







CONTRIBUTED PAPERS

Synthesizing habitat connectivity analyses of a globally important human-dominated tiger-conservation landscape

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Abstract

As ecological data and associated analyses become more widely available, synthesizing results for effective communication with stakeholders is essential. In the case of wildlife corridors, managers in human-dominated landscapes need to identify both the locations of corridors and multiple stakeholders for effective oversight. We synthesized five independent studies of tiger (*Panthera tigris*) connectivity in central India, a global priority landscape for tiger conservation, to quantify agreement on landscape permeability for tiger movement and potential movement pathways. We used the latter analysis to identify connectivity areas on which studies agreed and stakeholders associated with these areas to determine relevant participants in corridor management. Three or more of the five studies' resistance layers agreed in 63% of the study area. Areas in which all studies agree on resistance were of primarily low (66%, e.g., forest) and high (24%, e.g., urban) resistance. Agreement was lower in intermediate resistance areas (e.g., agriculture). Despite these differences, the studies largely agreed on areas with high levels of potential movement: >40% of high average (top 20%) current-flow pixels were also in the top 20% of current-flow agreement pixels (measured by low variation), indicating consensus connectivity areas (CCAs) as conservation priorities. Roughly 70% of the CCAs fell within village administrative boundaries, and 100% overlapped forest department management boundaries, suggesting that people live and use forests within these priority areas. Over 16% of total CCAs' area was within 1 km of linear infrastructure (437 road, 170 railway, 179 transmission line, and 339 canal crossings; 105 mines within 1 km of CCAs). In 2019, 78% of forest land diversions for infrastructure and mining in Madhya Pradesh (which comprises most of the study region) took place in districts with CCAs. Acute competition for land in this landscape with globally important wildlife corridors calls for an effective comanagement strategy involving local communities, forest departments, and infrastructure planners.

KEYWORDS

central India, circuit theory, coexistence, corridors, human wildlife, infrastructure, land use, movement

Resumen

Conforme los datos ecológicos y los análisis asociados están cada vez más disponibles, la síntesis de los resultados para la comunicación efectiva con los actores es esencial. En el caso de los corredores de fauna, los gestores en los paisajes dominados por humanos

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Article Impact statement: Independent studies agree on priority conservation areas for connectivity and management challenges for spaces shared by humans and wildlife

necesitan identificar tanto la ubicación de los corredores como a los múltiples actores para tener una vigilancia efectiva. Sintetizamos cinco estudios independientes sobre la conectividad de tigres (*Panthera tigris*) en el centro de la India, un paisaje de prioridad global para la conservación de esta especie, para cuantificar la armonía sobre la permeabilidad del paisaje para el movimiento de tigres y las vías potenciales de movimiento. Usamos el segundo análisis para identificar a los actores asociados con estas áreas y las áreas de conectividad en las que los estudios estaban de acuerdo para determinar a los participantes relevantes en la gestión de los corredores. Tres o más de las capas de resistencia de los cinco estudios estuvieron de acuerdo en un 63% del área de estudio. Las áreas en las que todos los estudios estuvieron de acuerdo sobre la resistencia fueron principalmente las de resistencia baja (66%, p. ej.: bosques) y alta (24%, p. ej.: áreas urbanas). La armonía de acuerdos fue más baja en las áreas de resistencia intermedia (p. ej.: paisajes agrícolas). A pesar de estas diferencias, los estudios tuvieron una armonía generalizada en las áreas con niveles altos de movimiento potencial: >40% de los píxeles de flujo continuo de promedio alto (20%) estuvieron también en el 20% de los píxeles armónicos de flujo continuo (medidos por la baja variación), lo que indica que las áreas de conectividad unánime (ACUs) son prioridades de conservación. Aproximadamente el 70% de las ACUs se ubicaron dentro de los límites administrativos de las aldeas, y el 100% se traslapó con los límites de gestión del departamento de bosques, lo que sugiere que las personas viven y usan los bosques dentro de estas áreas prioritarias. Más del 16% del área total de las ACUs se ubicó a un kilómetro de la infraestructura lineal (437 cruces de carreteras, 170 de vías férreas, 179 de líneas de transmisión y 339 cruces de canales; 105 minas a un kilómetro de las ACUs). En 2019, el 78% de las desviaciones del suelo forestal para la infraestructura y la minería en Madhya Pradesh (que conforma la mayoría de la región de estudio) ocurrió en distritos con ACUs. La feroz competencia por tierras en este paisaje con corredores de fauna de importancia mundial exige una estrategia de comanejo efectivo que involucre a las comunidades locales, los departamentos de bosques y a los planeadores de infraestructura.

PALABRAS CLAVE

coexistencia, corredores, humano-fauna, India central, infraestructura, movimiento, teoría de circuitos, uso de suelo

摘要

一个全球重要的人类主导的虎保护景观中生境连接度的综合分析

随着生态学数据和相关分析越来越普遍,对结果进行综合分析以便与利益相关者有效沟通也变得十分重要。就野生动物廊道而言,人类主导景观中的管理者需要确定廊道的位置和多方利益相关者,以进行有效监督。我们综合了对印度中部——一个全球虎(*Panthera tigris*)保护优先景观中的虎种群连接度的5项独立研究,确定了对老虎移动的景观渗透性和潜在移动路径的共识。我们还利用潜在移动路径的分析确定了研究中一致的连通区域以及这些区域的利益相关者,以确定廊道管理中相关的参与者。63%的研究区域在5项研究的至少3项中被认为是阻力层。所有研究一致得到的阻力区域主要是低阻力(66%,如森林)和高阻力(24%,如城市)地区,而中等阻力(如农业)的地区一致性较低。尽管存在以上差异,但这些研究得到的潜在移动水平高的地区基本一致:超过40%的高平均(前20%)电流像元同时也是前20%的一致电流像元(用低变异衡量),表明一致连接区(CCA)是保护的重点。大约70%的CCA位于村庄行政边界内,且全部与林业部门的管理边界重叠,这表明人们在这些保护优先区域内生活并利用森林。超过16%的CCA总面积在线性基础设施的1公里范围内(437条公路、170条铁路、179条输电线路和339个运河交叉口;还有105个矿场在CCA的1公里范围内)。2019年,中央邦(包括了大部分研究区域)78%被改用于基础设施和采矿的林地都位于有CCA的地区。在这种具有全球重要性的野生动物廊道景观中存在着对土地的激烈竞争,这要求人们采取有效的共同管理战略,让当地社区、林业部门和基础设施规划者共同参与管理。【翻译:胡怡思;审校:聂永刚】

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INTRODUCTION

Unprotected areas (i.e., matrix) are important for wildlife and threatened in human-dominated landscapes (Habib et al., 2021; Smith et al., 2019), particularly where high-density human populations share space and resources with local fauna. As such, promoting coexistence is essential for long-term viability of wildlife. Large-scale infrastructure projects in the Global South frequently cut across areas connecting the remaining habitat for endangered species (Laurance et al., 2009). Protecting large landscapes from all anthropogenic impacts is infeasible and often unjust because largely rural and disadvantaged populations depend on the landscape and its development for their livelihoods and well-being. Thus, protection of habitat corridors (areas for the safe movement of wildlife between core habitat) is frequently proposed, especially for wide-ranging species that depend on movement between core population areas to maintain genetic connectivity (Ripple et al., 2014).

Connectivity predictions are made with movement or spatial-spread algorithms (e.g., resistant kernel [Compton et al., 2007] and circuit theory [McRae et al., 2008]) to “resistance surfaces” (Cushman et al., 2013), which represent degrees of landscape permeability for animal movement (Spear et al., 2015). A diverse array of methods and data are used to produce resistance layers, which can result in variability in connectivity maps (Koen et al., 2012). Cumulative connectivity maps have been derived comparing predictions from multiple species in a shared landscape (e.g., Plissock et al., 2020). However, to our knowledge, no one has compared multiple, independent connectivity analyses in the same landscape.

