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Predicting landscape connectivity for the Asian elephant in its largest remaining subpopulation

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Abstract

Landscape connectivity between protected areas is crucial for the conservation of megafauna. But often, corridor identification relies on expert knowledge that is subjective and not spatially synoptic. Landscape analysis allows generalization of expert knowledge when satellite tracking or genetic data are not available. The Nilgiri Biosphere Reserve in southern India supports the largest wild populations of the endangered Asian elephant *Elephas maximus*. Current understanding of connectivity in this region is based on corridors identified by experts, which are not empirically validated and incongruent with each other. To more rigorously assess population connectivity for the Asian elephant, we evaluated a combination of three resistance layers and three dispersal abilities. The resistance models were based on the combined contributions of land cover, topographical slope, elevation, roads and buildings. A spatially explicit connectivity modeling tool predicted optimal movement corridors as a function of factorial least-cost routes across the resistance maps. A resistant kernel approach produced maps of the expected frequency of elephant movement through each cell to define core areas. We conducted a sensitivity analysis to determine the influence of resistance and dispersal. We selected the resistance surface and dispersal ability that produced the highest correlation with observed elephant densities. We evaluated the optimality of expert corridors by using a path randomization method. Eleven out of 24 expert corridors had connectivity values significantly higher than expected by chance, while only two corridors were spatially congruent between expert teams. Areas with the highest connectivity corresponded well with priority areas identified by conservationists and elephant density predicted by the resistant kernel connectivity model correlated significantly with surveys (Spearman's $\rho = 0.85$, $n = 500$, $P \ll 0.001$). The results provide the first rigorous, spatially synoptic and empirically validated evaluation of the connectivity of the elephant population across the reserve.

Introduction

Improving connectivity with corridors between terrestrial protected areas (PAs) enhances gene flow and reduces the deleterious effects of small population size (Hanski, 1998; Rabinowitz & Zeller, 2010; Theobald *et al.*, 2012; Cushman, Landguth & Flather, 2013). Identification of corridors for megafauna in south-east Asia (Moinuddin *et al.*, 2011), Thailand (Suksawang & Temchai, 2014) or India (Menon *et al.*, 2005) mostly rely on expert knowledge. Conventionally, corridors were defined as 'a relatively narrow strip of a particular type that differs from the areas adjacent on both sides' (Forman, 1995; Turner, Gardner & O'Neill, 2001). In recent years, however, this structural definition of corridors was complemented by a functional definition considering corridors to be areas with relatively high connectivity (e.g. Cushman, McKelvey & Schwartz, 2009; Landguth *et al.*, 2012). There are several advantages to this definition: (1) it is more general because animal dispersal proceeds along the same basic rules modulated by habitat quality within or between reserves; (2) it is valid over the entire landscape and not only in a particular area of focus; (3) it is more comprehensive for conservation because connectivity outside reserves is not independent from connectivity within reserves.

Functional connectivity is a product of how landscape structure affects the dispersal of organisms (Baguette & Van Dyck, 2007; Cushman, Evans & McGarigal, 2010a; Cushman, Chase & Griffin, 2010b; Elliot *et al.*, 2014). It is assessed by combining resistance maps, which measure the facilitation or reduction in movement through different landscape conditions such as land use, slope, roads and vegetation cover (Cushman, McKelvey & Schwartz, 2006; Spear *et al.*, 2010), with connectivity modeling analyses (Cushman *et al.*, 2010b, 2013; Mateo-Sánchez, Cushman & Saura, 2014; Elliot *et al.*, 2014; Cushman *et al.*, 2016). Least-cost path modeling is a method to identify corridors (Adriaensen *et al.*, 2003). It depends upon resistance maps that ideally would be parameterized from radio or satellite telemetry (Cushman & Lewis, 2010; Reding *et al.*, 2013; Elliot *et al.*, 2014; Zeller *et al.*, 2014, 2016) or from empirical optimization of gene flow data (Cushman *et al.*, 2006; Shirk *et al.*, 2010; Castillo *et al.*, 2014). In many instances, such data are still unavailable. Integrating expert knowledge within a least-cost path model is an improvement relative to the urgent task of reducing arbitrary demarcation of corridors and provides a more accurate, spatially synoptic understanding of connectivity (Riordan *et al.*, 2015; Moqanaki & Cushman, 2016).

The Nilgiri Biosphere Reserve (NBR) forms the link between the Eastern Ghats and the Western Ghats of India, two major geographic ranges of peninsular India, and holds the key to survival for the largest remaining populations of the Asian elephant *Elephas maximus* (Baskaran, 2013) and the Bengal tiger *Panthera tigris* (Jhala *et al.*, 2011). Increasing pressures for development and infrastructure expansion, coupled with inadequate planning, pose urgent threats to the ecological integrity and connectivity of this region (Puyravaud & Davidar, 2013).

