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RESEARCH ARTICLE

Dog in the matrix: Envisioning countrywide connectivity conservation for an endangered carnivore

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Abstract

1. Elevated rates of anthropogenic impacts on land-use regimes have pushed terrestrial megafauna to the brink of extinction. Consequently, it is critical to adopt conservation approaches that safeguard individual populations while retaining connectivity among these populations. Conserving spatially structured populations of imperiled species at large scales is often complex; and the past decades have therefore seen a rise in spatial conservation prioritization exercises aimed at shaping landscape-scale conservation programmes.
2. We present a framework for informing nationwide connectivity conservation, linking ecological and administrative scales, to maximize relevance for management. We assessed connectivity of the endangered dhole *Cuon alpinus* among 155 potential source populations across India using a data-driven approach combined with graph and circuit theory. We used clustering algorithms to identify ecologically meaningful conservation landscapes; within each landscape, we identified priority source populations based on their connectedness and quantified pixel-specific habitat *accessibility*. We superimposed administrative boundaries on our findings to provide conservation recommendations at this management-relevant scale.
3. We first mapped potential dhole movement across India. Dhole populations fell within three primary clusters—Western and Eastern Ghats (WEG), Central Indian Landscape (CIL) and North-East India (NEI)—of which NEI had the highest forest cover, most diffuse connectivity and lowest human density, while WEG had the highest protected area coverage and overall connectedness. Within each conservation landscape, we evaluated the relative importance of Protected Areas and accessibility to high-quality patches. Parts of the Eastern Ghats had low habitat accessibility, yet high potential for dhole landscape connectivity. In 114 identified administrative units of priority for habitat restoration, we highlight those with low accessibility, that is, areas where restoration needs to be spatially targeted for maximum benefits.
4. *Synthesis and applications*. We make recommendations for spatially informed habitat restoration to enhance dhole connectivity in India, highlighting the importance of improving matrix permeability where dhole movement is currently restricted. More broadly, the framework we present is useful across species and management contexts, as it combines spatial and administrative scales to make ecologically

informed assessments of high relevance to management. Synergistically integrating species ecology, threats and administrative considerations in connectivity conservation plans can enhance success of species conservation programmes.

KEYWORDS

circuit theory, connectivity, conservation landscapes, dhole, India, management, modularity, spatial prioritization

1 | INTRODUCTION

Rapid changes in global land-use patterns and increase in human footprint are driving habitat loss and fragmentation (DeFries et al., 2010; Laurance et al., 2014). This has led to elevated extinction risks for a number of species, particularly terrestrial fauna (Crooks et al., 2017), with a 68% decrease in vertebrate populations being attributed to land-use change in the last 50 years (IPBES, 2019; WWF, 2020). With increased isolation of populations, movement of individuals among populations or habitats can be pivotal for reducing negative consequences of demographic stochasticity, facilitating recolonization of empty habitat, avoiding inbreeding and enabling climate-driven range shifts (Åkesson et al., 2016; Huang et al., 2020; Tensen et al., 2019). Loss of connectivity has been shown to have negative consequences for species behaviour, spatial genetic structure and demography across taxa and geographies (Fletcher et al., 2016). Safeguarding imperiled species today therefore calls for a shift from a population- or Protected Area-centric focus to a broader landscape- or even regional-scale perspective that includes connectivity conservation (Worboys et al., 2010). By ensuring movement and dispersal of individuals, connectivity conservation holds the potential to ensure long-term viability of populations (Benson et al., 2016; Thatte et al., 2018), and is a crucial tenet for the conservation or management of endangered species (Tensen et al., 2019; Vasudev et al., 2017).

Scale plays an important role in the assessment of spatial processes, and shapes our inferences on the ecological underpinnings that govern connectivity (Wu, 2004). At the rangewide scales or across countries, we are often interested in delineating conservation landscapes. Besides national species conservation plans, such assessments can provide a basis for transboundary conservation interventions and forging international collaborations for conservation action (e.g. Riordan et al., 2016). Modelling connectivity at regional scales can aid in the identification of metapopulations, potential population sources and sinks, and connectivity corridors (Cushman et al., 2009; Reichert et al., 2016). At smaller spatial scales, such as the population or landscape level, connectivity assessments can help determine optimal movement routes and generate directives to local managers on areas to target for corridor design and maintaining corridor functionality (Joshi et al., 2013; McRae et al., 2012). They can also help assess *accessibility* of habitat to prioritize locations for interventions such as habitat restoration such that individual animals have sufficient access to resources. Another consideration is the scale at which conservation action typically occurs, which may be within administrative units such as Protected Areas (PAs), districts or states; and these may not always align with ecological scales. Taken together, there are advantages to investigating connectivity at multiple scales, since ecological processes and consequences to conservation actions are inherently linked (see Pitman et al., 2017). Such a multi-scale approach can also help link landscape-scale conservation science—which occurs at large scales that spans diverse land ownership and administration—to management of endangered species, which typically may occur at region-specific administrative scales.

Most terrestrial large carnivores are wide-ranging, have high resource requirements and are dependent on large, intact habitat patches (Ripple et al., 2014). Many large carnivoran mammals have expansive geographical ranges that show high spatial overlap with human-use areas (Carter & Linnell, 2016). Unfortunately, most populations are currently confined to insular, small habitat patches of varying degrees of quality and are extremely vulnerable to concomitant effects of habitat fragmentation and habitat loss (Wolf & Ripple, 2017). Those species that are forest dependent face higher risks of extinction, given the current rates of forest fragmentation and loss worldwide (Ripple et al., 2014; Vancutsem et al., 2021). Ensuring the persistence of such large carnivores in insular or isolated patches often requires management interventions to be implemented at the metapopulation level in addition to those that focus on securing individual populations (Dolrenry et al., 2014). Such conservation strategies can account for movement of individuals between patches, facilitate gene flow between sub-populations and allow for rescue effects, thereby prolonging the overall viability of populations (see Akçakaya et al., 2007).

In this paper, we demonstrate an approach for informing connectivity conservation at multiple spatial scales, tailored to a species' ecological requirements while also being conducive for management interventions (Figure 1a). The framework we use is ideally suited for species like large carnivores, which have expansive distribution ranges and are found in spatially structured populations (i.e. higher densities clustered in high-quality habitats as population sources, together with smaller trace populations occurring across a wider landscape matrix of habitats and non-habitats; Rich et al., 2017). We first consider the countrywide scale, where connectivity assessments can be integral for making national species conservation plans. Assessments at this scale are relatively uncommon due to their computationally intensive nature, especially when using fine-scale data. At this scale, we employ methods based in circuit theory that model

