J. Indian Inst. Sci.
A Multidisciplinary Reviews Journal
ISSN: 0970-4140 Coden-JIISAD

REVIEW ARTICLE

Trends in Wildlife Connectivity Science from the Biodiverse and Human-Dominated South Asia

Prachi Thatte[1], Abhinav Tyagi[2,3], Amrita Neelakantan[4], Meghana Natesh[5], Mihika Sen[6] and Tarsh Thekaekara[2,6]*

Abstract | The threat of habitat fragmentation and population isolation looms large over much of biodiversity in this human-dominated epoch. Species-rich South Asia is made particularly vulnerable by its high human density and anthropogenic habitat modification. Therefore, reliably estimating wildlife connectivity and the factors underpinning it become crucial in mitigating extinction risk due to isolation. We analysed peer-reviewed literature on connectivity and corridors for terrestrial mammals in South Asia to identify trends in connectivity research. We identify key research gaps and highlight future directions that may aid efforts to robustly study connectivity. We found a significant bias towards charismatic megafauna and their habitats. Methodologically, although we observed a range of approaches reflecting some of the advances and innovations in the field, several studies lacked data on animal movement/behaviour, leading to potentially biased inferences of how species disperse through human-modified landscapes. New avenues for connectivity research, though currently under-explored in South Asia, offer alternatives to the heavily used but less-reliable habitat suitability models. We highlight the advantages of landscape genetic methods that reflect effective dispersal and are made feasible through non-invasive and increasingly more cost-effective sampling methods. We also identify important gaps or areas of focus that need to be addressed going forward, including accounting for animal movement/behaviour, human impacts and landscape change for dynamic and adaptive connectivity planning for the future.

Keywords: *Connectivity, Corridors, South Asia, Wildlife, Mammals*

1 Introduction

Ensuring connectivity between wildlife populations is a critical aspect of nature conservation in the Anthropocene, the present human-dominated geological epoch[1,2]. As humans convert natural habitats to other land-use types, wildlife populations face greater extinction risk due to isolation[3,4]. Protected areas (PAs) are the cornerstone for the conservation of endangered species, but individual PAs are often smaller than species' home ranges or provide sub-optimal habitat, undermining the resilience of populations of wide-ranging terrestrial mammals[5,6]. Movement restriction to protected habitat patches curtails the natural ranging behaviour of animals, often with detrimental impacts over their life cycles. Restricted dispersal can have negative impacts on natural patterns of colonization, reducing genetic variation due to lack of gene flow among populations, in turn affecting long-term population viability[7–9].

Humans have modified 75% of the earth's terrestrial surface and a projected 90% is predicted to be modified by 2050[10]. Mammals occurring in

[1] World Wide Fund for Nature-India, New Delhi, India.
[2] National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bangalore, India.
[3] SASTRA Deemed to be University, Thanjavur, India.
[4] Network for Conserving Central India (NCCI), Nagpur, India.
[5] Indian Institute of Science Education and Research (IISER), Tirupati, India.
[6] The Shola Trust, Nilgiris, India.
**prachi.thatte@gmail.com*

these altered landscapes are increasingly exploiting areas that are shared with humans, extending well beyond PA boundaries[11,12]. There is an urgent need to reorient connectivity science and practice to look beyond PAs and include diverse land-use types that enable wildlife movement and dispersal. The foundational concepts in connectivity science had a "structural" perspective, with efforts to conserve "linear landscape elements" or strips of natural habitat[13]. The IUCN's Connectivity Conservation Specialist Group (CCSG) takes a broader view of connectivity than structural linkage between habitat patches, defining connectivity as the "ability of plants or animals to move freely through a landscape, seascape, or freshwater environment" (www.conservationcorridor.org). The broader and more recent IUCN CCSG definition of connectivity belies the historical arc of connectivity science—expanding from a purely structural connectivity emphasis to landscape-wide permeability of multiple landscape features supported by data on individual dispersal providing insights into functional connectivity[14].

Understanding connectivity in the future will depend, in large part, on the ability to model dispersal between distinct populations' habitat patches reliably and dynamically, in a way that reflects real-world animal movement. Methodological advances increasingly provide deeper insights into species ability to move through heterogeneous landscapes (incorporating animal behaviour, observed dispersal events, individual variation, seasonality, etc. and even human activity) allowing for more robust and accurate models[15]. However, these advances are often not reflected in connectivity modelling studies, which still rely on (arguably biased) expert opinion and species presence/absence, despite a growing number of empirical studies on animal movement[16,17]. Examining the methods used to predict animal movement is therefore essential, to understand if they reflect functional connectivity or real-world animal movement in an increasingly human-dominated world.