Although a wealth of knowledge on the importance of landscape-level conservation via wildlife corridors can provide a clear path to stakeholder collaboration and effective management of multiuse areas, incompletely aligned results may disrupt the process, leading to misunderstandings and distrust (Pouyat, 1999). Accordingly, effective synthesis of the results of multiple analyses is vital to conservation research (Sutherland et al., 2019). We synthesized five independent studies of tiger (*Panthera tigris*) connectivity in central India, a globally recognized priority landscape for tiger conservation (Sanderson et al., 2010), to inform management outside protected areas (PAs) and serve as a model for science-based management of the matrix in other important, relatively well-studied corridor areas. Tigers, now in only a few relict populations throughout Asia, are a keystone species throughout their range. Fewer than 5000 individuals, living in ~7% of their historical range (Dinerstein et al., 2007), remain in the wild (Jhala et al., 2021); thus, planning efforts for tigers focus on protecting source populations and permeable habitat between population-source sites (Ash et al., 2020; Seidensticker, 2010).

The central India landscape (CIL) is a heavily populated region with a mosaic of PAs, forest patches, small-scale farms, villages, and cities (DeFries et al., 2016). Here, humans and wildlife coexist and wide-ranging species depend on movement through the matrix between small (relative to their range) PAs

to connect source populations and maintain genetic diversity (Dutta et al., 2013, 2015; Seidensticker, 2016; Thatte et al., 2018). Despite their small populations and extensive habitat loss, tigers in the CIL have substantial levels of genetic diversity and gene flow, indicating that animals move and breed between the PAs in the landscape (Joshi et al., 2013; Sharma et al., 2013a, 2013b; Thatte et al., 2018; Yumnam et al., 2014). Because the human population and infrastructure are expanding (Habib et al., 2016), tiger conservation efforts focus primarily on identification, prioritization, and restoration of areas for connectivity between PAs to maintain tigers’ abilities to exchange genetic material.

Connectivity for tigers (e.g., Dutta et al., 2016, 2018; Krishnamurthy et al., 2016; Mondal et al., 2016; Reddy et al., 2017; Thatte et al., 2018; Yumnam et al., 2014) and multiple other species in the CIL (Jayadevan et al., 2020; Thatte et al., 2020) has been mapped over the past decade, and India’s National Tiger Conservation Authority (NTCA) has delineated tiger corridors throughout the country (Qureshi et al., 2014). Yet, the spatial concordance of corridor locations across these studies in the CIL has not been assessed.

An analysis of existing tiger connectivity studies in central India would provide a cohesive representation of important locations for landscape connectivity and thus a coherent message to landscape managers and policy makers. Accordingly, we collaborated to inform landscape-level conservation efforts for tigers and the many other connectivity-dependent species in central India within the realities of complex management involving multiple stakeholders.

We compared and synthesized tiger connectivity research in central India in order to distill a unified result for in situ stakeholders and land managers. We compared results from five independent tiger connectivity studies (Dutta et al., 2018; Mondal et al., 2016; Reddy et al., 2017; Thatte et al., 2020; Yumnam et al., 2014) in the CIL to quantify agreement on the permeability of matrix areas to tiger movement and important areas for connectivity throughout the landscape. Both metrics are uniquely informative because permeable areas facilitate movement and may become core habitat (e.g., Harihar et al., 2018; Talegaonkar et al., 2020) and connectivity accounts for spatial configuration of core areas (i.e., the potential of various patches to connect to other areas of the landscape). Using locations where studies agree on potential areas for tiger movement (consensus connectivity areas [CCAs]), we identified various stakeholders whose decisions affect the viability of the corridors, particularly in light of rapidly expanding infrastructure.

Biophysical setting

The CIL spans multiple states without a clearly defined boundary. The studies in this analysis used different spatial extents within the CIL (Figure 1). The area of overlap among the studies was a portion of the CIL in an agroecological zone known as the Central Indian Highlands (CIH). The full extent of the CIH is

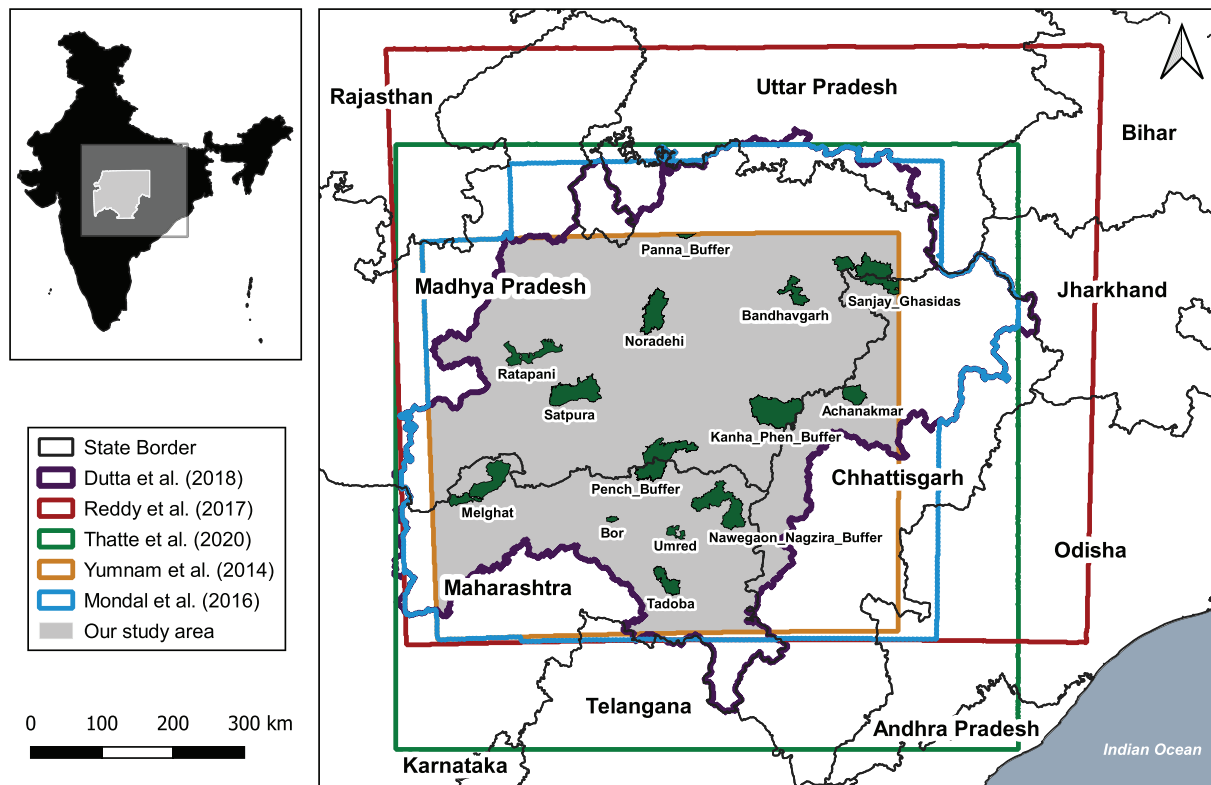


FIGURE 1 The central India landscape with the extents of the five studies on tiger connectivity synthesized to assess agreement among studies (gray, overlapping extent of all studies; green, protected areas; “_Buffer,” protected area displayed with an administrative buffer). We expanded the layer produced by Mondal et al. (2016)

384,508 km², spread mainly across three states in central India: Madhya Pradesh, Maharashtra, and Chhattisgarh (Gajbhiye & Mandal, 2000). The CIH encompasses 16 PAs, 11 of which are recognized as Tiger Reserves by the NTCA.