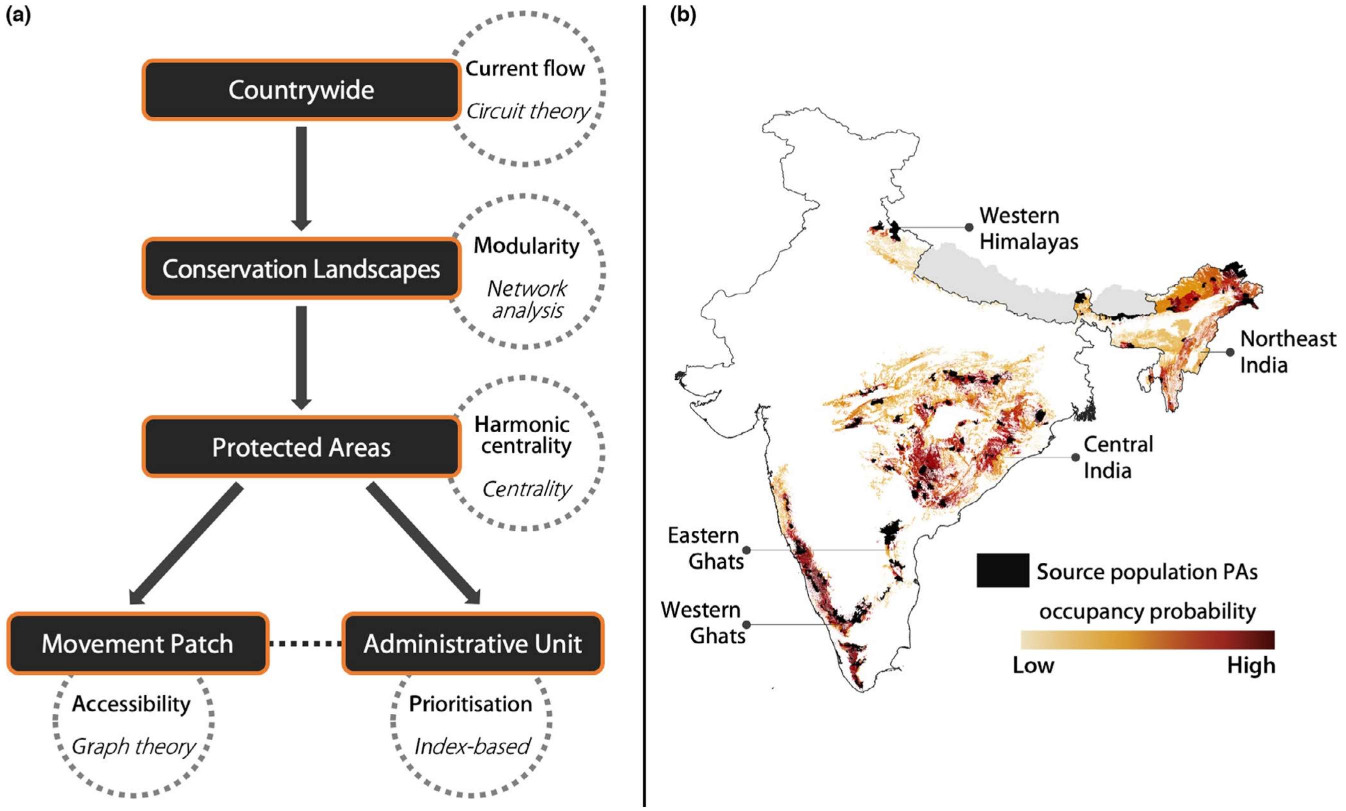

FIGURE 1 (a) Framework used for making multi-scale connectivity assessments. Black boxes represent individual scales at which assessments were made. The corresponding circles in dotted lines include the specific aspect examined (normal typeface) and the analytical method or concept used (italicized typeface). (b) Map of India showing dhole source population PAs, probabilities of dhole occupancy (reproduced from Srivathsa, Majgaonkar, et al., 2020), and major regions or landscapes. Shaded grey areas are geographically contiguous dhole range countries Nepal (left) and Bhutan (right)

potential species movement as analogous to current flow in an electrical circuit (McRae et al., 2008). At the smaller regional scale(s), our goal is to discern metapopulations within ecologically meaningful 'conservation landscapes'. Such landscapes may be defined using clustering algorithms rooted in network analysis paired with movement data (Fletcher et al., 2013). Next, we focus on Protected Areas (PAs), which may represent population sources; here, we use a centrality index to assess the connectedness of PAs in the landscape as a measure of each PA's relative contribution to maintaining connectivity. Lastly, at the finest scales, we consider species movement across habitat patches, and use a combination of cost-distance and graph theoretical approaches to assess connectivity, inferred as the accessibility of habitat patches within the larger landscape. By computing this patch-level metric within relevant administrative jurisdiction boundaries, we prioritize administrative units in need of targeted conservation efforts. A schematic of this framework is presented in Figure 1a, and is applicable across species and management contexts.

India harbours 23% of all known terrestrial carnivore species. Around 5% of the country's land area is designated as PAs, averaging at a size around 250 km^2 (UNEP-WCMC & IUCN, 2018). Most forest-dwelling carnivore populations spill over into heterogeneous landscapes, using these areas as secondary habitats and movement conduits (Mathur & Sinha, 2008). We apply the aforementioned framework to inform connectivity conservation for the endangered, forest-dependent dhole or Asiatic wild dog *Cuon alpinus* in India, presenting novel insights into dhole spatial population structure. This also represents one of the first such applications of species ecological information to countrywide connectivity conservation planning in India.

2 | MATERIALS AND METHODS

2.1 | Study species and location

Dholes are endangered social carnivores and apex predators found in forests of south and southeast Asia (Kamler et al., 2015). Historically, dholes showed widespread distribution across Asia, from lower parts of the Russian Federation in the north to the Indonesian islands in the south. Following local extirpations in many locations, they currently occupy only ~20% of their former range (Wolf & Ripple, 2017). Recent rangewide assessments indicate that there may be only 949–2,215 mature, adult individuals left (Kamler et al., 2015). India is an important range-country with the largest global dhole population. Yet, the species has been extirpated from nearly 60% of its historic range in the country, in just the last century (Karanth et al., 2010). Presumed to be habitat sensitive, most dhole populations are found in the Western Ghats, Eastern Ghats, Central India and Northeast India (Figure 1b), with some recent records indicating that a disjunct population may occur in the Western Himalayas of north India (Srivathsa et al., 2020). Extant populations occupy an area of 249,606 km^2, largely restricted to forested PAs (Srivathsa, Majgaonkar, et al., 2020). Unprotected multi-use forest fragments sustain smaller populations, and certain agroforest production areas (coffee and tea plantations) serve as secondary habitats for the species (Gangadharan et al., 2016; Srivathsa et al., 2014, 2019, 2019). Administratively, PAs that house most of India's dholes are managed by the state or federal government(s) of the country. Conservation planning is typically implemented at the level of PAs, or administrative units called *taluks* (henceforth, 'sub-districts'; mean size = 1,400 km^2; range = 3–51,000 km^2), but can also occur at the scale of the country. Our study area included 3,279,013 km^2 of mainland India, encompassing potential dhole habitats and movement routes, including PAs, unprotected forests, agricultural and plantation lands, and human settlements (Figure 1b). The connectivity assessment we describe in this paper was part of a larger project examining dhole status, conservation planning and prioritization in the country.

