14	208.4	5
20	Lepar	183.2	6,641.0	11	198.5	6
28	Temiang	55.7	7,574.1	1	174.9	7
4	Endau	2,143.6	2,978.0	30	173.0	8
10	Gunung Inas	1,057.0	903.2	15	158.6	9
30	Mersing	36.7	451.9	8	149.0	10

TABLE 2 Landscape variables that have an effect on the probability of movement of Asian elephants in Peninsular Malaysia. Variables are ranked according the standardized coefficient values. This model includes quadratic terms. The values in the parenthesis after the names of the variables indicate the spatial scale used in each environmental variable

Variable	Standardized coefficient	z value	p
Wetness	0.92290	20.268	<.00001
Wetness ²	-0.55976	-13.896	<.00001
Distance to forest (196 m)	-0.43088	-10.009	<.00001
Elevation	-0.30899	-11.077	<.00001
Distance to roads (30 m)	0.27813	1.919	.054
Slope	-0.26408	-24.576	<.00001
Percentage of regrowth and new plantations (1,961 m)	0.19310	12.518	<.00001
Distance to plantations (30 m)	-0.15900	-2.666	<.01
Percentage of plantations (1,961 m)	-0.06671	-5.298	<.00001
Percentage of water (196 m)	0.04280	3.019	<.01
Mean of nightlight (4,016 m)	-0.03134	-2.218	<.05

plantations (“percentage of regrowth and new plantations at the 1,961 m scale”) but avoided areas with high coverage of plantations (“percentage of plantations at the 1,961 m scale”). Elephants also avoided high human densities (“nightlight at the 4,016 m scale”) and roads (“distance to roads at the 30 m scale”; Table 2).

3.3 | Functional connectivity of elephants' populations in peninsular Malaysia

We identified 57 potential cost-weighted corridors using LCP and circuit theory analysis to maintain functional connectivity between the 34 focal forest patches (Figure 3, Table 3). According to current-flow centrality scores, the most important focal forest patches are Taman Negara (patch #1) and Temengor (#2; Figure 3, Table 3). These forest patches are important both because of their large area and role maintaining the whole connectivity network for elephants in Peninsular Malaysia (Figure S2). Another forest patch, Ulu Jelai 1 (#6), is important

because it allows connectivity between Taman Negara and Temengor (Table 3).

The five most important cost-weighted corridors identified were Temengor-Ulu Jelai, Taman Negara-Ulu Jelai, Taman Negara-Lepar, Endau-Nenasi, and Ibam-Temiang (Table 3). These corridors showed the highest values of centrality ranking, while their resistance was relatively low (Table 3, Figure S2). Our model suggests that connectivity is more compromised in the southern part of Peninsular Malaysia. Circuit theory analysis, through visual inspection of the current density map, suggests that elephant movements would be more restricted for corridors in southern Peninsular Malaysia (Figure 3). The current density map suggests that landscapes in the north and center of Peninsular Malaysia still provide good connectivity for elephant movements (Figure 3).

We validated our elephant movement model by comparing predicted movements from the model with random points. Predicted movements showed lower resistance values (95% CI: 0.16–0.18 vs. 0.20–0.23) and higher cumulative current density (95% CI: 0.61–0.66 vs. 0.54–0.59), indicating that our model has high potential for predicting the movements of Asian elephant across Peninsular Malaysia.

3.4 | Evaluation of the functional connectivity of the central Forest spine linkages

According to the functional connectivity evaluation of 28 CFS linkages, 57% of them provided high functional connectivity (i.e., classified as “good” or “very good”), 28% provided acceptable connectivity, and 14% provided low to no connectivity (i.e., “poor” or “non-functional”; Figure 4, Table 4). The four CFS linkages with the highest centrality values (PL1-I, PL3-I, PL2-II, and SL1-II; Table 3) all provided good or very good landscape connectivity (Table 4). Five CFS linkages showed lower connectivity levels than their associated LCP and boundaries and two of them (SL6-I and PL4-II; Table 4) were classified as non-functional, suggesting that they have completely lost their connectivity. SL6-I has lost one of its focal patches as a consequence of deforestation and the area of PL4-II was identified as a barrier for elephant movements in our functional connectivity model (Figure 4).