Tigers are classified as “endangered” on the IUCN Red List of Endangered Species (IUCN, 2021). Certain regions of their remaining range have been highlighted as tiger conservation landscapes (TCLs)—large blocks of contiguous or connected areas that contain tiger habitat that can support at least five adult tigers and where tiger presence has been confirmed in the past 10 years (Dinerstein et al., 2006). The TCLs are generally composed of isolated PAs embedded in a mosaic of natural and human-altered areas and are ranked in order of conservation priority. Central India harbors four of the 17 class I TCLs (highest priority), according to the latest designation (Sanderson et al., 2010). India as a whole harbors ~60% of the global tiger population—approximately 2967 (2603–3346) free-ranging adults and juveniles (~1–1.5 years old) as of 2018—and ~28% of India’s tigers live in the three states covered by our study (Madhya Pradesh, Chhattisgarh, and Maharashtra) (Jhala et al., 2019). Jhala et al. (2015) estimated that one-third of wild tigers in central India live outside PAs, highlighting the importance of the matrix. Dispersal data are limited, but genetic data suggest that individuals disperse up to 690 km, including through human-dominated landscapes (Joshi et al., 2013; Sharma et al., 2013b).

As rural development continues, previously permeable matrix is becoming a hard barrier to tigers, adding to existing threats from poaching, electrocution, and retaliatory killings (Habib et al., 2017; Karanth et al., 2013; Saxena et al., 2020). National and regional linear infrastructure intersects the CIL, and mining projects and reservoir construction for water security and hydropower are planned throughout the landscape (Appendix S1) (Habib et al., 2016).

Social setting

Local livelihoods are sustained mostly through small-scale agriculture, cattle rearing, and collection of forest products. Historically, agriculture expanded to almost all arable areas and the increasing human use has led to large-scale degradation of forests, soil, and water resources (Meiyappan et al., 2017). More than 50 million tribal households in India depend on nontimber forest products (NTFPs) for 40–60% of their household income (Ghate et al., 2009). The CIL has a high density of indigenous, officially recognized “scheduled tribes” or *adivasis* that reside in the region (>25% of all inhabitants) (Mohindra & Labonté, 2010; Revankar, 1971). The region encompasses thousands of villages (mean population >750) and a growing number of towns that also rely on forest goods, primarily to supplement agricultural incomes (Neelakantan et al., 2020).

Land management

In India and the CIL, land management is a complicated mix of areas under the Forest Department (FD), other governmental entities (e.g., Revenue Department and Defence Forces), and private land holdings (Appendix S2). Additionally, managers' spatial jurisdictions overlap between local administration and the FD hierarchy (Appendix S3). Proposed corridors in the CIL largely track historically forested areas that are now a mosaic of agriculture, villages, and remaining forests (Qureshi et al., 2014). The NTCA provides status reports of tiger populations in India and management guidelines for all tiger habitat, including lands in corridors. The NTCA guidelines for tiger conservation plans mandate PA FD staff provide comprehensive corridor management plans and coordination for the multiuse areas. A multilayered and hierarchical framework applies to forest use, protection, and diversion for other land uses via interactions with other stakeholders (e.g., industry and local communities) (Appendix S2).

METHODS

This study was based on five previously published studies on tiger connectivity in central India (Dutta et al., 2018; Mondal et al., 2016; Reddy et al., 2017; Thatte et al., 2020; Yumnam et al., 2014). Despite differences in underlying data and methodologies, all studies incorporated land use or land cover and accounted for human populations in the matrix in a variety of ways (e.g., population density and nightlights) (details in Table 1). We used the common extent among all resistance layers of the five respective studies (Figure 1) and reprojected all data layers to a 250 m resolution. We defined our PA boundaries to reflect recent changes and reclassifications of PAs (details in Appendix S4), resulting in 14 PAs within our study extent that were used as core areas in the movement analysis. We quantified agreement between studies on two focal metrics: landscape resistance (habitat permeability) and potential movement through the landscape (connectivity areas) (Appendix S5).

Landscape resistance

We used the landscape resistance layers from each study to measure the amount of agreement on resistance values between layers (Appendix S5). Due to the variety of input data and modeling methods used in the studies, the original resistance layers were highly varied. The large variation in numerical distributions of these layers (Appendix S6) precluded the use of traditional summary metrics (mean, standard deviation, etc.). Thus, to draw conclusions on agreement, we discretized each layer into five quantiles, resulting in five discrete levels of resistance: 1 (low), 2 (medium low), 3 (medium), 4 (medium high), and 5 (high). We then calculated the mode value and percentage agreement on this value between the five layers for each raster pixel. To investigate the effect of land cover on our analysis, we overlaid

our resulting layers with a land cover map of the study region (Roy et al., 2015). We aggregated several forest classes for the purposes of this analysis (Appendix S7).

Potential movement

We used the original resistance layers from each study to simulate movement via Circuitscape (McRae & Shah, 2009), with PAs as nodes, and then compared the resulting layers to quantify agreement between them (Appendix S5b). In this case, the similar distributions of the current flow outputs from Circuitscape allowed us to confidently use the mean and coefficient of variation (CV) to measure agreement among normalized (range 0–1) layers. To remove areas of low agreement between layers, we masked pixels that were above the 20th percentile CV for all pixels (sensitivity analysis for this cutoff in Appendix S8). We refer to the remaining areas as *consensus current flow* areas.

Calibration

To decide on a cutoff for current flow values within consensus current flow (which shows both high and low levels of current flow), we compared several upper (60th, 70th, 80th, and 90th) percentile cutoffs of the consensus current flow output to a data set of newspaper reports of human–tiger conflicts throughout the CIL from 2012 to 2015 (Appendix S20 [csv file]). We restricted the calibration to a convex hull encompassing the four southern-most PAs from the study area because this was the area with the densest conflict data (number of points = 15). For each percentile cutoff of the consensus current flow layer, we calculated the proportions of random versus real conflict points that intersected the layer. We then chose the percentile cutoff layer with the greatest positive difference between the proportion of intersecting conflict points and intersecting random points as our CCA layer. This layer represented areas where there was both high average current flow and high agreement between the studies throughout the landscape (i.e., areas where the studies had similarly high levels of potential movement). Unless specified, all analyses detailed thus far were carried out in R/R Studio 3.6.2 and QGIS 3.12.1.

Management in CCAs

We used open access data on development activities and governance to spatially identify the management regimes and stakeholders in the CCAs layer. Specifically, we explored the overlaps between the CCAs and FD management, land diverted for infrastructure, and land within village boundaries. All spatial analyses for management and stakeholders were conducted on NextGIS QGIS 9.6.0 - QGIS base 2.18.28.

Details on all methods, including workflows, are in Supporting Information.