2.2 | Generating a countrywide resistance surface

We created a countrywide conductance surface across India based on findings by Srivathsa, Majgaonkar, et al. (2020). The aforementioned study used data from 690 records of dhole presence across India, and across land uses, to find that occurrence was positively influenced by forest cover, PAs and production agroforests, and negatively by terrain ruggedness, human population density and linear infrastructure (Table 1). We used the same inference on covariates to predict landscape conductance to dhole movement, that is, the estimated coefficient values for each covariate were taken from the global occupancy model derived for dholes in Srivathsa, Majgaonkar, et al. (2020). The value for the coefficient of each covariate is listed in Table 1. While we would ideally use dhole movement data to parameterize resistance, we note that these values concur with existing, limited, knowledge of dhole ecology and movement: that dholes avoid non-forested lands with high human disturbance (Habib et al., 2021; Jenks et al., 2015; Singh et al., 2020; Srivathsa et al., 2014), that they face local extinction with loss of forests (Srivathsa, Karanth, et al., 2019) and that other human-associated factors, such as the presence of free-ranging dogs, impedes dhole use of human-inhabited lands (Srivathsa, Puri, et al., 2019).

We first reprocessed the covariate data at a 1-km^2 resolution across the country (see Appendix S1 in Supporting Information for data descriptions and sources). We considered this resolution well-suited for dholes, considering their home range size, movement behaviour and ecology, as it is significantly smaller than their home ranges, and likely to be a relevant scale for movement decisions. Conductance C, interpreted as permeability and related to the 'likelihood of a walker choosing to move through a cell' (McRae et al., 2008), of each 1-km^2 pixel was calculated as:

TABLE 1 Input variables and their respective weights used for generating countrywide conductance surface for modelling dhole connectivity in India

Input variables	Conductance weights	Rationale
Forest cover	3.13	Dholes are highly forest-dependent species
Production agroforests	2.52	Agroforests serve as secondary habitats and likely support movement of individuals
Terrain ruggedness	−2.27	Densities of large herbivore ungulates are generally higher in mixed- to dry-deciduous habitats in relatively less heterogeneous terrains
Human population density	−4.94	Dholes are sensitive to human presence and avoid areas with high human densities
Density of linear infrastructure	−4.94	Roads and railway lines impede large carnivore movement
Protected Areas	5.97	Forested-Protected Areas represent high-quality, low-threat habitats for dholes
Forest fragmentation[a]	3.13 (±2.35)	Spatial configuration of forest habitats (in this case, cohesion of patches) positively influences dhole movement
Density of built-up infrastructure[a]	−20.00	Built-up areas (and associated human activity) represent completely unsuitable habitats for dholes
Water bodies[a]	−20.00	Current knowledge of dhole behaviour indicates that it is unlikely that the species would traverse large water bodies like rivers or lakes

Note: Conductance weights were taken from Srivathsa, Majgaonkar, et al. (2020).

[a]These variables were assigned reasonable, ecologically informed values. For forest fragmentation, we used the same score as that for forest cover, but additionally tested for mean score ± *SE* to evaluate sensitivity.

$$\text{logit}(C) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n, \quad (1)$$

where X_i is the pixel-level value for covariates described above and in Table 1, and β_i is the corresponding coefficient taken from Srivathsa, Majgaonkar, et al. (2020).

We additionally used four covariates that we deemed important for connectivity, and which were not incorporated in the global model of Srivathsa, Majgaonkar, et al. (2020): forest fragmentation, linear infrastructure, water bodies and density of built-up infrastructure. We assumed that forest fragmentation, calculated as 'patch cohesion' index, would influence dhole movement to the same degree as forest cover extent, that is, $\beta_{\text{frag}} = \beta_{\text{fcov}}$. To test the sensitivity of our results to this assumption, we considered two additional scenarios, where $\beta_{\text{frag}} = \beta_{\text{fcov}} \pm SE(\beta_{\text{fcov}})$. Linear infrastructure was assumed to have the same inference as human population density. We expected the density of built-up infrastructure (buildings) and presence of large water bodies to pose a barrier to dhole movement, and these covariates were accordingly assigned high negative values (Table 1).

Conductance values calculated in this manner were constrained between 0 and 1; we rescaled them to 0–100 for ease of interpretation. Nepal and Bhutan are both dhole range countries that are geographically contiguous and ecologically similar to the Himalayan landscape in north–northeast India (Figure 1b). To ensure that the political boundaries between the three countries were not inaccurately treated as ecological barriers, we generated 1-km^2 pixels across these two countries and assigned conductance values that were averages from neighbouring pixels in India. Resistance was calculated as the inverse of conductance (McRae et al., 2008), thereby providing a data-driven approach to estimate landscape resistance.

2.3 | Potential connectivity among source populations

Application of circuit theory in ecological studies was initially proposed for modelling movement and gene flow in animals (McRae et al., 2008). Circuitscape (McRae & Shah, 2011), a software designed to model movement of animals in a heterogeneous environment similar to current flow in an electrical circuit, has been applied to study connectivity in several threatened species (McClure et al., 2017; Rio-Maior et al., 2019). We defined source populations as PAs with high predicted habitat occupancy probability (>0.45; Figure 1b) following Srivathsa, Sharma, et al. (2020). We then used circuitscape.jl (Hall et al., 2021) to model connectivity across the country among these source populations. This provides us with (a) pixel-specific current flow across the entire region, representing projected movement through each pixel, or alternatively, the contribution of each pixel to dhole connectivity and (b) pairwise effective resistance distances between dhole source populations, a realistic relative measure of isolation between PA pairs. Pixel-wise current flow from the three scenarios (β_{frag} mean, +*SE* and −SE) were highly correlated ($r > 0.99$).

2.4 | Defining conservation landscapes

Identifying the spatial structure of metapopulations is crucial for development of landscape-scale conservation action plans. Such landscapes may be viewed as management units (Palsbøll et al., 2007), comprising populations that are closely linked to each other. These discrete units can be identified using network-theoretic approaches such as modularity (Fletcher et al., 2013; Peterman et al., 2016). To identify conservation landscapes for dholes, we created networks of source populations and parameterized links between pairs of source populations using the effective resistance distances estimated above. We applied a negative exponential function (Royle et al., 2013) to the pairwise resistance distances to calculate association metrics between populations. We assessed the modularity of this network, and considered clusters of closely linked source population PAs as 'modules'. Modularity analyses were performed using the IGRAPH package in R v4.0.3 (R Core Team, 2020). See Appendix S2 in Supporting Information for additional details and code.

To include the matrix surrounding source populations (which potentially serves as secondary habitat and movement conduit) within conservation landscapes, we created a buffer of 50 km around each source population of a module. We refer to the spatial extent encapsulated by PAs and their corresponding buffers for each module as a '*dhole conservation landscape*'. In the absence of reliable knowledge on dhole dispersal kernels, this buffer width was chosen as (a) it allowed for demarcating conservation landscapes with zero overlap between adjacent landscapes, (b) this buffer size would account for most, if not all, dispersal events, considering the median dispersal distance for dholes (~30 km) calculated based on their body weight and home range size (Bowman et al., 2002). Thus, our nodes represented PAs; a group of interconnected PAs formed a module; and these interconnected PAs along with a 50 km buffer formed dhole conservation landscapes.