We focus this study on South Asia (https://www.cia.gov/the-world-factbook/SouthAsia/) to explore connectivity science in the context of human-dominated landscapes which are important for wildlife conservation, regionally and globally. South Asia is one of the world's strongholds for charismatic megafauna—tigers (*Panthera tigris*), leopards (*Panthera pardus*), Asiatic lions (*Panthera leo*), snow leopards (*Panthera uncia*) and Asian elephants (*Elephas maximus*)—and holds multiple globally recognized biodiversity hotspots spread across five of the worlds' 14 biomes[18]. Incredibly, one fourth of all humanity also lives in the same geographic region, spanning 5 million km^2. Millions of socially and economically vulnerable people rely on forests for goods and services in this densely populated and biodiverse sub-continent[19]. Much of all available arable land has been under cultivation for generations and conversion of lands from agriculture to peri-urban and urban land-use is on the rise[20–22]. The larger threat for connectivity and conservation in these human-dominated landscapes is likely to be the change of permeable matrix habitats (e.g. smallholder agriculture) to land uses that impede or serve as barriers to animal movement (industrial use, linear infrastructure and cities). South Asian countries face some of the highest pressure on land that is shared by both humans and wildlife, and future connectivity research must, therefore, attempt to better understand functional connectivity and how species navigate human-dominated landscapes.

In this systematic review, we examine trends in peer-reviewed connectivity literature from South Asia, with a focus on terrestrial mammals as one of the most studied taxonomic groups[23], and arguably the most impacted by anthropogenic land-use change. We attempt to first get a coarse-scale overview of the literature in terms of geographic distribution of studies and species being researched, and whether it maps onto existing taxonomic bias.[16,23,24]. The thrust of the review is then a deeper understanding of the existing literature on connectivity science from a functional perspective, or how terrestrial mammals move in multi-use landscapes consisting of forests, grasslands, agro-ecosystems and human settlements, with a keen focus on the approaches and methods and whether these reflect real-world animal movement. Finally, we examine the policy and conservation implications of this research and touch on future directions and applicability of recent methodological advances for connectivity studies to be more relevant in an increasingly crowded planet.

1.1 Definition of Key Terms Used in the Review

Term	Category	Definition	Relevant references
1. Structural connectivity	Type of connectivity	A measure of the degree to which some landscape elements of interest are contiguous or physically linked to one another, independent of any attributes related to species movement/with no direct link to any behavioural attributes of organisms	Tischendorf- and Fahrig (2000)[25]; Taylor et al. (2006)[26]
2. Functional connectivity	Type of connectivity	A measure of connectivity that incorporates species-specific responses to different landscape elements and accounts for the actual movement of individuals through the matrix between habitat patches. Based on the extent to which species-specific responses/behaviour are incorporated, it may be further classified as below	Taylor et al. (2006)[26]
2.1. Potential functional connectivity	Type of connectivity	A measure of connectivity that uses physical attributes of the landscape to predict connectivity among patches for a species, with limited information about dispersal ability or animal movement data	Calabrese and Fagan, (2004)[27]; Fletcher et al. (2016)[17]
2.2 Realised functional connectivity	Type of connectivity	A measure of connectivity that incorporates observed data (e.g. radio tracking, molecular genetic data) that reflects actual rates of the movement of individuals (or their genes) between focal patches or in a landscape to estimate the species-specific connectivity between landscape elements or habitat patches	Calabrese and Fagan (2004)[27]; Fletcher et al. (2016)[17]
3. Resistance surface/cost surface	Method/tool used for studying connectivity	A landscape map (raster) in which the value of each pixel/cell is the cost or resistance that a particular landscape feature in that pixel/cell offers to movement of dispersing individuals	McRae et al. (2008)[28]; Spear et al. (2015)[29]
4. Least cost path algorithm	Method/tool used for studying connectivity	A route optimization algorithm that finds the path between two locations that costs the least to those travelling along it to determine the most cost-effective route between a source and destination	Beier et al. (2009)[30]; Alexander et al. (2016)[31]
5. Habitat suitability modelling	Method/tool used for studying connectivity	Habitat suitability modelling (sometimes called species distribution modelling) is a method for predicting the suitability of a location for a species, or group of species, based on their observed relationship with environmental conditions	Hirzel and Le Lay (2008)[32]; Ziólkowska et al. (2016)[33]
6. Circuit theory-based modelling	Method/tool used for studying connectivity	A modelling approach that assumes that ecological processes such as gene flow and dispersal are analogous to how electrical circuits function, relating resistance, current, and voltage in electronic circuits to random walks on analogous graphs. Circuit theory is applied to predict movement patterns and probabilities of successful dispersal of random walkers moving across complex landscapes, to generate measures of connectivity	McRae et al. (2008)[28]; Spear et al. (2015)[29]
7. Graph theory-based modeling	Method/tool used for studying connectivity	A mathematical approach used to model pairwise relationships between nodes. In the context of connectivity modeling, the landscape is represented as a graph with nodes (habitat patches) and edges that join pairs of nodes (interpreted as connectivity)	Bunn et al. (2000)[34]; Kindlmann and Burel (2008)[35]; Godet and Clauzel, (2021)[36]
8. Landscape genetics	Discipline	An approach for analysing spatial genetic data to understand how geographical and environmental features structure genetic variation at both the population and individual levels	Manel et al. (2003)[37]