4 | DISCUSSION

We used a movement probability model based on actual movement decisions of 53 elephants to evaluate the functional connectivity of landscapes and linkages in

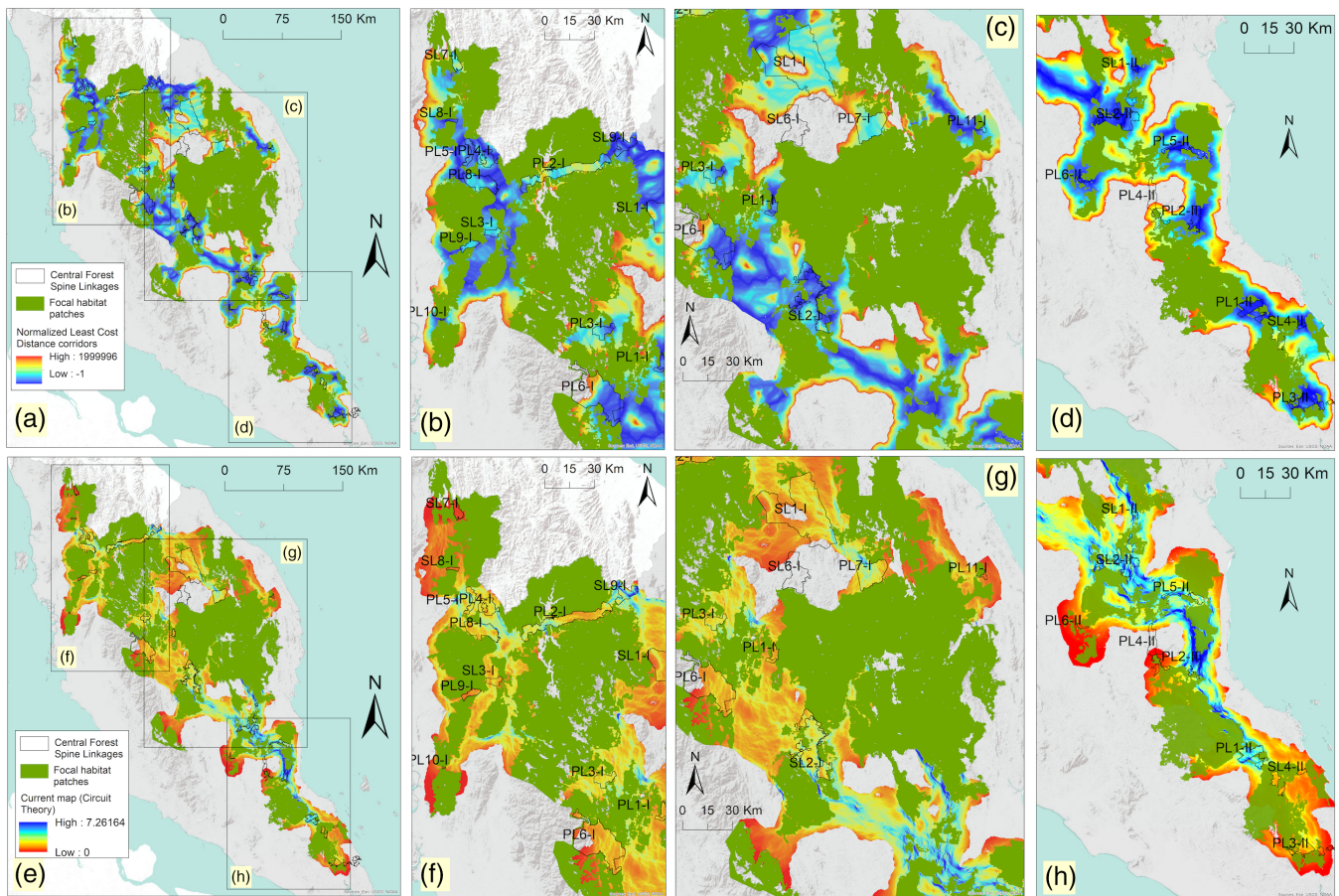


FIGURE 3 Connectivity areas identified according our Least Cost Path analysis (low resistance in blue, higher resistance in red), (a) throughout all Peninsular Malaysia, and (b) northern; (c) central; and (d) southern areas; and current density derived using Circuit Theory analysis (higher current densities in blue, lower in red), (e) throughout all Peninsular Malaysia, and (f) northern; (g) central; and (h) southern areas