2.5 | Source populations and habitat accessibility

Within conservation landscapes, we were first interested in evaluating the relative importance of individual source population PAs. Taking connectivity considerations into account, securing the habitat that holds these populations can be a priority for management. We estimated source-specific harmonic centrality (Ashtiani et al., 2019), calculated as the sum of reciprocals of the effective resistance distances from a focal source population to all other populations within each conservation landscape. The metric indicates the relative importance of each source population in being connected to all populations within a conservation landscape.

At a finer spatial scale, we were interested in calculating accessibility to optimal habitats (considered as a proxy for resources) in each conservation landscape. For this analysis, we considered each 1-km^2 pixel within the landscape as a node in a network. We calculated a modification of the Probability of Connectivity index or PCi (Saura & Pascual-Hortal, 2007) as demonstrated by Mestre et al. (2016), as an index of habitat accessibility. PCi is a dispersal-based connectivity index designed with the aim of integrating connectivity in landscape planning and decision-making. It incorporates concepts from graph structures, inter-patch dispersal probabilities and habitat availability and has found widespread application in identifying priority habitats for planning landscape conservation and assessing importance of patches for connectivity (Mohammadi et al., 2021; Suttidate et al., 2021). We defined PCi here as the probability of any habitat patch being connected to other habitat patches, given a network of habitat patches and connections between them. We estimated PCi as:

$$\mathrm{PCi} = \sum_{j=1, j \neq i}^{n} a_i a_j p_{ij}^{*}. \tag{2}$$

Here, a_i and a_j are suitability values of pixel i and pixel j, respectively, and p_{ij}^{*} is the maximum product probability of all possible paths connecting i to j. To create the network, each pixel was treated as a node. Based on knowledge from previous studies, we considered forested PAs to be optimal habitats, followed by non-protected forests and agroforest production areas. We generated a 'habitat suitability' score for each 1-km^2 pixel as a weighted sum of the proportion of each pixel under forested PA, non-protected forests and agroforest production areas with weights 3, 2 and 1, respectively. Pixels that did not have any of the above land-cover types were treated as non-habitats and assigned a score of 0. We considered that this habitat suitability map would better reflect habitat quality of patches in the landscape (as destination points with varying degrees of resource quality) as opposed to the conductance values generated earlier, which were intended for capturing *movement* at the 1-km resolution. For estimating p_{ij}^{*}, we calculated the least-cost distance between each pair of pixels using the GDISTANCE package, with resistance calculated as the inverse of conductance values (McRae et al., 2008). To translate this distance to a probability, we used a negative exponential function, setting 30 km as the median dispersal distance (Bowman et al., 2002). We then iteratively calculated p_{ij}^{*} for each pixel pair, and calculated PCi for each pixel following Equation (2) provided above. See Appendix S3 in Supporting Information for additional details.

2.6 | Locations to target management interventions

Implementing management actions aimed at improving, consolidating or increasing habitats is typically shaped by administrative boundaries and jurisdiction (see Game et al., 2013). Srivathsa, Sharma, et al. (2020) identified 145 sub-districts across India where dhole conservation called for forest restoration, based on dhole occupancy probability and forest habitat availability. We overlaid those prioritized sub-districts on our habitat accessibility maps, obtained from the above analysis and referring to the accessibility of habitat from each pixel, to further recommend sub-districts for forest restoration efforts. For sub-districts that were spatially enclosed within our conservation landscapes, we calculated the average PCi value across all pixels that fell within each of these units. Here, our interpretation was that units with higher scores are most amenable to habitat recovery initiatives with relatively lower focus on the spatial location of restoration efforts, whereas units with low scores would require strategic and intensive focus on spatially locating restoration efforts to maximize accessibility.

3 | RESULTS

3.1 | Countrywide potential connectivity

Mapping potential connectivity countrywide helped identify regions and linkages that were most and least conducive for dhole movement (Figure 2). At this scale, most areas in southern India's Western Ghats appeared to be well connected: pairwise effective resistance distances between source populations, a measure of the degree of isolation, across south India ranged from 9.90×10^{-5} to 21.82×10^{-3} resistance distance (or cost-distance) units. Dhole source populations of central India appeared to be relatively more isolated, indicative of weakly connected sub-populations within the region (range of resistance distances 3.34×10^{-5} to 12.39×10^{-3} units). In northeastern India, potential connectivity between source populations decreased longitudinally from the western to eastern parts, with pairwise resistance distances ranging from 1.85×10^{-4} to 34.32×10^{-3} units.

3.2 | Identification of conservation landscapes

Modularity analyses suggested that dhole populations spatially segregated into three distinct conservation landscapes: (a) the Western and Eastern Ghats (henceforth, WEG) in southern India, (b) Central Indian Landscape (CIL) and (c) North-East India (NEI; Figure 3). WEG covers an area of 219,261.2 km^2 and has the highest number of source population PAs (n = 68) along with the largest proportion of land under protection (Table 2). CIL is the most expansive, harbouring 59 source population PAs in a human-dominated land-use matrix, together comprising an area of 560,113 km^2; this landscape also had the highest human population size and lowest proportion of land under protection (Table 2). NEI is around 254,946.2 km^2 in size, and has a higher proportion of area under forest cover compared to the other two landscapes (~50% under forest cover), along with the lowest human population size. NEI also has the least number of source populations (n = 28) among the three landscapes. Current flow was also more diffused in NEI, with few pinch-points and substantial redundancy in movement paths. Potential linkages between conservation landscapes—which were lower than linkages within landscapes—are presented in Appendix S4 in Supporting Information.