Concerns about megafauna landscape connectivity within the NBR emerged in the late 1970s. However, to date, only two studies, Davidar (1981; refer to Davidar *et al.*, 2012 for a published summary) and Menon *et al.* (2005), have attempted to assess connectivity over the entire landscape. Meanwhile, efforts to restore or even simply maintain connectivity have been the source of intense social and economic conflict (Taghioff & Menon, 2010). Ongoing debates regarding conservation and development in the region are limited by the apparent subjectivity of expert corridor position and number. To synthetize data and make the results less dependent on personal choices, we assessed elephant habitat connectivity in the NBR with least-cost path and resistant kernel modeling on a resistance map produced through the composite of land cover, slope, elevation, human habitations and obstacles such as canals and penstocks.

We parameterized the resistance layers based on movement relationships described in the published literature (Baskaran *et al.*, 1993; Douglas-Hamilton, Krink & Vollrath, 2005). We used spatially explicit synoptic methods (e.g. Cushman, Lewis & Landguth, 2014) to predict population connectivity across this resistance model and validated the resulting connectivity predictions with observed elephant densities (Baskaran, 2013) and assessed the degree of agreement with corridors identified by experts (Davidar, 1981; Menon *et al.*, 2005). This enabled us to generate a more reliable and spatially complete assessment of the elephant population connectivity in the NBR. This approach can help with the urgent task of more robust wildlife corridor identification in regions where satellite tracking or genetic data are still lacking.

Methods

Study area

The NBR (5220 km^2) is located in the Western Ghats–Sri Lanka biodiversity hotspot, India (Fig. 1). It lies at the confluence of four distinct climatic zones: tropical monsoon, tropical savanna, temperate dry winter warm summer, and temperate dry winter hot summer (Peel, Finlayson & McMahon, 2007). The rainfall (from *c*. 800 to 5000 mm per year) occurs mostly during the south-west monsoon (May–August) and the north-east monsoon (September–December). The rain shadow of the Nilgiri Mountains results in a gradient of increasing aridity from west to east. The NBR's topographic and climatic diversity favors a wide range of ecosystems, from lowland evergreen rainforest to scrub jungles and from montane evergreen forest to high-elevation grasslands and wetlands (Prabhakar & Pascal, 1996). It harbors important populations of several endangered mammal species including the Asian elephant *E. maximus* and the Bengal tiger *P. tigris*.

Land use

GRASS-GIS (GRASS Development Team, 2015) was used for raster calculation and QGIS (Quantum GIS Development Team, 2015) for outputs. We used Survey of India 1/50 000 topographic maps for reference. The ASTER GDEM data provided the digital elevation model or DEM (ASTER GDEM is a product of METI and NASA). Two geometrically corrected images provided by the medium resolution Linear Imaging Self-Scanner (LISS-III) of the IRS-P6 satellite (NRSA, 2003) with 23.5 m spatial resolution were used to classify land cover. The land cover classification was based on the Normalized Difference Vegetation Index of the satellite Digital Number. Data were projected to UTM zone 43N in a WGS 84 datum (see Supporting Information Appendix S1 for details).

Resistance map

We defined a focal (also called original) movement resistance model based on a combination of land cover (Table 1), topographical slope, elevation, roads and human habitations. The cost assigned to each cover type in the resistant surface is supposed to represent an integration of the willingness of an animal to cross this cover type, the physiological cost of moving and the reduction in survival (Compton *et al.*, 2007). To follow a systematic resistance ranking method, we considered the pixel resistance to be a divisor of the maximum daily movement of elephants (see Supporting Information Appendix S2 for details over resistance attribution). African bush elephants can move at an average pace of 26.40 km per day in unprotected corridors (Douglas-Hamilton *et al.*, 2005). This distance was reduced to 23.50 km per