TABLE 1 Details on studies synthesized in the analysis of landscape permeability for tiger movement and potential movement areas^a

Authors	Year	Title	Spatial resolution	Inputs for resistance layer	Derivation of resistance
Yumnam et al.	2014	Prioritizing Tiger Conservation through Landscape Genetics and Habitat Linkages	1 km	forest metrics (area, core area, and patch size) NDVI elevation ruggedness drainage density rainfall distance to PA distance to roads distance to nightlights human and livestock observations prey availability	occupancy model (PRESENCE) tiger presences as response
Mondal et al. ^b	2016	Tiger Corridors of the Eastern Vidarbha Landscape	1 km	human and livestock population forest cover (Forest Survey of India 2009) land cover (Bhuvan) nightlights distance to roads distance to drainage distance to forest or protected area	Maximum entropy (Maxent) tiger presences as response
Reddy et al.	2017	Tiger Abundance and Gene Flow in Central India are Driven by Disparate Combinations of Topography and Land Cover	500 m	land cover (Forest Survey of India 2013) topography (roughness and slope) road density nightlights	restricted multivariate optimization (generalized linear model) genetic data as response
Dutta et al.	2018	Targeting Restoration Sites to Improve Connectivity in a Tiger Conservation Landscape in India	90 m	hybrid land cover map (four data sets) human population density infrastructure (mines, reservoirs, and power plants)	review of literature (with weighting optimization)
Thatte et al.	2020	Human Footprint Differentially Impacts Genetic Connectivity of Four Wide-Ranging Mammals in a Fragmented Landscape	250 m	land cover (Bhuvan) human population density (2011 census) roads with passenger car units density of linear features (roads + railway lines + irrigation canals)	restricted multivariate optimization (generalized linear mixed model) genetic data as response

^aSee Figure 1 for the spatial extents of the studies. For further detail, refer to original publications.

^bThe area from Mondal et al. (2016) we used is an enlarged version of the 2016 study layer.

RESULTS

Landscape resistance

The variety of methodologies and data sources resulted in what appears as a diverse set of resistance maps (Appendix S9). Using the discretized layers (Appendix S10), we derived mode values for each pixel (Figure 2a) and the percentage of studies that agreed on that value (Figure 2b). We found the highest agreement in the low and high resistance categories (Figure 3a). Of all pixels where four of five studies agreed on a resistance category (80% agreement), 45% and 24% were low and high resistance, respectively. The remaining 31% were split among the three intermediate resistance categories. Where all studies agreed on a resistance category (100% agreement), 66% and 24% of pixels were low and high resistance, respectively. The remaining 10% were split among the three intermediate resistance categories. Areas with lower agreement were more evenly distributed between resistance categories. The majority of pixels

showed only two or three studies agreeing on the mode value; these two levels of agreement displayed predominantly intermediate mode resistance (Figure 3a).

Our land-cover analyses revealed that, among our five studies' resistance values, areas classified as forest and human settlement were in relatively high agreement on resistance value, whereas the agriculture and scrub land-cover categories exhibited lower agreement (Figure 3b).

Potential movement

We observed high agreement in current flow among studies (Figures 4 & 5, & Appendices S11 & S12). Overall, high-agreement (<20th percentile CV) current-flow pixels—consensus current flow areas—overlapped with the high mean current pixels (>80th percentile mean current flow) 41% of the time (Appendix S12). The percentile cutoff of consensus current flow that best captured our conflict data points was

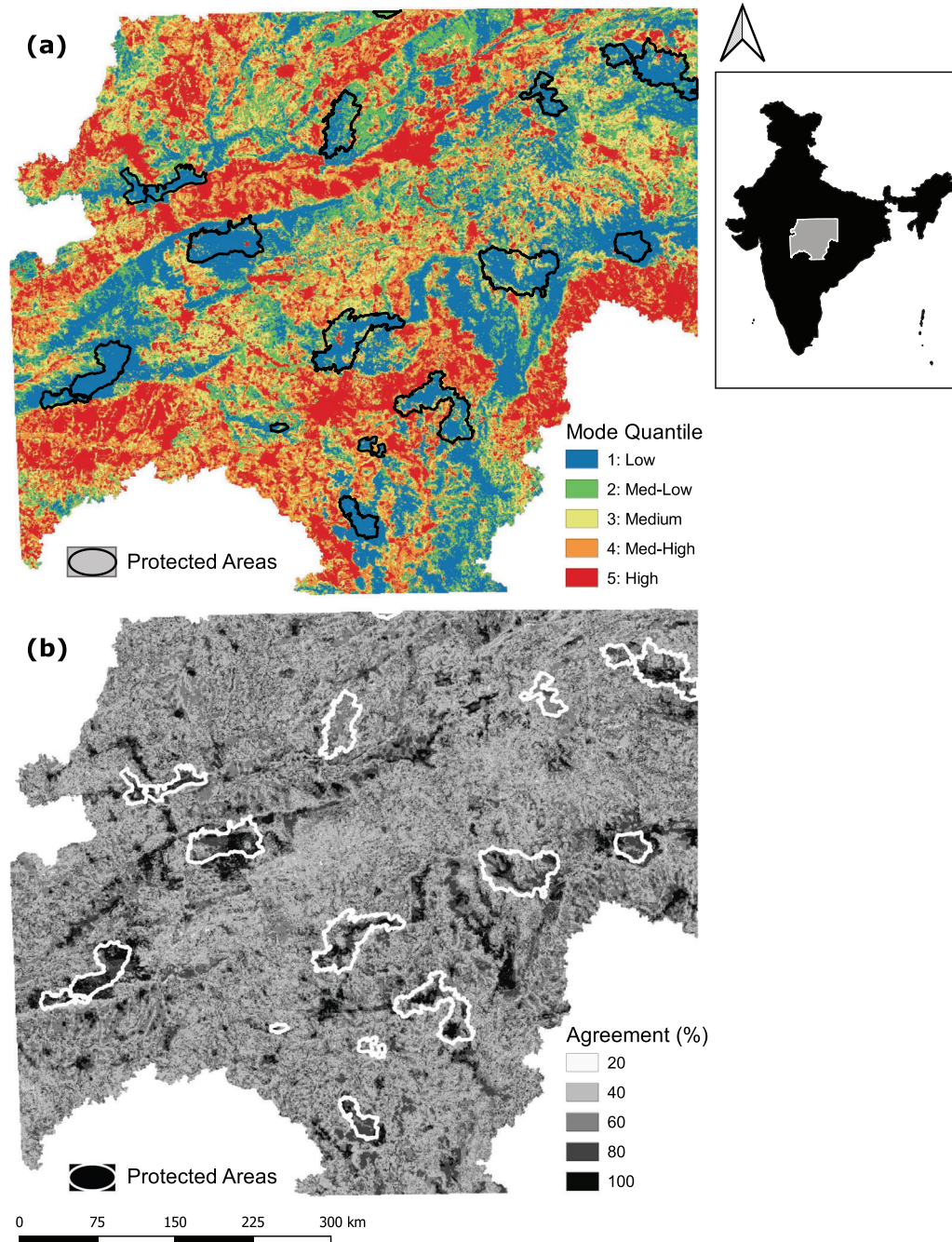


FIGURE 2 Agreement among five independent studies on landscape resistance to tiger movement: (a) mode quantile and (b) percent agreement on mode value (the darker the pixel, the higher the agreement)

the 70th percentile (Figure 5; Appendices S8 & S13). These CCAs overlapped with conflict data significantly more than expected by random (observed points = 0.67; mean of random points = 0.40; one-sample t test, $p = 3.4e-9$).

Management in CCAs

Connectivity areas for long-term tiger conservation are largely managed by the state FDs. The spatial overlap between tiger

CCAs and other land-use was extensive, highlighting management with multiple objectives for conservation, forestry, and livelihood activities (Figure 6 & Appendix S14). Nearly, 70% of CCAs in our study region overlapped village boundaries (Figure 6a).