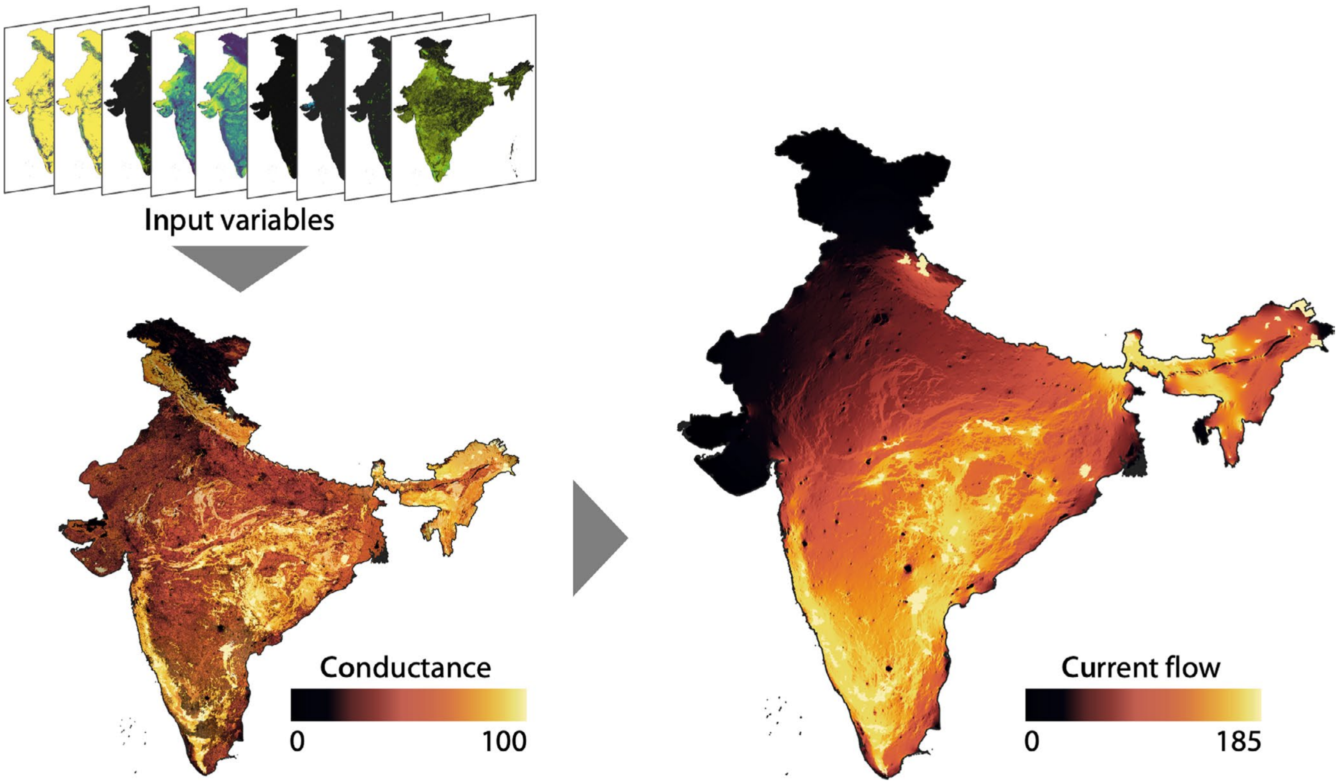

FIGURE 2 Schematic representation of connectivity modelling across India, showing all input variables used for parameterizing conductance (or 1/resistance; top left); conductance scores thus generated (bottom left); and patterns of current flow, or movement, among source population PAs assessed using a circuit-theory-based approach (right)

3.3 | Important source populations

Four source population PA clusters in WEG had high harmonic centrality, that is, they were regionally important in that they were highly connected to other source populations (Figure 4). In the Eastern Ghats—a highly fragmented section of WEG—source population PAs had lower harmonic centrality values, indicating that accessibility across this region could be constrained. In CIL, potential source population PAs of moderate and low centrality values were interspersed across the landscape, with high centrality source population PA clusters situated at landscape extremities characterized by relatively lower human populations and lower density of linear infrastructure. A large proportion of NEI is forested and therefore structurally well connected for dhole movement. Our results suggest that five source population PAs in the northern part are well connected in the landscape (Figure 4).

3.4 | Habitat accessibility

PCi values across WEG suggested that a combination of high centrality source population PA clusters, and large, intact forest patches provide high accessibility across most of the northwestern extent of the landscape. Accessibility to habitat in the eastern parts was lower, and highly constrained outside source population PAs (Figure 5). Compared to the other two landscapes, dholes had lower access to optimal habitat outside source population PAs in CIL, pointing to low overall connectivity in the landscape. Notably, source populations PAs here are not surrounded by forest buffers, and for the most part, remnant forests form structural corridors but with little corridor redundancy. Higher values of PCi were thus mostly within the bounds of extant source population PAs. Accessibility to high-quality habitats in NEI was largely limited to the forest-covered eastern and central parts of the landscape (Figure 5); this might be a manifestation of the low PA coverage in this landscape.

3.5 | Management in sub-districts

We identified 114 priority sub-districts—58, 48 and 8 in WEG, CIL and NEI, respectively—where habitat consolidation or recovery would contribute towards improving connectivity for dholes, shortlisted from the units prioritized in Srivathsa, Majgaonkar, et al. (2020). In Figure 5, we present these sub-districts whose scores in each landscape reflect the average PCi values across all 1-km^2 pixels within the corresponding unit. We also provide statewise locations and numbers of important sub-districts in Appendix S4.