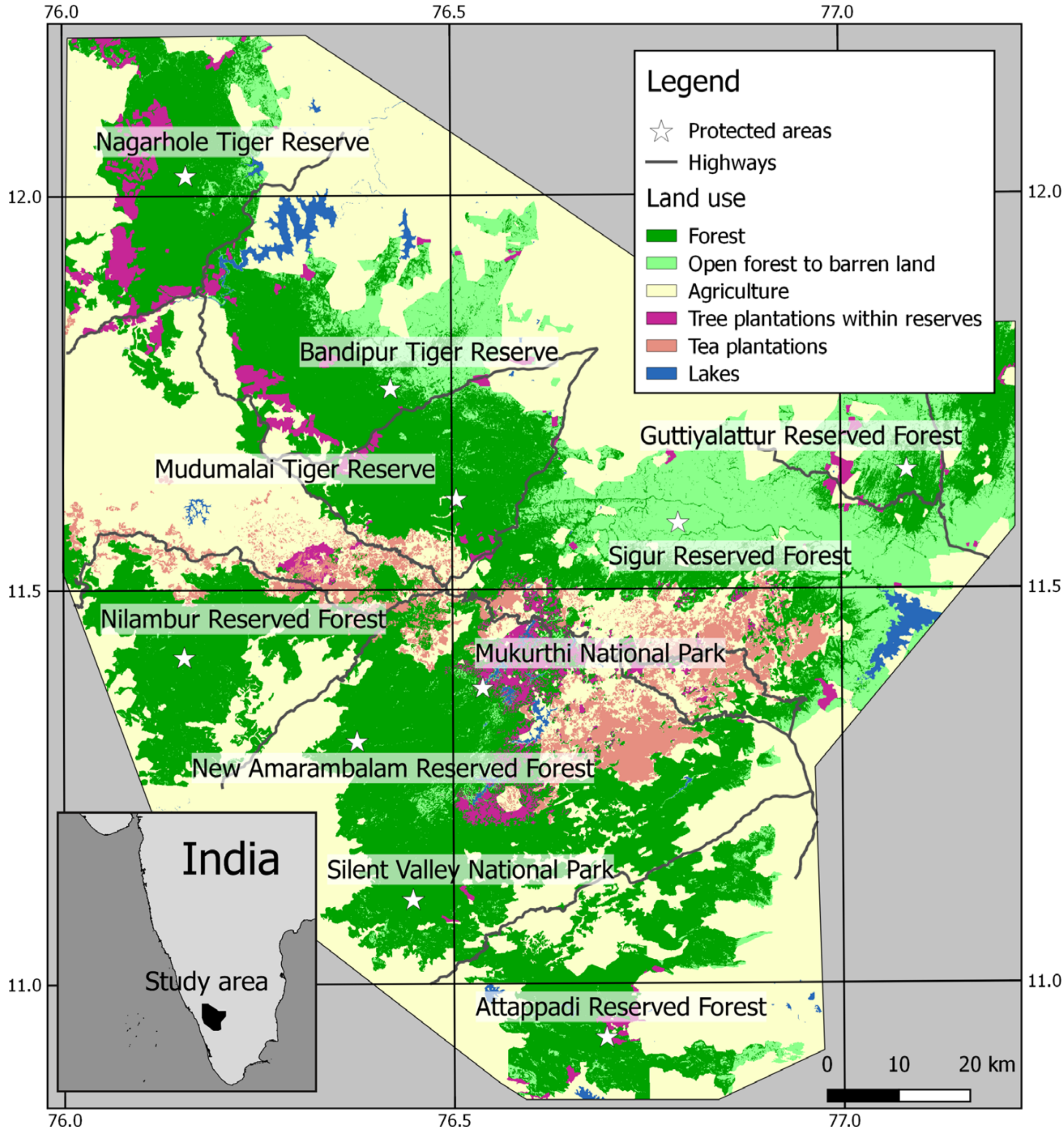

Figure 1 Land use of the Nilgiri Biosphere Reserve.

day to correspond to 1000 pixels (given the land-use spatial resolution) per day in ideal conditions. Elephants are unlikely to choose their movements based on their immediate surroundings only. However, at the landscape level, their density is higher in relatively more productive (Baskaran, 2013) or less disturbed areas (Jathanna *et al.*, 2015), which is consistent with the assumption that presence in less than optimal habitats has a cost to the animal. The resistance of elevation, slope, human habitation density (Fig. 2) and linear structures were added to that of the land-use resistance. Trenches and fences were not taken into consideration because there is an ongoing effort by the Forest Department to remove fences in elephant corridors. For the focal resistance model, we worked with a dispersal ability of 500 000, which authorized elephants to cover an absolute maximum of 21 km.

Core habitat

We used the resistant kernel approach in UNICOR (Landguth *et al.*, 2012) to produce maps of the expected frequency of elephant movement through each cell over the study area, which is the basis of defining core habitat areas (Cushman *et al.*, 2013). The resistant kernel approach builds a least-cost dispersal kernel around each source cell. The kernel maps surrounding all sources are summed to give the total expected density at each location on the landscape. The kernel reflects the attenuation of movement frequency as a function of resistance. We defined core habitat patches as contiguous units with resistant kernel values above 90th percentile.

To validate the kernel map and the underlying resistance surface, we compared its values to average elephant density in eight PAs (Baskaran, 2013) representing 3614 km^2. The values of the kernel map and of the elephant density map were divided by their respective range to rescale between 0 and 1. We distributed a total of 500 random points over the eight PAs comprising the NBR and recorded the kernel and density values. The Spearman's ρ statistics was used to estimate the measure of association between the two variables.