Village populations were generally lower in CCAs than state or regional averages (Appendix S14). The density of villages per square kilometer was also lower in CCAs (1.0 village per 10 km²) than outside of CCAs (1.8 villages per km²) in the study region. The spatial distribution of villages

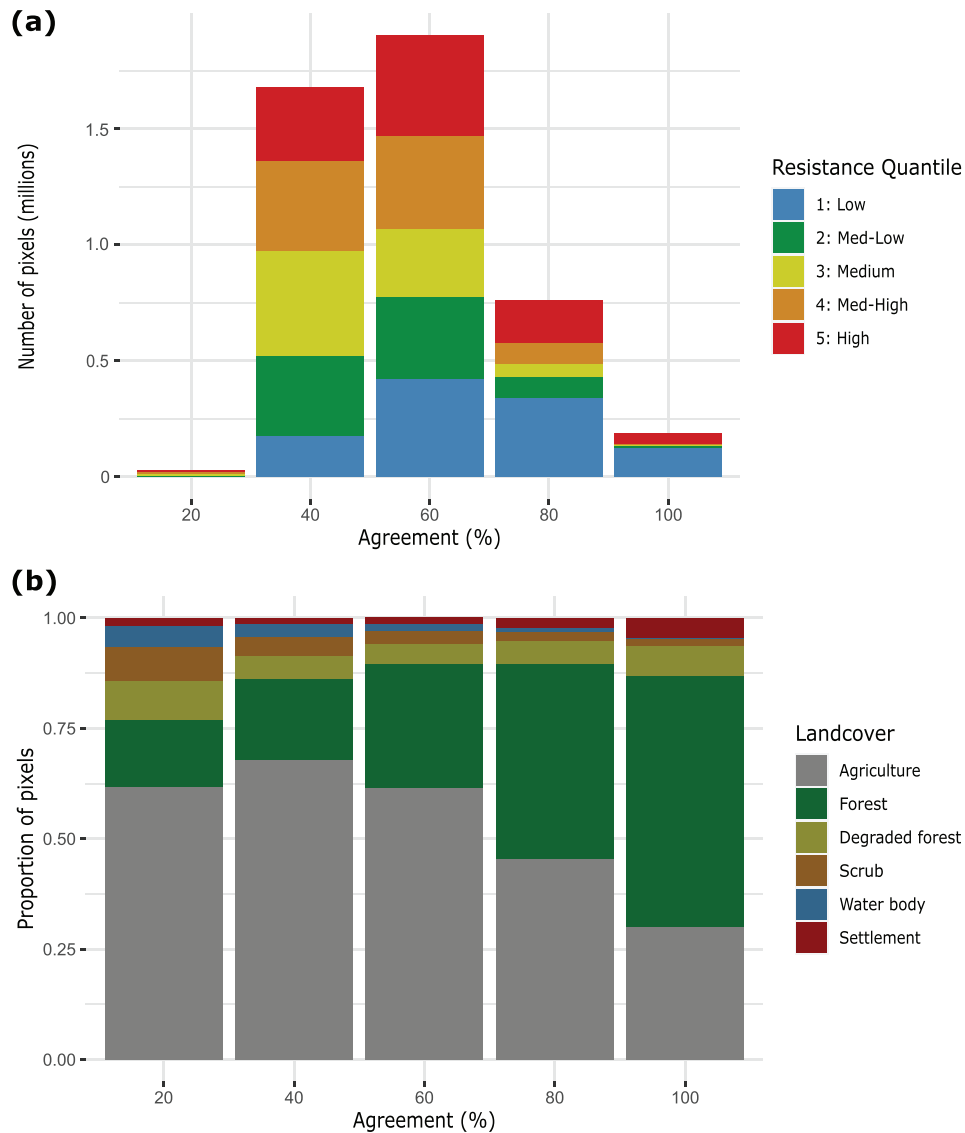


FIGURE 3 (a) Number of pixels in resistance quantiles by percent agreement among five studies on landscape resistance to tiger movement and (b) proportion of land-cover classes by level of agreement among studies. Land-cover classes are the six most common in the study area

clarifies that CCAs were, and likely will remain, largely multiuse areas.

Linear infrastructure cut across CCAs several hundred times: road 437 times, railway 170, transmission line 179, and canal 339 (Figure 7a–e). Of the total area of CCAs, 16.4% was within 1 km of linear infrastructure. We found a total of 271 km of roads, 1165 km of railway lines, 3741 km of transmission lines, and 1732 km of canals within 1 km of CCAs (total area of CCAs with 1-km buffer was 65,641 km²). We also found 105 mines within 1 km of CCAs. Mineral deposits closely tracked remaining forests in central India; mining activities were, therefore, predominantly in connectivity areas for tigers (Figure 7f).

Collection of NTFPs was extensive in the CCAs, particularly the collection of tendu leaves used for rolling tobacco. Seasonal tendu leaf collection is extensive in the districts that are inter-

sected by the CCAs. Approximately 82% (1,887,200 bags of 50,000 leaves) of tendu leaf was collected from these districts in the state of Madhya Pradesh in 2014 (Appendix S15). Finally, central Indian forest lands outside of PAs were diverted for mixed land use—predominantly for linear infrastructure, mining, and irrigation—based on 2019 data from the Indian government (Appendices S16 & S17). In Madhya Pradesh, 78% of all forest land diversions in 2019 was in districts that have CCAs (data from other states in Appendices S16 & S17).

Spatial layers are available from <http://www.conservingcentralindia.org/data-collab.html>, and all code used to perform the synthetic analysis is available on Github (<https://github.com/jaymschoen/ci-tiger-connectivity-synthesis>). Independent tiger connectivity data may be requested from the respective authors.