TABLE 3 Top 10 ranked potential corridors according their centrality value. Potential corridors were identified using Least Cost Path and Circuit Theory analysis and connect the 34 focal forest patches within Peninsular Malaysia's MERs and the CFS master plan (see Table S5 for the complete list)

Corridor ID	From habitat patch	To habitat patch	Cost weighted distance to path	Effective resistance	Cost weighted distance to effective resistance	Centrality	Rank
13	(2) Temengor	(6) Ulu Jelai 1	131.2	2,286.5	196.8	207.5	1
3	(1) Taman Negara	(6) Ulu Jelai 1	82.7	1,171.6	155.8	188.2	2
6	(1) Taman Negara	(20) Lepar	60.1	2,797.7	87.6	182.4	3
28	(4) Endau	(18) Nenasi	61.0	6,498.1	117.5	168.0	4
61	(11) Ibam	(28) Temiang	33.9	1,483.0	96.5	149.6	5
31	(4) Endau	(30) Mersing	42.7	1,285.6	113.9	145.0	6
16	(2) Temengor	(16) Papulut	85.7	478.2	152.9	126.3	7
44	(8) Lenggong Tengah	(30) Mersing	57.3	901.7	47.7	120.0	8
58	(11) Ibam	(18) Nenasi	79.5	4,822.3	132.5	108.8	9
67	(14) Pekan	(18) Nenasi	51.5	427.5	30.1	106.9	10