Table 1 Resistance to elephant movement for each land use. Original (or focal), Alternative 1 and Alternative 2 resistance values

	Resistance		
Land use	Original	Alternative 1	Alternative 2
Evergreen forest and degradation	1	1	1
Deciduous forest and degradation	1	1	1
Very degraded forest	4	1	4
Sparse scrubs and grass	10	1	10
Irrigated agriculture	50	20	10
Non-irrigated fields	30	20	10
Barren fields	20	20	10
Tree plantations, tree gardens	50	20	50
Fields	50	20	10
Habitations/barren land	20	20	20
Tree plantations within reserves	4	10	4
Tea	10	10	10
Water bodies	50	100	50
Roads	125	100	125

Corridors

We used the UNICOR connectivity modeling tool (Landguth *et al.*, 2012) to predict optimal movement corridors across the area as a function of factorial least-cost routes (Cushman *et al.*, 2014) across the resistance map. We placed 1166 source points for the dispersal model in a uniform grid at a 5-km spacing. The graph edges, which represent possible movement paths between source points, are weighted by the resistance value of the cell times the distance to the next pixel center, which gives the total edge length in terms of cost. All paths found are optimal paths of movement computed for every paired combination of starting and ending source points. The combination of the shortest paths creates a raw path density map or connectivity graph. The raw corridor map with a spatial resolution of 50 m was smoothed by applying a 750-m × 750-m square window (Cushman, Shirk & Landguth, 2012).

Corridor spatial randomization test

We evaluated the optimality of 12 Davidar (1981) and 12 Menon *et al.* (2005) corridors (Fig. 3) by using a path randomization method (Cushman *et al.*, 2010b; Cushman & Lewis, 2010; Cushman *et al.*, 2014). Each corridor was shifted (between 0 and 5000 m) and rotated randomly 100 times to obtain a distribution of randomized corridors paired to each of the expert corridors.

We calculated the sum value of the factorial least-cost path corridor network predicted by UNICOR down each expert corridor, and along its 100 randomized permutations. The agreement between the UNICOR corridor network and an individual expert corridor would be indicated by the number of standard errors the expert corridor was from the mean of the distribution of matched randomized corridors (e.g. Cushman *et al.*, 2010b). We evaluated 100, 250, 500, 750 and 1000 m radius smoothing with the focal mean function

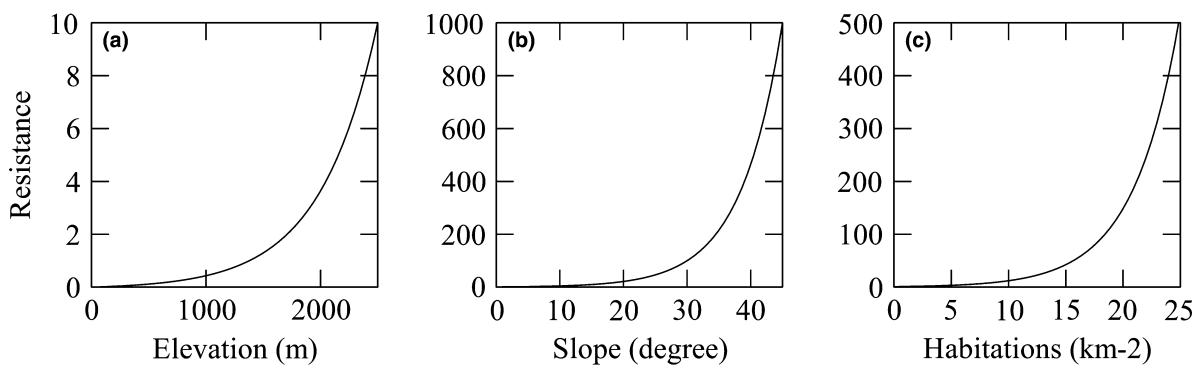

Figure 2 Resistance values allocated to elevation (a), topographic slope (b) and building density (c).