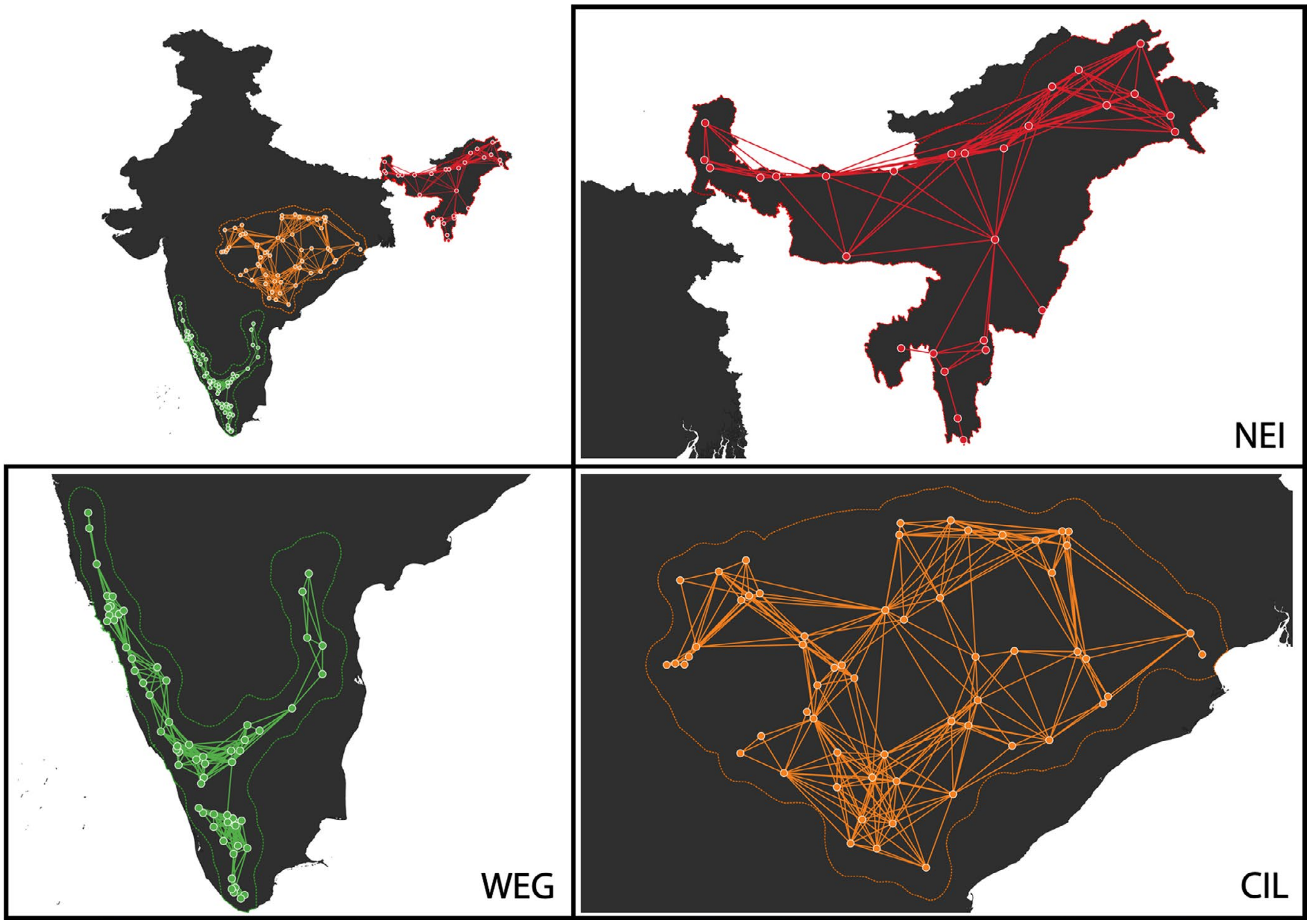

FIGURE 3 Dhole conservation landscapes determined based on modularity analyses. The three landscapes are Western and Eastern Ghats (WEG), Central Indian Landscape (CIL) and Northeast India (NEI). Dots represent centroids of dhole source populations PAs, solid lines are 'links' assessed using pairwise effective resistance distance values between PAs, and dotted lines indicate outer limits of each conservation landscape

TABLE 2 Landscape attributes relevant for conservation policy and action across three dhole conservation landscapes in India

Landscape attributes	Western and Eastern Ghats (WEG)	Central Indian Landscape (CIL)	North-East India (NEI)
Total area (km^2)	219,261	560,113	254,946
Number of source populations[a]	68	59	28
Proportion of area under protection	14.39%	5.89%	8.84%
Proportion of area under forest cover	30.76%	37.31%	49.81%
Proportion of area under production agroforest	4.54%	0.35%	3.47%
Total human population size (in millions)	91.17	125.98	58.64
Length of linear infrastructure (km)	201,663 (0.91 per km)	172,495 (0.31 per km)	85,818 (0.34 per km)

[a]Source populations are Protected Areas with suitable dhole habitat and high dhole occupancy probabilities.

4 | DISCUSSION

In this study, we demonstrate how a carefully designed framework allowed for making multi-scale connectivity assessments for the dhole such that the results generate ecological insights while also being relevant for implementing conservation actions. Our results at the countrywide scale represent the first ever national-scale potential connectivity map for the species across its distribution range; this also serves as a model for other species-specific conservation plans within India and elsewhere. At the regional scale, we present the first connectivity-based evidence for defining dhole metapopulations within their corresponding conservation landscapes. We also

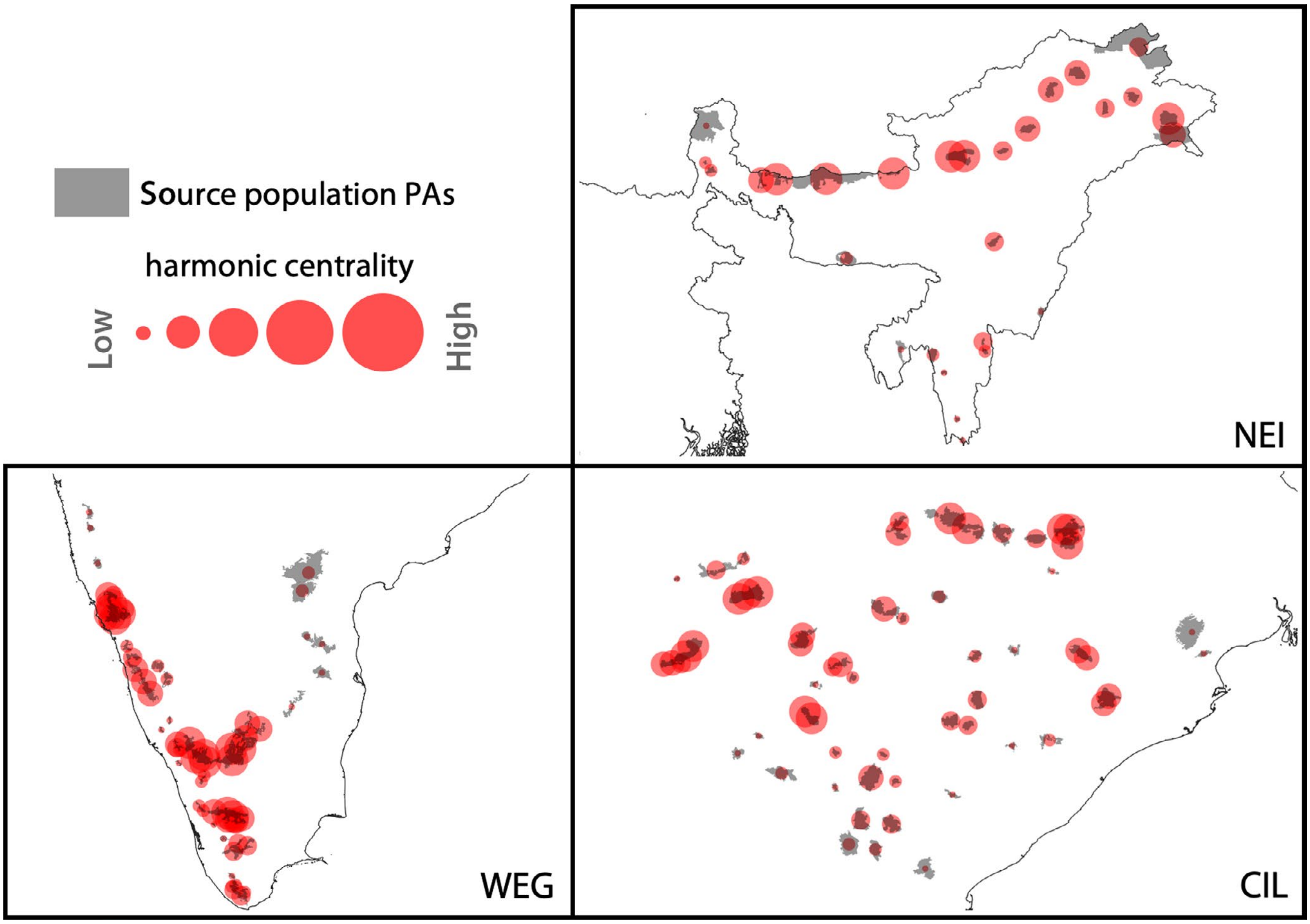

FIGURE 4 Harmonic centrality metrics for each dhole source population PA across the three conservation landscapes. Larger circles represent higher values of centrality, indicating higher relative importance of the PA(s) in the corresponding landscape

identified the relative importance of source population PAs in each landscape. Finally, we show how accessibility to high-quality habitats at more localized scales can be a key consideration while planning management interventions. Taken in conjunction with select, recent studies of dholes, this paper signifies an advancement in knowledge for a relatively under-studied, endangered carnivore in need of conservation attention, and also exemplifies how incrementally building knowledge can be beneficial to species that do not have a long history of targeted, systematic quantitative assessments.