2 Methods

This review drew on the Collaboration for Environmental Evidence guidelines for evidence synthesis (www.environmentalevidence.org), aimed at creating an objective and replicable systematic map of the literature to identify the gaps from the perspective of functional connectivity.

2.1 Boolean Search String

Based on a number of preliminary search phrases in the database Scopus (www.scopus.com) a "catch-all" Boolean search string was formulated to capture the maximum number of studies related to connectivity in South Asia: TITLE-ABS-KEY ((connectivity OR corridor) AND (wildlife OR animal OR species OR habitat OR landscape) AND (("India" OR "Pakistan" OR "Bangladesh" OR "Sri Lanka" OR "Nepal" OR "Bhutan" OR "Afghanistan" OR "Maldives") OR (("Indian" OR "Pakistani" OR "Bangladeshi" OR "Sri Lankan" OR "Nepali" OR "Nepalese" OR "Bhutanese" OR "Afghanistani" OR "Afghani" OR "Maldivian"))).

Capturing papers relating to South Asia was a challenge since the "Affiliation" search field in the database is related to the geographic affiliation of the author rather than the study region. Further, the adjective form of countries has to also be used, since some papers describe subnational regions (e.g. "Central Indian Landscape" in Thatte et al. (2018)[9]).

This search string yielded 841 results, and these were then divided among the authors, and then filtered and tagged using the flowchart in Fig. 1. The bibliographic software Zotero was used, and tags were capitalised to differentiate from existing article tags. The screening and tagging process was validated by each set of tags being checked by two authors to ensure consistency.

2.2 Eligibility Criteria

The eligibility criteria for inclusion in the review were (1) study region is within the terrestrial realm of South Asia (209 papers tagged with "Indian Ocean" were also captured with the above search string, while a further 287 mentioned a South Asian country though the study was from elsewhere), (2) is related to wildlife/conservation (130 papers not related to wildlife/conservation but related to studies around development/infrastructure 'corridors' were also captured), and (3) connectivity and animal movement is a key part of the study—267 papers mentioned the terms "corridor" or "connectivity" in the abstract or title, but did not actually study them. A number of articles relating to phylogeography, paleogeography or biogeography were excluded, since these studies deal with phylogenetic relationships between populations/subspecies, referring to isolation on a much longer temporal scale, and may not be informative in the context of contemporary animal movement.

We found 108 papers had a wildlife connectivity focus, and 36 of these were related to species other than mammals, while another 19 were species-independent connectivity studies. Our final dataset consisted of 53 research papers[7–9,38–87] on terrestrial mammal corridors and connectivity in South Asia. While we have considered these 53 articles to be a representative sample of peer-reviewed research focused on wildlife corridors and connectivity in South Asia over the past 3 decades, we also emphasize that this search may not have captured all the published work on this topic. We have followed the principles of a systematic review while designing our methodology and search string and for this to be a standardised, replicable process we have not included grey literature in our search. From these 53 articles, various fields of data were extracted and tabulated into a spreadsheet (Appendix 1) for further analysis, presented in subsequent sections.

3 Results and Discussion

3.1 Overview

First, we present an overview of the literature in terms of (a) regional distribution, (b) species studied, and (c) the geographical scale of the analysis.