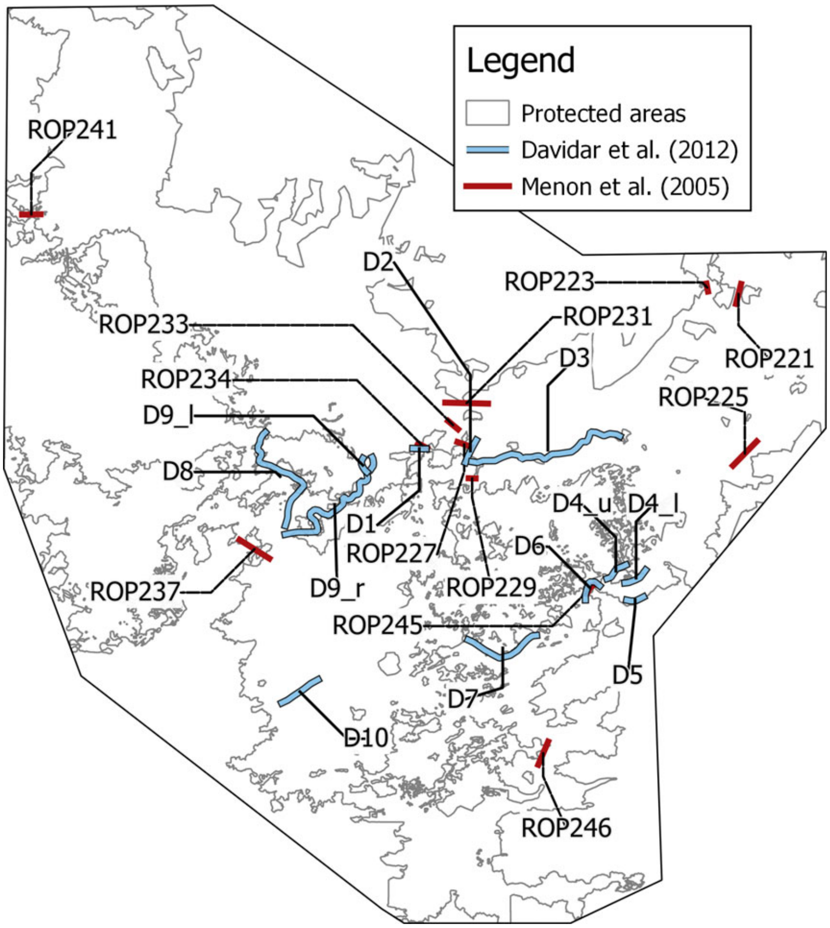

Figure 3 Location and identification of expert corridors.

in ArcGRID. We assessed which of these radii provided the best performance by calculating the average value of standard errors of actual expert corridors from the distributions of matched randomized corridors, and identified the scale that had the largest positive value, indicating highest discrimination of expert corridors. Next, we evaluated the ranking of corridor performance by sorting the expert corridors by the number of standard errors each was from the mean of the distribution of available corridors at each scale.

Sensitivity analysis

Provided resistance values were not actual measurements, we performed a sensitivity analysis (Supporting Information Appendix S3). Given the high computational demands of this synoptic analysis, we reduced the extent analyzed to the southern two third of the full Nilgiri study area, since it contained most expert corridors we sought to evaluate, the majority of the protected lands and a full range of the land-use mosaic.

We compared the original resistance model to two other resistance models (Table 1). Each kernel resistance model and each least-cost path model was tested with three dispersal abilities (500 000, 1 000 000 and 2 000 000). The least-cost path models were evaluated with smoothing radii of 250, 500 and 750 m. The nine density models were checked against actual elephant density and the 27 least-cost path maps where evaluated with spatial randomization compared to expert corridors. Correlation of connectivity surfaces were produced for comparison and reciprocal causal modeling (Cushman *et al.*, 2006) helped identify the most important source of variation.

Results

The reciprocal analysis of partial Mantel tests (Supporting Information Appendix S3) suggested that, at least under the dispersal distances used in this analysis, the varying dispersal abilities had relatively little effect on predicted patterns of elephant population connectivity, while variation in the resistance surface had a larger and statistically significant effect. The sensitivity analysis indicated that the original resistance surface at a 500 000-cost unit dispersal threshold was most supported, and that a 750-m smoothing parameter was optimal for the factorial least-cost paths. The results presented below are based on this optimal set of parameters.

The 90th percentile of the kernel on the map original resistance surface at a 500 000-cost unit dispersal threshold displayed only one core area from the Bandipur National Park to the Sigur Reserved Forest (Fig. 3a). Adjoining areas, such as the Nagarhole Tiger Reserve and the Sigur Reserved Forest, also constituted relatively strong core elephant habitats. The south of the NBR, however, does not contain core habitat due to terrain, elevation, less than optimal habitat and disturbance. There was a high agreement between the kernel model and observed density (Spearman's $\rho = 0.85$, $n = 500$, $P \ll 0.001$). The kernel model, however, tended to overestimate density in the Nilgiri North, Nilgiri South, Mukurthi, and part of the Coimbatore Division (Fig. 3b).