4.1 | Insights from countrywide connectivity assessment

Holistic rangewide conservation models that combine priority-setting exercises with population connectivity are pivotal for identifying and understanding threats that imperil large carnivore persistence (Rabinowitz & Zeller, 2010). Plans for species recovery, conservation and management tend to possess maximum traction when generated at the countrywide level, and promulgated in consonance with the corresponding legal frameworks of the nation-state; many recent studies have contributed towards such an approach (e.g. see Ahmadi et al., 2017; Haidir et al., 2021). In our country-level assessment, the macro-scale perspective provided certain key insights. First, despite their spatial proximity, CIL and WEG may be disjunct in terms of enabling movement between the two landscapes, mostly owing to the fragmented nature of the Eastern Ghats. Enhancing habitat consolidation here could have a disproportionately positive influence on the persistence of dhole populations; habitat expansion will likely help reduce landscape resistance while also providing habitat for local colonizations. Second, CIL is characterized by large number of narrow pinch-points, highlighting the need for increased redundancy in movement path; path redundancy has been shown to improve population connectivity and resilience, especially in relatively impermeable or hostile matrix (Fletcher et al., 2014). Third, most dhole populations in NEI (and the small populations in western Himalayas) exist along geopolitical borders, and are likely to be functionally connected to populations in countries that share these borders. We propose that a national-level plan for conserving dholes should be cognizant of the opportunities and challenges in multi-state collaborations within the country. Our findings also suggest that conservation plans explore international collaborations across

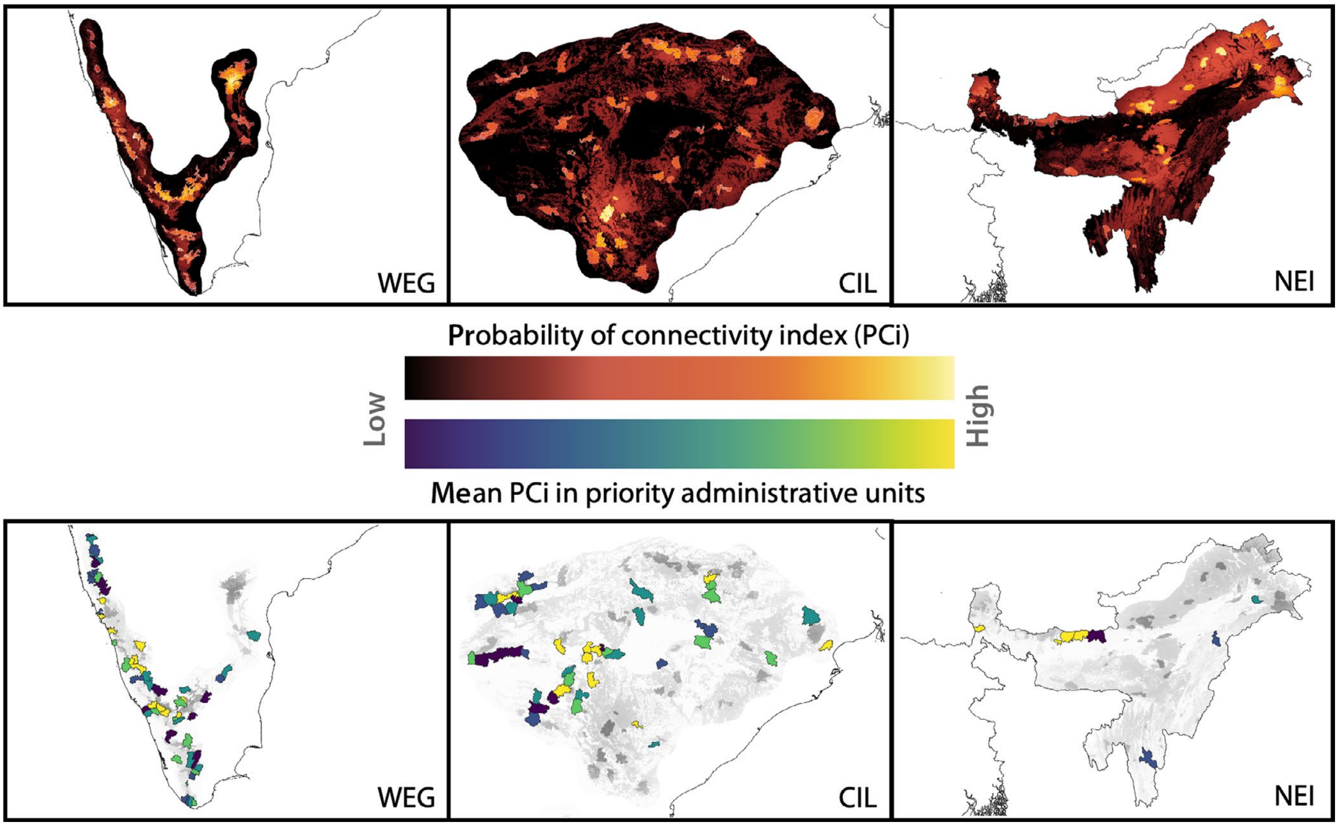

FIGURE 5 Top panel—Probability of connectivity index (PCi) at the scale of 1-km^2 resolution in the three dhole conservation landscapes, Western and Eastern Ghats (WEG), Central Indian Landscape (CIL) and North-East India (NEI). Higher values represent locations with greater access to optimal habitats. The brightest hotspots are source population PAs (demarcated with white boundary). Bottom panel—Mean PCi scores for priority administrative units (sub-districts) deemed important for habitat recovery and connectivity conservation in each conservation landscape

Bangladesh, Bhutan, China, Myanmar and Nepal, highlighting how such assessments can additionally direct transboundary conservation efforts (Farhadinia et al., 2015).

4.2 | Landscape-scale considerations for conserving metapopulations

Ensuring long-term persistence of wide-ranging, large-bodied carnivores that are habitat-restricted requires a landscape-scale approach, protecting multiple populations while allowing for movement of individuals among them (e.g. Karanth et al., 2020). This first calls for identifying priority population sources, based on, among other considerations, connectedness. Second, permeability outside sources (PAs) and anthropogenic impacts are key considerations for such plans. Our framework encompasses both these requirements. Past assessments, based on distribution patterns, have suggested the idea that dholes in India are distributed as metapopulations across three main landscapes (Kamler et al., 2015; Srivathsa, Sharma, et al., 2020). Our results corroborate this from a connectivity standpoint; we also report the first evidence for potential linkage between the Western Ghats and Eastern Ghats populations. The Western Ghats is a global stronghold for dholes (Srivathsa, Karanth, et al., 2019) but also a hotspot for many large-scale infrastructure projects in recent years (Jayadevan et al., 2020; Table 2). The landscape's peculiar arrangement of source populations as a narrow linear stretch emphasizes the importance of linkages between high and low centrality source population PA clusters, rendering it sensitive to forest fragmentation, potentially hampering dhole metapopulation dynamics. In CIL, many source populations appear to be comparatively isolated (low centrality values), or have spatially restricted corridors (Figures 4 and 5). This could coerce dispersing dholes to traverse increasingly risky mosaics which, as evidence suggests, they appear to be avoiding (Srivathsa, Puri, et al., 2019). Unless conservation practitioners enhance permeability of the matrix in this landscape, we could see deleterious effects on individual survival in the short term and metapopulation viability and genetic diversity in the long term (Day et al., 2020; Newby et al., 2013). In NEI, a large proportion of forests exist outside PAs and on community-owned lands. Functional connectivity between populations here may be constrained by low prey densities (Datta et al., 2008) and conflict-induced persecution of dholes by local communities (Lyngdoh et al., 2014). There is strong emphasis on community-based conservation here, but little data exist on the potential of community-managed forests to support dhole source populations.