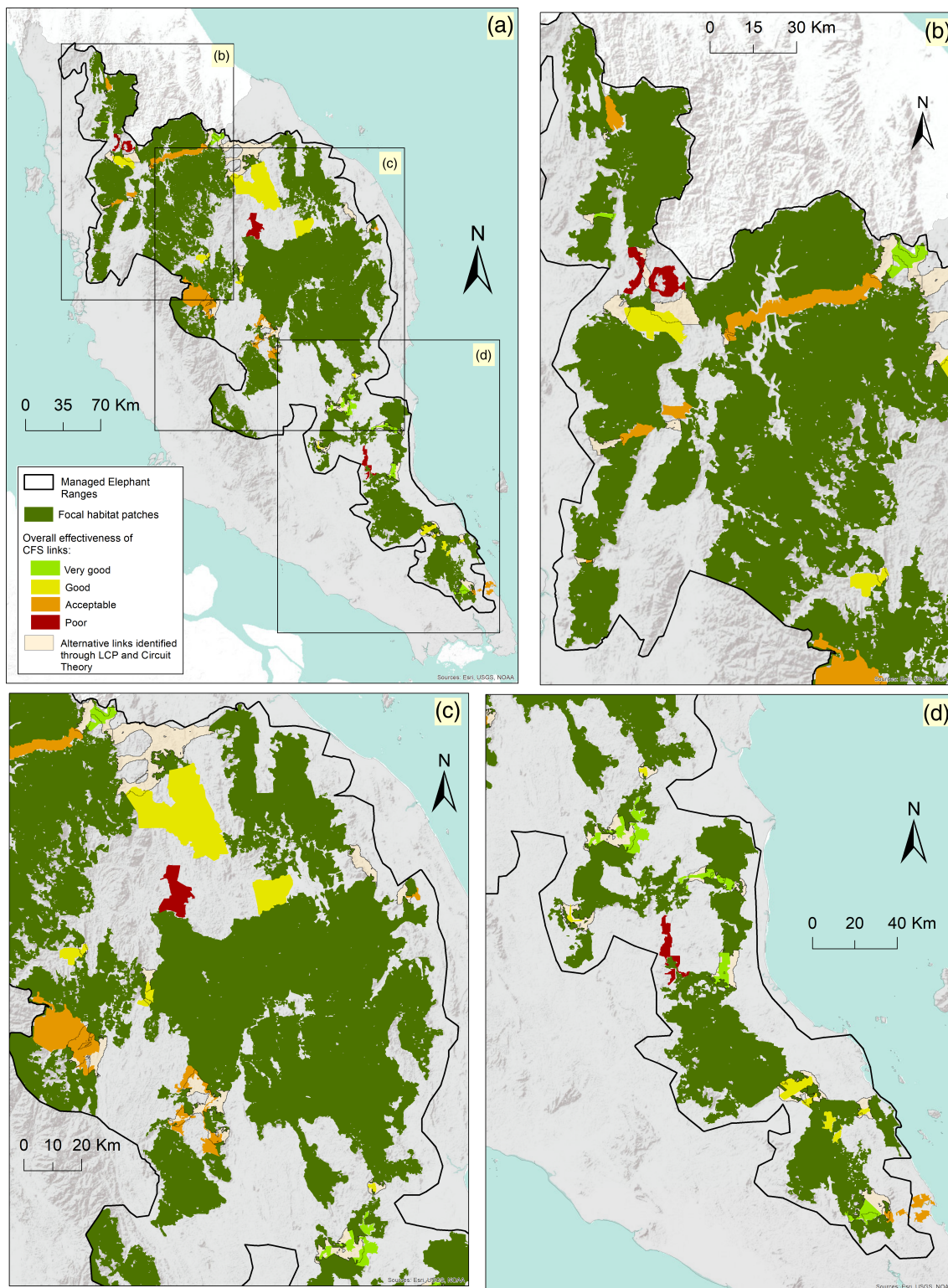


FIGURE 4 Central forest spine effectiveness to maintain functional connectivity for Asian elephants in Peninsular Malaysia and alternative corridors between focal habitat patches. Total area covered by the 28 Central Forest Spine (CFS) links is $\sim 3,798 \text{ km}^2$ and area covered by their, respectively, alternative least cost path (LCP) corridors encompassed $\sim 2,522 \text{ km}^2$. The proportion of overlap between the CFS links polygons and LCP polygons is 19% (724 km^2)

Peninsular Malaysia's CFS master plan. This is the first evaluation of CFS's effectiveness with biological data and our results present a relatively positive picture of the

plan, highlighting its capacity to maintain functional connectivity at large scale, at least for Asian elephants. A very important and positive finding is that the CFS

TABLE 4 Effectiveness of Central Forest Spine ecological linkages according to their functional connectivity for Asian elephants

CFS linkage	From habitat patch	To habitat patch	Area covered (km ²)	Connectivity compared with least cost path	Connectivity compared with surrounding buffer	Score	Overall effectiveness
PL1-I	(1) Taman Negara	(6) Ulu Jelai 1	43.5	Lower	Higher	2	Good
PL2-I	(2) Temengor	(5) Royal Belum	279.8	Lower	Equivalent	1	Acceptable
PL3-I	(2) Temengor	(6) Ulu Jelai 1	68.0	Equivalent	Equivalent	2	Good
PL4-I	(5) Royal Belum	(29) Belukar Semang	76.3	Lower	Lower	0	Poor
PL5-I	(7) Ula Muda	(29) Belukar Semang	46.6	Lower	Lower	0	Poor
PL6-I	(6) Ulu Jelai 1	(13) Ulu Jelai 2	529.3	Lower	Equivalent	1	Acceptable
PL7-I	(1) Taman Negara	(3) Tembat	225.2	Lower	Higher	2	Good
PL8-I	(10) Gunung Inas	(29) Belukar Semang	153.7	Equivalent	Equivalent	2	Good
PL9-I	(10) Gunung Inas	(15) Bukit Larut	36.7	Lower	Equivalent	1	Acceptable
PL10-I	(15) Bukit Larut	(17) Bubu	2.0	Equivalent	Equivalent	2	Good
PL11-I	(1) Taman Negara	(31) Jerangau	12.6	Lower	Equivalent	1	Acceptable
SL1-I	(3) Tembat	(25) Sokortaku	1,037.2	Lower	Higher	2	Good
SL2-I	(1) Taman Negara	(26) Bencah	190.8	Lower	Equivalent	1	Acceptable
SL3-I	(10) Gunung Inas	(16) Papulut	36.6	Lower	Equivalent	1	Acceptable
SL6-I	(1) Taman Negara	—	205.3	—	—	—	Not functional
SL7-I	(7) Ula Muda	(19) Pedu	44.2	Lower	Equivalent	1	Acceptable
SL8-I	(7) Ula Muda	(22) Rimba Telui	11.3	Equivalent	Higher	3	Very good
SL9-I	(2) Temengor	(34) Jeli 2	81.2	Equivalent	Higher	3	Very good
PL1-II	(8) Lenggong Tengah	(30) Mersing	143.7	Lower	Higher	2	Good
PL2-II	(4) Edau	(18) Nenasi	66.9	Equivalent	Higher	3	Very good
PL3-II	(8) Lenggong Tengah	(24) Panti	67.4	Equivalent	Higher	3	Very good
PL4-II	(4) Endau	(11) Ibam	104.1	—	—	—	Not functional
PL5-II	(14) Pekan	(18) Nenasi	66.5	Equivalent	Higher	3	Very good
PL6-II	(11) Ibam	(21) Tasik Bera	12.5	Equivalent	Equivalent	2	Good
SL1-II	(1) Taman Negara	(20) Lepar	10.5	Equivalent	Equivalent	2	Good
SL2-II	(20) Lepar	(11) Ibam	150.6	Equivalent	Higher	3	Very good
SL4-II	(8) Lenggong Tengah	(23) Tenggaroh	11.7	Equivalent	Equivalent	2	Good
SL5-II	(24) Panti	(32) Ulu Sungai	84.3	Lower	Equivalent	1	Acceptable