The smoothed path density map (Fig. 5) based on the original resistance surface at a 500 000-cost unit dispersal threshold and a 750-m smoothing parameter, provided the best prediction of the connectivity network across the landscape of all hypothesis tested (Supporting Information Appendix S3). A smoothing of 750-m radius applied to the UNICOR network provided the best discrimination between actual expert corridors and their randomized matched distributions (Table 2 and Supporting Information Appendix S3). At 750-m smoothing radius, 11 out of 24 expert corridors had large (>2) positive values for standard errors from the mean of the randomized distribution, indicating that these corridors detected significantly high level of connectivity. Out of these 11 corridors, 5 belonged to the Davidar (1981) and 7 to the Menon *et al.* (2005) study. By comparison, only two corridors (D1 = ROP333 and D6 = ROP245) were common to both expert teams.

Corridors defined as areas above the 90th percentile of the factorial least-cost path connectivity values with 750-m smoothing, form a network mainly within PAs and around the periphery of the Nilgiri Mountains (Fig. 5), with the highest number of branches in or near the core area. Above the 95th percentile, branches span from the Nagar Hole Tiger Reserve to Guttiyalatur Reserved Forest in the East or to Silent Valley National Park. A corridor also encircles the Nilgiri Plateau, with a gap in the Attapadi Reserved Forest. There is only one corridor with values above the 99th percentile, ranging from Nagar Hole Tiger Reserve to Guttiyalatur Reserved Forest. Within this corridor, the highest connectivity value was in between the Mudumalai National Park and the Sigur Reserved Forest, where this most important corridor crosses several villages.

Discussion

Maintaining connectivity between PAs is crucially important to biodiversity conservation (Blake *et al.*, 2008; Wilcove & Wikelski, 2008). Regional conservation strategies such as maintaining landscape connectivity for large mammals are sometimes deliberated with insufficient data. Spatial analysis can improve the available knowledge base for more rigorous evaluation of corridors. In this paper, we present the first synoptic evaluation of elephant population connectivity in the NBR. We combined expert opinion, extensive sensitivity analysis and *post hoc* validation of connectivity predictions. We chose to do so because telemetric data or genetic data were still unavailable or too sparse to validate a much needed landscape connectivity model.

We used factorial least-cost path modeling (Cushman *et al.*, 2009) and resistant kernel modeling (Compton *et al.*, 2007) implemented with UNICOR (Landguth *et al.*, 2012) to identify elephant corridors. The resistance map on which the focal study rested was selected after a sensitivity analysis spanning three choices of resistance values for land-use classes, three dispersal abilities and three path smoothing radii (Supporting Information Appendix S3). The original resistance surface (Table 1) at a 500 000-cost unit dispersal threshold and a 750-m smoothing parameter was most supported in sensitivity analysis and selected for final analysis of connectivity patterns.

We found a high agreement between predicted movement frequency from the resistant kernel model and observed elephant density (Baskaran, 2013). Our prediction of population connectivity matches the actual pattern of elephant occurrence in the landscape with high levels of concordance, and tends to confirm that the resistance map upon which the connectivity predictions were based reliably reflects the effect of

Table 2 Ranks and standard errors (>2) the actual corridor (Menon *et al.*, 2005; Davidar *et al.*, 2012) were from the distribution of randomized corridors across all expert corridors, across five smoothings of the UNICOR factorial least-cost path network

	100-m wide		250-m wide		500-m wide		750-m wide		1000-m wide	
Rank	Corridor	S.E.	Corridor	S.E.	Corridor	S.E.	Corridor	S.E.	Corridor	S.E.
1	ROP225	55.6	ROP225	68.0	D3	58.4	D3	56.2	D3	54.3
2	D3	46.9	D3	55.2	ROP225	52.8	ROP225	43.8	ROP225	36.3
3	D1	25.7	ROP241	25.1	ROP241	36.4	ROP241	25.5	ROP231	19.8
4	D2	21.0	D8	20.6	ROP223	24.0	ROP223	21.2	ROP241	19.5
5	ROP221	17.0	ROP223	19.7	D8	16.6	D2	13.2	ROP223	18.5
6	D8	12.4	D2	14.5	D2	13.3	ROP234	12.0	ROP234	14.8
7	D9_r	6.7	D1	13.1	D1	11.5	D8	11.8	D2	11.9
8	ROP241	5.6	ROP221	12.9	ROP221	9.4	D1	8.5	D8	8.8
9	–	–	D9_r	7.3	D9_r	8.1	D9_r	7.4	D9_r	7.2
10	–	–	–	–	ROP234	4.1	ROP221	5.2	D1	7.2
11	–	–	–	–	–	–	ROP231	3.7	–	–

landscape features on elephant movement. The path randomization analysis confirmed that 11 out of 24 expert corridors had significantly high levels of connectivity, compared with only two corridors in common between the expert teams. Agreement with expert corridors is therefore much higher than agreement among experts. Moreover, if corridor mapping by experts had been done with global positioning system, agreement with our study might have been even higher. Cushman *et al.* (2014) used a similar randomization method to validate resistance maps and corridor predictions for American black bears and found resistant kernel and factorial least-cost path methods effective at predicting locations where bears crossed highways. Our results therefore provide one of the first empirical validations of predicted corridor networks for large mammals.