4.3 | Habitat accessibility and management interventions

Studies addressing topics at the intersection of large carnivore ecology and conservation have alluded to the integral role of politics and administrative capacity in influencing management and policy (see Darimont et al., 2018). Since most locations where connectivity conservation needs to be achieved tend to be outside PAs, optimizing intervention outcomes would need to account for jurisdiction boundaries, politics, governance and local stakeholders (Harihar et al., 2018). We approached this by first examining habitat accessibility within the three landscapes. Higher accessibility in WEG is likely facilitated through a combination of multiple source population PAs, stepping-stone forest areas and relatively permeable agroforest patches (Table 2). Of particular concern are the prominent zones of near-zero permeability in the Eastern Ghats (Figure 5), which may be rendering the large source PAs in the region functionally disconnected. In that sense, fostering permeable connectivity zones in the Eastern Ghats is critical and could, in the future, forge a link between WEG and CIL, which are currently identified as disparate landscapes. CIL is characterized by many locations with potential dhole habitats but sub-optimal population sizes (Srivathsa, Sharma, et al., 2020). Given the importance of connectivity-linked immigration of individuals in reviving small populations (Reichert et al., 2021), consolidating and maintaining corridors for dholes and ensuring redundancy of connectivity should be prioritized in CIL.

Debates on whether conservation efforts should be focused on habitat loss or fragmentation notwithstanding, some studies have argued for a simultaneous redressal of both the threats (Fahrig, 1997, 2017; Fletcher et al., 2018; Geldmann et al., 2013). The PCi metric we use is one step towards a holistic approach, wherein the conservation target is to have *accessible* habitat. Our findings were tailored to inform sub-district level habitat restoration efforts, so as to be directly relevant to landscape planners, wildlife managers and conservation practitioners. It is critical that the sub-districts that have low PCi values, in particular, should strategically locate their habitat restoration efforts to ensure that restored habitat is *accessible* to the rest of the sub-district; without such considerations, restoration efforts may prove ineffective. Demarcation of movement corridors and timely implementation of connectivity conservation measures in these locations can help prevent local extinctions and maintain regional persistence of dhole populations. Incorporating a data-driven assessment of resource availability, or population size and dispersal rates into our assessment would provide further insights into the conservation potential of the three landscapes.

4.4 | Methodological considerations

Studies aimed at identifying or designing conservation landscapes have traditionally relied on least-cost models or maximum entropy models in conjunction with prioritization-based or threshold-based analyses (Wibisono et al., 2018; Wikramanayake et al., 2004). Such approaches potentially underestimate the contribution of alternative routes and secondary habitats in facilitating movement; several studies have reported higher connectedness among local populations at larger spatial scales than initially predicted (Vasudev et al., 2017). Recently, network-based metrics for determining spatial scales that regulate ecological and evolutionary processes have gained some traction. These assessments rely on evidence such as genetic similarity (Peterman et al., 2016) and inter-patch movement (Fletcher et al., 2013). We used pairwise effective resistance distances between source populations ascertained through potential connectivity (not realized connectivity). We employed widely used tools for assessing connectivity—circuit and network theory based approaches—at multiple spatial scales to obtain a comprehensive view of connectivity patterns and their salient features at each scale.

These models rely on data on dhole movement in the matrix, or while dispersing; this information is typically difficult to obtain. A number of approaches address this critical information requirement using presence detections, movement data from radiotelemetry or other sources, and spatial genetic information; most studies use expert opinion to parameterize resistance surfaces (Zeller et al., 2012). With movement or space-use data on dholes outside PAs being extremely limited, we took matrix conductance, or permeability, to be similar to habitat suitability values at a 1-km^2 resolution (see Zeller et al., 2018). This allowed us to employ a data-driven approach to a countrywide connectivity prioritization exercise, using the best available information on a rare and endangered species. We note that factors determining species presence may not always equal those facilitating or impeding their movement (Keeley et al., 2016; Mateo-Sánchez et al., 2015). Further research into dhole movement behaviour could reveal finer-scale responses to barriers, such as responses to linear infrastructure. Adding such insights from dispersing dholes—obtained from intensive multi-population camera-trapping efforts, landscape genetics or telemetry—can help further validate and augment our findings. As such, we see our prioritization exercise as one that can evolve with additional knowledge on dhole behaviour, threats and land-use change going into the future.

5 | CONCLUSIONS

At present, initiatives involving connectivity conservation in India largely focus on forest corridors for tigers and elephants (Menon et al., 2017; Qureshi et al., 2014). These designated corridors, however, may be sub-optimal for the more habitat-sensitive dholes (see Srivathsa, Puri, et al., 2019), and are unlikely to ensure their population viability. Long-term persistence of dhole populations will depend on habitat consolidation outside PAs aimed at facilitating local colonization of patches with high potential for dhole occupancy (Srivathsa, Karanth, et al., 2019). Although protected under India's wildlife law, dholes have hitherto been afforded very little funding and proactive conservation efforts. Given the dearth of quantitative studies on the species, insights from potential connectivity assessments such as ours can have key implications for formulating management plans, designing infrastructure projects and allocating conservation funds and resources. While our study goes some distance in addressing this issue, we propose that future research should augment our findings by employing approaches like satellite telemetry and genetic tools to assess functional connectivity within landscapes.

In a broader sense, accelerated rates of habitat loss and fragmentation, and consequent impacts on animal movement (Pitman et al., 2017; Tucker et al., 2018), make landscape-scale conservation planning exercises all the more important; these necessarily incorporate both habitat availability and connectivity considerations. Implementing evidence-based mitigation strategies, such as targeted restoration, to counter, offset or reverse the deleterious effects of anthropogenic pressures almost always hinges on political will, and administrative jurisdictions and capacity. We believe adopting a combination of ecologically meaningful scales determined by species behaviour, and scales that are relevant for administrative action, can benefit prioritization exercises and organically link scientific findings to conservation planning and action. Synergistically integrating species ecology, conservation challenges and administrative considerations, as we demonstrate here, can significantly improve landscape-level and regional conservation plans, and ultimately, enhance the success of species conservation programmes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

R.G.R. and A.S. conceived the ideas and designed the study; R.G.R. and A.S. collated and processed data; R.G.R. analysed the data; A.S. and D.V. advised on the analyses; R.G.R., A.S. and D.V. interpreted the results; A.S. produced the figures; R.G.R., A.S. and D.V. contributed to writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.qv9s4mwfr (Rodrigues et al., 2021).

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