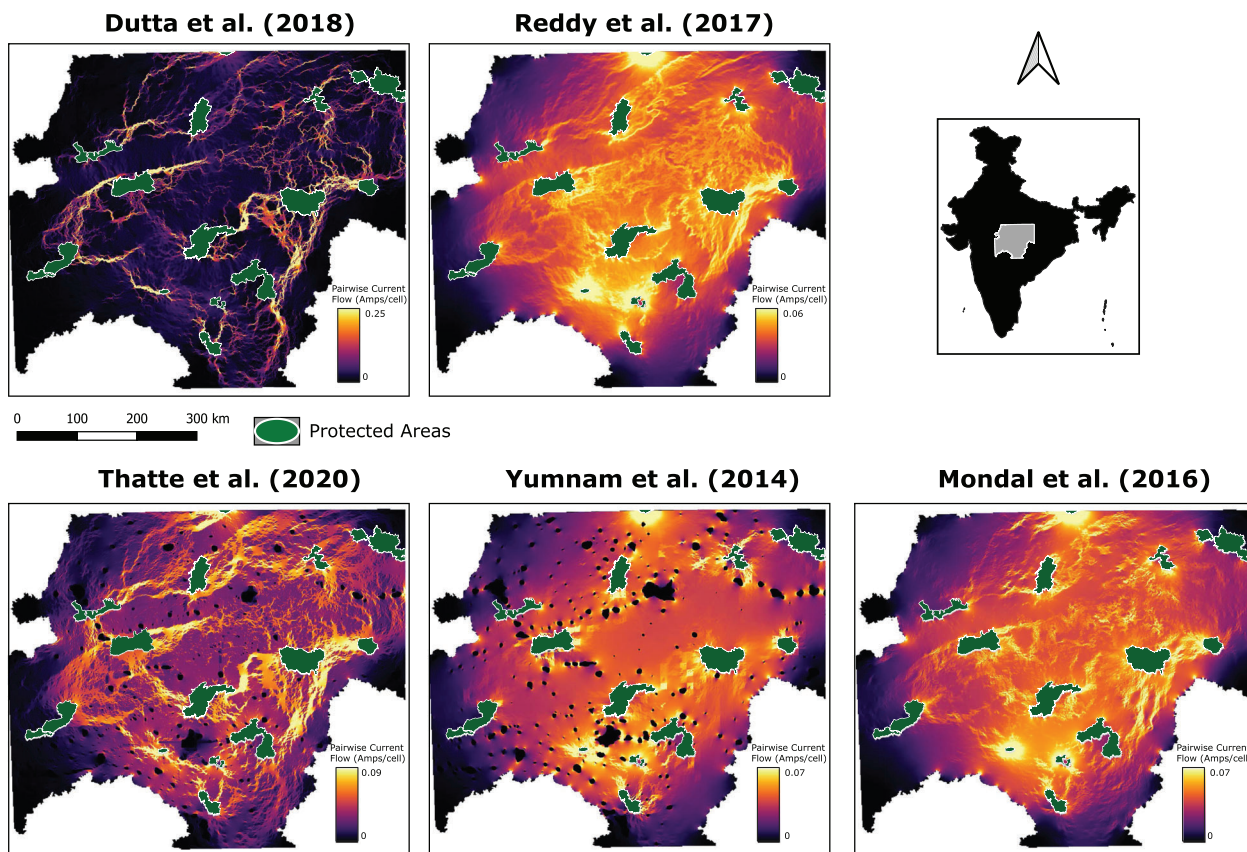


FIGURE 4 Current flow output from Circuitscape runs performed on each study's layer representing landscape resistance to tiger movement (dark areas, relatively low current flow; bright areas, relatively high current flow; protected areas, nodes of each Circuitscape run). We expanded the layer produced by Mondal et al. (2016)

DISCUSSION

By comparing results from five independent studies on tiger connectivity in a globally important and human-dominated landscape, we identified areas of agreement for both landscape resistance (habitat permeability) and potential movement (connectivity areas). Further, by quantifying the stakeholders and human impacts in these areas, we provide crucial context for land managers and policy makers in a multiuse landscape where humans and wildlife exist in close proximity. These results can be used as a basis for wildlife-supportive land-use and infrastructure planning in a rapidly developing region in India, whereas the synthetic framework can be applied to analogous spatial research scenarios and other tiger-conservation landscapes in Asia and throughout the world. We considered our results on the agreement of the individual studies' resistance layers, comparison of simulated movement via current flow, and the management implications of our results in the CIL.

Landscape resistance

Due to the variety of data sources and methods used to derive the resistance surfaces (Table 1), it is not surprising that study

results did not agree fully on resistance values throughout the landscape (Koen et al., 2012; Zeller et al., 2018). The lack of agreement likely reflects the different spatial and temporal scales and resolutions in the data sources, as well as various ways of parameterizing and optimizing resistance surfaces. The effects of this were clear when comparing original resistance layers (Appendices S6 & S9).

Our results demonstrated that seemingly discordant results from connectivity mapping and other spatial research can be synthesized. In our case, the results were in much higher agreement than would be expected on initial examination. Drastically different results from the original studies could be misconstrued as a lack of precision by the latest scientific efforts, thus straining trust in the scientific community. However, discretizing each resistance map prior to comparison (Appendix S10), rather than direct comparison of resistance values, enabled assessment of the degree to which they agree.

Our finding that the studies agreed on high (quantile 5) and low (quantile 1) resistance areas proportionally more than intermediate resistance areas (quantiles 2–4) (Figure 3a) would be expected because areas of highest (e.g., cities/settlements) and lowest resistance (e.g., forest) should have consistently high or low resistances (relative to the particular resistance surface) regardless of the method used to generate the resistance

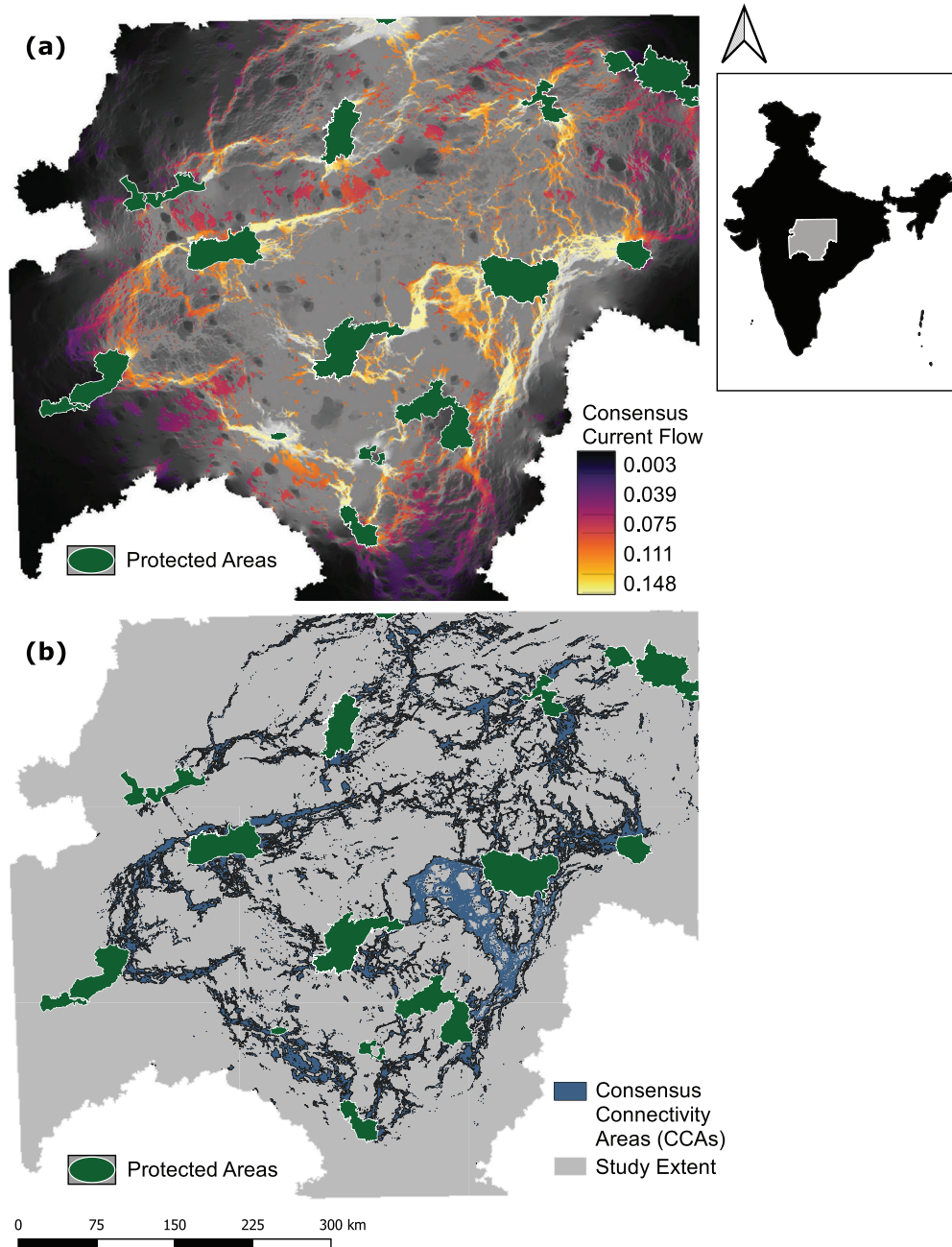


FIGURE 5 Consensus current flow (i.e., mean current flow in areas where the five studies agreed) and consensus connectivity areas (CCAs) (i.e., areas where the five studies agreed on high current flow) in the central Indian landscape: (a) mean current flow throughout the study area (grayscale) (highlighted consensus current flow, mean current flow in <20th percentile coefficient of variation [CV] of current flow areas [black to yellow color scale]) and (b) CCAs between protected areas (CCAs, 70th percentile of mean current flow in <20th percentile of CV of current flow areas)

surface. Contrarily, lower agreement areas would be expected to display land-cover types for which permeability is intermediate or highly variable (e.g., agriculture). Our investigation of the underlying land cover confirmed these expectations (Figure 3b). The effect of specific methodology on the resistance—as well as in situ wildlife use—of these intermediate areas is an intriguing area for future investigation.