The core elephant habitat was defined as contiguous units with limited restrictions on animal movement as indicated by resistant kernel values greater than 10% of the highest recorded (Cushman *et al.*, 2013). The resistant kernel model, however, overestimated elephant densities in a few reserves (Fig. 4b). This divergence may be due to the model itself or to the density data. We observed for example that (1) reserves with highest discrepancies were not as frequently surveyed as the National Parks where data agreement was higher, and (2) some areas such as Mukurthi National Park had no elephants according to (Baskaran, 2013), when elephants are actually observed at low densities (Davidar *et al.*, 2012). The kernel map (Fig. 4a) isolated one core area along the continuum of Bandipur Mudumalai and Sigur. In contrast, the southern portions of the NBR may be too fragmented, insufficient in extent or habitat quality to support a core area. This by no means indicates that the southern NBR is not important: elephants need to disperse in less than optimal areas that function as sinks within a metapopulation (van Aarde & Jackson, 2007).

The least-cost path corridor model (Fig. 5) offers a synoptic view of elephant corridors. A crucial difference between expert corridors and the present study is the evidence of a corridor network. This actuality was totally ignored by expert studies because of their structural definition of corridors and the spatial limitations of field studies. This difference is not trivial because corridors outside reserves are effective only when they form a continuum with corridors within reserves. This network also forms a hierarchy where small corridors merged into main corridors. Consequently, some corridors are more important than others, a fact that was also ignored by expert studies. This hierarchy allowed us to identify the most important corridor that crosses several problematic areas from Nagar Hole National Park to Kallar (Fig. 5). It threads through a maze of villages from Masinagudi to Sigur. This corridor with highest connectivity values was almost entirely described by Davidar (1981) and recently, the Tamil Nadu Forest Department (2009) proposed to give the surrounding region the status of 'Elephant Corridor' to increase its protection status. This management option is strongly supported by our analysis. Several other areas such as the 'Kallar corridor' (Johnsingh & Williams, 1999), the Ketambara corridor (http://www.tigernet.nic.in/Alluser/Parliament_Detail.aspx?

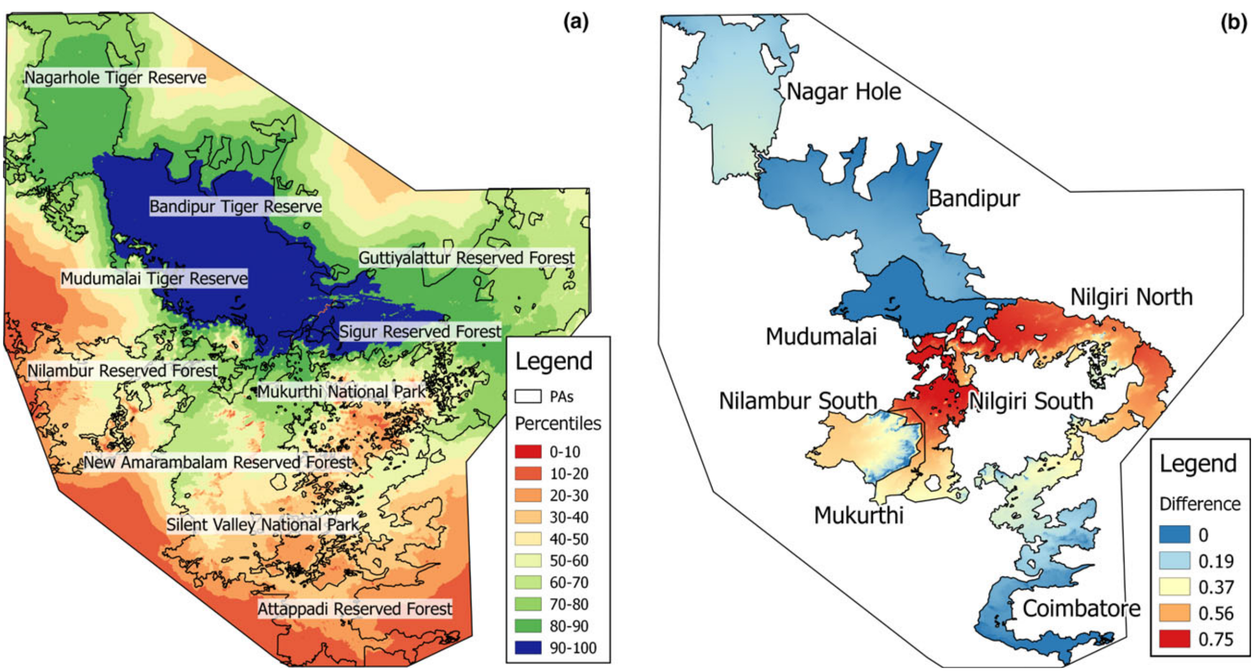

Figure 4 Core area the Nilgiri Biosphere Reserve based on UNICOR least-cost dispersal kernel calculation of elephant density (a) and difference between standardized elephant density as provided by UNICOR least-cost dispersal kernel and the Baskaran (2013) standardized elephant densities (b).