linkages with the highest centrality values (i.e., the most important to maintain overall connectivity in Peninsular Malaysia) also score highly in functional connectivity (i.e., they are actually effective corridors for elephant movement). This means that an adequate CFS implementation can lead to high levels of functional connectivity among Peninsular Malaysia's main forest blocks. Our connectivity model was also useful to identify specific problems and actionable solutions. For example, we identified non-effective linkages and suggested potential alternative alignments. Overall, connectivity is far more compromised in the southern part of Peninsular Malaysia

as a consequence of high development and extensive transformation of forests into monocultures such as palm oil. Further losses of CFS links in southern Peninsular Malaysia would seriously compromise connectivity due to the lack of alternative corridors.

Based on our assessment, we recommend Malaysia's authorities to conduct some revisions on the CFS plan to ensure its effectiveness. CFS's 37 linkages suffer serious limitations—for example, none of them was originally designed based on actual ground surveys, almost none of them has been afforded protected area status to prevent further forest losses, and most of them are bisected by

paved roads (Jain et al., 2014). In fact, as of 2019, forest loss is ongoing in many linkages (Authors, pers. obs.). Though half of the 28 CFS linkages evaluated here provide high or good functional connectivity for elephants, and 28% provide acceptable levels, 14% of them are not conducive for elephant movements and indeed two of them may have completely lost their functional connectivity due to land use change. Options to improve connectivity around poorly-functioning linkages include tweaking some of the original alignments or replacing old linkages for completely new routes, such as in the case of linkages PL4-I, PL5-I, SL6-I, and PL4-II (Figure 4, Table 4). Despite their great potential, CFS's linkages actual capacity to ensure long-term connectivity in Peninsular Malaysia is still uncertain, and it largely depends on adequate governance and coordination between the Federal and relevant State governments to successfully implement the project (Jain et al., 2014). Additionally, it is critical to ensure the conservation of the focal forest patches identified, especially those with high centrality values that contribute disproportionately to the overall maintenance of connectivity in Peninsular Malaysia (Table 1).

Our probability movement model showed the complexity of Asian elephants' movement behavior. Though the perception of many conservation practitioners is that elephants prefer "pristine" primary forests, the reality is that elephants are edge specialists (Campos-Arceiz 2013) and they are more likely to thrive in areas with at least some disturbed vegetation, such as forest gaps, logged and secondary forest, and areas of regrowth and new plantations (Figure 2 and Evans, Asner, & Goossens, 2018; Wadey et al., 2018). These are often human-dominated landscapes, or their interface with natural vegetation. As edge specialists, elephants require forest and they avoid moving across landscapes with extensive monocultures where there are no nearby forests to provide refuge (e.g., Wadey et al., 2018). These insights about elephant ecology, again, have important implications for conservation planners and practitioners—a conservation strategy based solely on protected areas will not be effective for Asian elephants. An approach like the CFS, based on wide conservation areas that include a network of protected areas embedded within integrated management landscapes (Reed, Van Vianen, Deakin, Barlow, & Sunderland, 2016; Sayer et al., 2013), is the best option for Asian elephant conservation.