The finding that a majority of pixels showed two or three of five studies agreeing on a mode value (Figure 3a) can be attributed in large part to the distributions of the five studies' resistance layers (Appendix S6). Dutta et al. (2018) and Thatte et al. (2020) classified the landscape as predominantly low resistance, with few high resistance areas. Yumnam et al. (2014), Mondal et al. (2016), and Reddy et al.'s (2017) layers show the

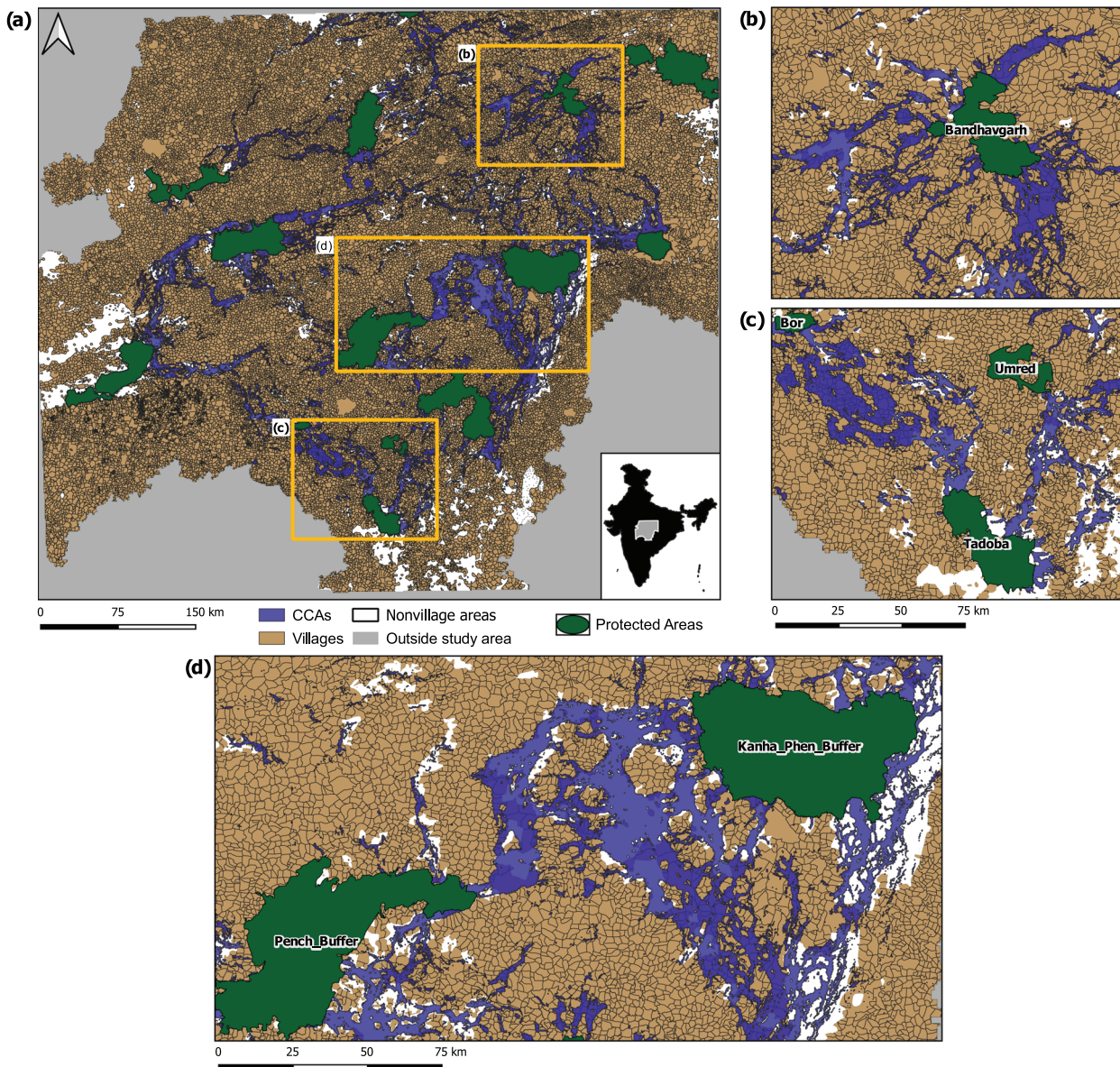


FIGURE 6 (a) Human-dominated central Indian landscape showing villages (which include towns and other inhabited hamlets); consensus connectivity areas (CCAs) (i.e., areas where all five studies agreed on high potential movement) overlaying villages (dark purple); CCAs not overlapping villages (light purple); and protected areas (PAs) (70% of CCAs overlap village boundaries and 30.39% are not within village boundaries); (b) high overlap around Bandhavgarh PA; (c) mixed or intermediate overlap among Bor, Umred, and Tadoba PAs; and (d) low overlap with villages between Kanha-Phen and Panch PAs. Nonvillage areas include some villages without accurate boundaries (points or very small circular shapes) (e.g., east and south of Kanha-Phen PA). “_Buffer” denotes a PA displayed with an administrative buffer

opposite pattern, with mostly high resistance and few low resistance areas. Because both methods of classifying resistance surfaces (left vs. right skew) produce viable results based on source data (Koen et al., 2012), the contrasting distributions are not concerning per se. This observation does, however, explain the pattern in agreement between layers; further, it accentuates the confidence we have in areas with more than three of five studies agreeing on a mode value. Accordingly, we consider 80% (four of five studies) agreement very high confidence in the mode resistance value.

Potential movement

The considerable overlap between high agreement and high current flow areas (Figure 5a, & Appendices S11 & S12) is encouraging. This finding suggests that even drastically different resistance layers may yield comparable results when movement is simulated via circuit theory. This method forces current to move somewhere within the resistance surface, which reduced the differences seen in the resistance layers (Figure 4). There are still considerable differences in the maps overall, but much less so