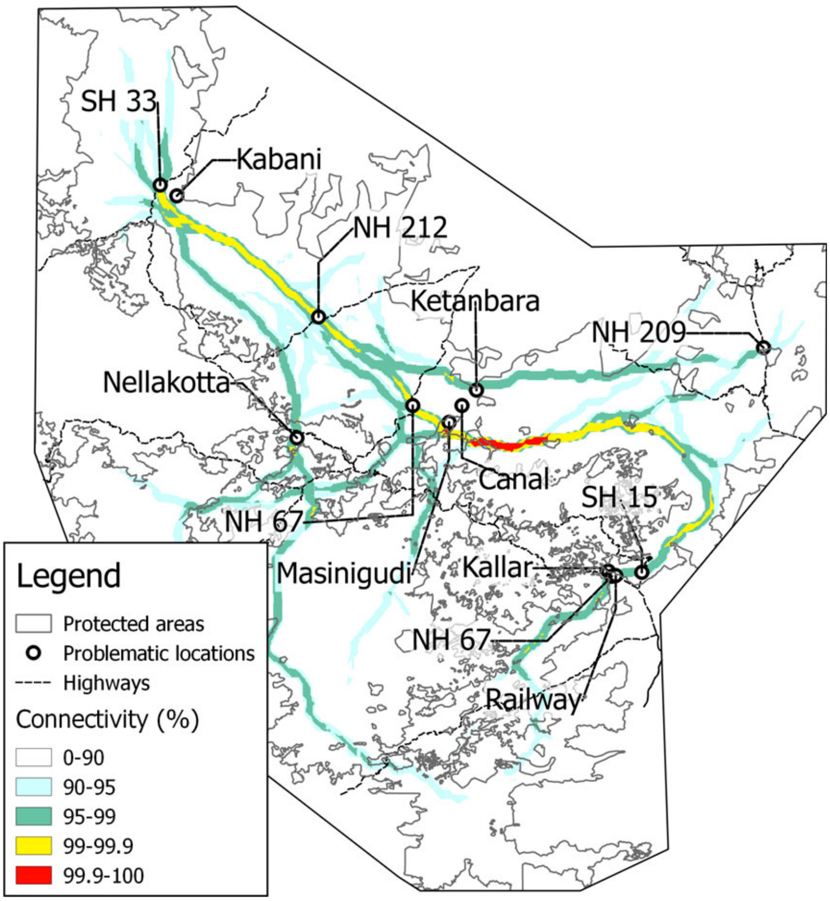

Figure 5 Connectivity patterns of the Nilgiri Biosphere Reserve as measured by UNICOR factorial least-cost path and problematic locations over main corridors.

Parliament_Id=586 accessed 19 November 2015) and the Nellakotta corridor (http://www.pucl.org/Topics/Industries-envirn-resettlement/2002/gudalur.htm; http://www.thehindu.com/news/cities/Coimbatore/it-is-rebirth-for-nilgiris-forest-land/article7303799.ece) are zones of concern and were clearly identified in this study. Other corridors circling the Nilgiris Plateau are also important in order to allow elephant movement across a relatively large set of ecological conditions.

It is unquestionable that the Asian elephant habitat connectivity in the NBR is in danger of being severed by infrastructure, development and disturbance. We noted 13 problematic areas where human activities interfere with major elephant corridors. Faced with the ominous possibility of lowered connectivity, our analysis provides maps and ranking of corridor importance that are easily understandable, objective and reproducible. They also provide evidence that targeted actions in a few areas might have disproportionately positive influence on the conservation of the Asian elephant in this region.

Our results could be further strengthened by incorporating movement data from satellite telemetry (Cushman & Lewis, 2010; Reding *et al.*, 2013; Elliot *et al.*, 2014) or model optimization with landscape genetics (Cushman *et al.*, 2006; Shirk *et al.*, 2010; Wasserman *et al.*, 2010). However, this study shows that currently available data can be generalized to a landscape, bringing better information on landscape connectivity for megafauna.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Methods for land-use classification.
Appendix S2. Methods for resistance coefficients.
Appendix S3. Sensitivity analysis.