Due to their extensive spatial requirements and foraging behavior (e.g., Mills et al., 2018; Poulsen et al., 2018; Terborgh, Davenport, Ong, & Campos-Arceiz, 2018), elephants will continue using forest edges and human-dominated landscapes and, inevitably, entering

into conflict with people in CFS and MER landscapes. After securing enough elephant habitat and functional connectivity between patches, the next priority for elephant conservation in Malaysia, and throughout the species range, is to mitigate the human–elephant conflict (HEC) that occurs largely in the form of crop raiding. Our probability of movement model suggests that elephant translocation, the current main form of mitigation in Peninsular Malaysia (Saaban et al., 2011), will not be effective in the long term. HEC mitigation therefore needs to promote coexistence by a combination of (a) spatial planning of new developments (e.g., avoiding when possible new plantations in high HEC risk areas), (b) reducing the cost of crop raiding (e.g., using electric fences to prevent elephants accessing the crops), (c) creating fair compensation mechanisms (e.g., crop raiding insurance schemes), (d) promoting tolerance and positive attitudes (e.g., by means of awareness campaigns), and, only as last resort, (e) elephant translocation and other highly invasive measures.

One potential caveat in our movement probability model is that 60% of the elephants tracked in this study were translocated individuals, whose movements might differ from those of non-translocated ones. We omitted the first 15 days of tracking data from all individuals to diminish potential biases from their behavior immediately after translocation and collaring, and we also assumed that movement patterns of the translocated elephants represent their capability of moving across the landscape. Importantly, over 600 elephants have been translocated in Peninsular Malaysia since 1974, approximately 40% of the entire estimated population (~1,500 individuals; Saaban et al., 2011), so a substantial proportion of the current elephant population in the country might have been translocated at some point. Another limitation is that the random walker model used by Circuit Theory analysis may oversimplify the actual movement behavior of our focal species. Elephants are known to follow routes that are consistent among years and generations (Polansky, Kilian, Wittemyer, & Polansky, 2015; Wall, Wittemyer, Klinkenberg, Lemay, & Douglas-Hamilton, 2013), and with the random walker model we only assessed the movements based on the surrounding 250 m raster cells of the resistance surface. This implies that learned movement routes or foraging behavior may not be adequately captured by the random walker model, since the perceptual ranges of elephants are much larger, and in consequence this might have implications in the precision of our connectivity model. Moreover, landscapes in Peninsular Malaysia undergo rapid transformations due to deforestation and development, and some of the areas evaluated have already changed since 2015, the

year from which most of our forest cover data were derived (Miettinen et al., 2016). Finally, it is important to keep in mind that our evaluation of functional effectiveness is based on just one species, Asian elephants, and their movement patterns are likely to differ from many other wildlife species in Peninsular Malaysia. Hence, caution is needed when extrapolating the results of our assessment to other species. Evaluating CFS's effectiveness for other species should be a priority in coming years.

This study is an example of applied conservation science in one of the global hotspots for megafauna and biodiversity. Studies of this kind are costly in time and resources, but this cost is just a tiny fraction of the overall CFS budget. It is crucial that conservation agencies incorporate in their plans the necessary resources for monitoring and evaluation (M&E), to apply adaptive management and evaluate the long-term effectiveness and impacts of programs like the CFS. The CFS is far from perfect, since several of its linkages require realignment and it still suffers risk from deforestation, shortage of resources, and governance conflicts between Federal and State governments (Maniam & Singaravelloo, 2015). But overall, our work shows that implementing the CFS is a worthwhile endeavor for the Malaysian authorities. A successful implementation of the CFS would contribute greatly to promote connectivity for Asian elephants, and other wildlife, in Peninsular Malaysia.

4.1 | Impact statement

An adequate implementation of Malaysia's Central Forest Spine land use plan will provide functional connectivity for Asian elephants.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

All authors meet the author contribution criteria. ACA and JAT conceptualized the study. EPW, DM, SS, and ACA collected the elephant movement data, while JAT and AL collected the remote sensing data. JAT led the analyses and writing with advice from ACA and AL. All authors contributed to revision and preparation of the final manuscript.

DATA AVAILABILITY STATEMENT

The data used in this study contains sensitive geographic information on the location of an Endangered species but can be shared for legitimate research and conservation purposes upon contacting the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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