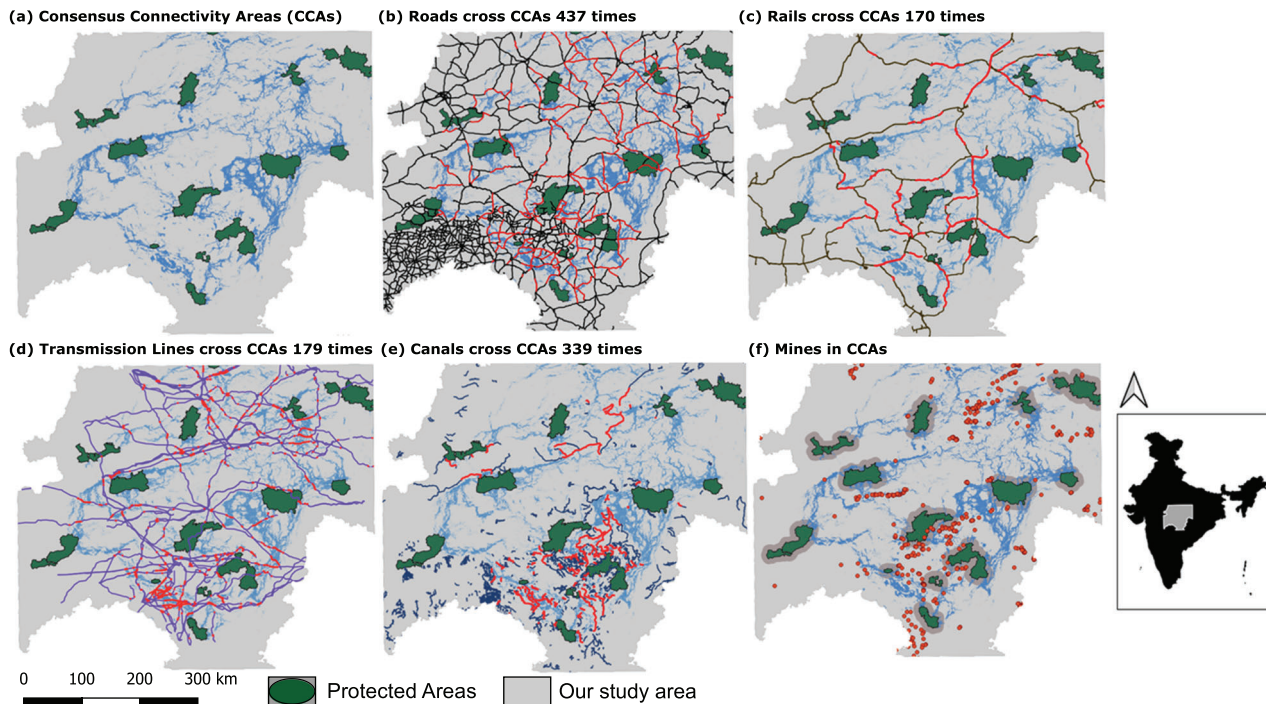


FIGURE 7 (a) Consensus connectivity areas (CCAs) (i.e., areas where all five studies agreed on high potential movement) for tigers in central India and linear infrastructure—(b) roads (black), (c) rail (brown), (d) transmission lines (purple), and (e) canals (cyan)—that crosses CCAs (red, crossings) and (f) mining activity (orange dots) (53 mines within 10 km of protected-area boundaries [light brown, 10-km buffer] and 105 mines within 1 km of or within CCAs)

than the original resistance layers (Appendix S9). We do not suggest that diverging distributions of resistance layers is a desirable scenario; rather, using circuit theory may be a better way to compare results than simply comparing resistance layers (e.g., Cushman et al., 2014).

Because the objective of our analysis was not to create a current flow model, but rather to highlight specific high flow areas in all studies, we elected to use independent occurrence records to select a percentile cutoff (70%) for current flow (Appendices S8 & S13). This CCA layer (Figure 5b) provides guidance for landscape-wide delineation, planning, and management of corridors.

Our results do not come without limitations, however. Specifically, the amount of current flow generated by Circuitscape depends on node centrality and the proximity of nodes to each other (e.g., Carroll et al., 2012; Dutta et al., 2016). Koen et al. (2014) suggest a “nodeless” method of Circuitscape that places nodes around the perimeter of the extent, rather than within it, to simulate movement throughout the entire landscape. We posit that the use of the PAs as nodes is the appropriate approach for our study, however, due to the network of PAs known to contain viable tiger populations (more information in Appendices S18 & S19). Nevertheless, to account for the artifacts of node centrality and proximity inherent to Circuitscape, it may be important to consider the current flow between centrifugal nodes relative to each other rather than in relation to more central PAs or to consider other methods, such as resistance kernels (Compton et al., 2007), which are not as sensitive to this and can also account explicitly for dispersal distance.

Finally, we used the terminology *connectivity areas* rather than *corridors* to describe our CCA layer for several reasons. The term *corridor* connotes a continuous area from point A to point B for future planning and protection. We recommend that our CCA layer be validated with movement data to illuminate suitable methods (e.g., addition of buffers) of forming the A to B connections necessary for corridors. Accordingly, our CCAs should serve as the basis for corridor planning, but are not delineated corridors themselves. We hope our analysis can support the NTCAs and the management of formally acknowledged tiger corridors in central India (Qureshi et al., 2014) and bolster collaborative efforts among researchers and managers for tiger conservation in central India.

Management implications

Management of CCAs in the CIL requires the inputs of multiple stakeholders in the rapidly developing human-dominated landscape of central India. Land ownership in CCAs is complicated, with overlapping or contested ownership among multiple arms of the FD and villages. Furthermore, our assessment of overlap between CCAs and village boundaries was conservative because several villages east of Kanha PA do not have resolved public boundaries (Figure 6a & d). The legacy of historical top-down management frameworks and little communication between government departments creates a challenging context for comanagement (Macura et al., 2016). Moreover, important and deep concerns remain about rights of

forest dwellers in the region (Gupta et al., 2020). Efforts by the FD, the main governing agency within CCAs, to include local communities have had mixed results. Some efforts have led to elite capture, whereas others have led to decentralization without equitable power distribution, highlighting the importance of strong local institutions (Agarwal et al., 2017; Kumar, 2002).

In central India—particularly forest areas within CCAs—a large proportion of vulnerable local (largely tribal) communities continue to rely on forests for daily fuelwood and grazing cattle as well as seasonal economic opportunities (Nair et al., 2021). Notably, people in central India extensively collect tendu leaves for commercial trade, supplementing their single-cropping agrarian livelihood by converting natural capital to financial capital in local markets (Lele et al., 2015; Neelakantan et al., 2020) (Appendix S15). The changing aspirations of the younger generation as well as large spatial overlap of connectivity and human-use areas reinforce the need for incorporation of local perspectives in corridor management.

Finally, another crucial stakeholder—regional infrastructure development actors—adds a challenge for managers of CCAs. Strong barriers to movement from linear infrastructure are increasing across all three central Indian states considered in this study (Figure 7). Our estimates of the numbers and areas of linear infrastructure crossings across CCAs are conservative as infrastructure continues to expand, whereas spatial data on proposed projects are difficult to access (Nayak et al., 2020). Moreover, while forest cover remains intact within PAs, forest cover outside of PAs (of which CCAs are largely comprised) is rapidly lost to infrastructure development and other drivers of land-use change (Banerjee et al., 2020). In building relationships with all stakeholders, researchers and managers could use CCAs to plan infrastructure in the future by avoiding areas important for conservation and restoration.

The management complexity we identified highlights the need for dialogue among the diverse and multiple stakeholders. Globally, strong evidence exists for long-term gains from stakeholder-driven goal-setting within conservation landscapes (Chester, 2015; Kremen & Merenlender, 2018). The NTCA clearly recognizes the importance of multiple-stakeholder coordination within TCLs in India by formally guiding FD plans to include mechanisms to manage corridors. With the synthesis of these studies, the scientific community has broad agreement on the locations and the diverse stakeholders to be engaged in management of CCAs that benefits wildlife, people, and development in central India.

Our results demonstrate a mode of empirical analysis with growing importance in modern ecological and conservation research: synthesis of multiple results. As more research is conducted in important biodiversity areas, analogous situations (in which multiple models exist) will demand synthetic analyses. Rather than differences in studies of the same subject or area connoting inadequacies in the scientific method and groups involved, methods to analyze where and to what degree such studies agree or disagree can bolster faith in scientific results while promoting transparency and healthy relationships within and outside of the scientific community. Our method provides a framework for synthesizing results from spatial research in

other regions throughout the world to support applied conservation work.

We also provide a practical application of spatial synthesis by outlining CCAs for tigers in a human-dominated landscape. By highlighting important areas for wildlife to maintain connectivity and identifying the stakeholders affected by land-use decisions in these areas, we aimed to provide a multipronged input to local and national managers. Our results emphasize that successful management of CCAs will require consensus among stakeholders on the appropriate balance between potentially competing objectives for safe passage of dispersing wildlife, livelihood needs for local communities, and infrastructure development.

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This article has earned an Open Materials badge for making publicly available the components of the research methodology needed to reproduce the reported procedure and analysis. All materials are available at <https://github.com/jaymschoen/ci-tiger-connectivity-synthesis>.

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SUPPORTING INFORMATION

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