Regional distribution: At a national level, India ($n=45$) had considerably more studies than the other South Asian nations, followed by Nepal (10), Pakistan (3) and Afghanistan, Bhutan and Bangladesh (1 each). Our search yielded no studies for the island nations of the Maldives or Sri Lanka, even though Sri Lanka harbours 126 mammalian species of which 97 are terrestrial[88].

We also classified studies from a biogeographic perspective of landscapes that most studies attributed themselves to, presented in Fig. 2. The Central Indian Landscape and The Terai Arc Landscape (across India and Nepal) are the most studied. While these are recognised as important regions for tiger conservation, connectivity research does not map onto the broader conservation priority landscapes from a scheme such as the biodiversity hotspots[89] with comparatively lower research in the Western Ghats–Sri Lanka and Indo-Burma (Northeast India) hotspots.

Species: Connectivity studies were found to have been conducted for a total of 18 terrestrial mammal species (Fig. 3). This accounts for only 3.7% of the total number of terrestrial mammal species in South Asia[90]. Further, tigers (27) and Asian elephants (9) account for 68% of all the studies, which could in part be on account of their relatively large home ranges, but there remains a significant bias against other less charismatic wide-ranging terrestrial mammal species also threatened by habitat fragmentation, which is similar to other global trends in conservation research in general[23]. Three studies adopted a multi-species modelling approach[44,67,81].

Scale: Ten papers studied single corridors, while the majority, 75% ($n=40$) assessed connectivity at the landscape scale (landscapes encompass multiple corridors). Only three papers conducted country-wide studies looking at multiple (tiger) landscapes in India for identification of conservation priorities.

3.2 Varying Approaches to Connectivity and Associated Limitations

There is a wide range of approaches to studying connectivity, making any classification or clustering of these studies a challenge. We identified three thematic areas based on the objectives and focus of the studies: (i) evidence of use—studies that validated potential corridors or established use of known corridors ($n=8$), (ii) population genetics—studies that used genetic tools to study gene flow, migration rates, clustering or isolation of populations ($n=15$) and (iii) connectivity modelling—studies that quantified connectivity, investigated drivers of connectivity patterns and identified corridors ($n=32$), which can further be split into (a) structural connectivity, (b) potential (functional) connectivity and (c) realised (functional) connectivity (Fig. 4).

(i) Evidence of use: These studies ($n=8$) had the explicit objective of documenting wildlife use of corridors. Seven of the studies relied on information from camera traps and sign surveys to validate the use of the corridor by one or more species. There was again a species bias: five related to tigers, one elephant, one tiger and elephant, and one fishing cat. They noted the presence/absence of the species, while two studies estimated occupancy in the corridor based on camera trapping surveys. One used conflict locations, indirect signs, and the tracking of individuals to assess the use of a trans-border corridor between India and Bangladesh[60].

The key limitation of these studies is that they restrict their investigations to an area assumed a priori to be a corridor, without clearly defining the geographic area or looking for evidence of use outside its assumed boundaries.

(ii) Population Genetics: Studies assigned to this thematic group primarily examined population genetic structure, calculated heterozygosity-based statistics, and investigated the presence of migrants in the populations sampled. Such studies provide useful information on how heterozygosity is partitioned in space and help in the identification of isolated and/or inbred populations. Some studies explicitly modelled gene flow and identified more and less connected populations. A few studies interpreted this in the light of identified structural corridors or change in landscape over time[8,53]. However, the lack of landscape information in these studies makes them less useful for the identification of potential corridors or any kind of on-ground spatial conservation planning. Nevertheless, the lack of directly actionable conservation insights is not necessarily a shortcoming, since the studies did not claim to provide specific insights for conservation planning.

(iii) Connectivity Modelling: Studies assigned to this theme constituted the majority of published research on connectivity (58% of studies), and was further grouped into studies that (a) investigated *structural connectivity* using physical attributes of the landscape, based on maps alone, to determine connectivity ($n=3$); (b) modelled *potential connectivity* ($n=20$) using information on landscape configuration, species distribution, habitat use, and expert opinion to predict linkages or connectivity; and (c) those that modelled *realised connectivity* ($n=8$), using information on animal movement from telemetry or gene flow to investigate connectivity.

Structural connectivity studies used information on vegetation and other land use features to visually identify connectivity and potential corridors[68,72,86].

Potential connectivity studies were largely motivated by the goal of identifying potential movement corridors for the study species (19/20). These studies predominantly (16/20) used a resistance-surface-based modelling approach, which assigns resistance values to landscape features based on whether they impede or facilitate movement[91]. Parameterisation of the resistance

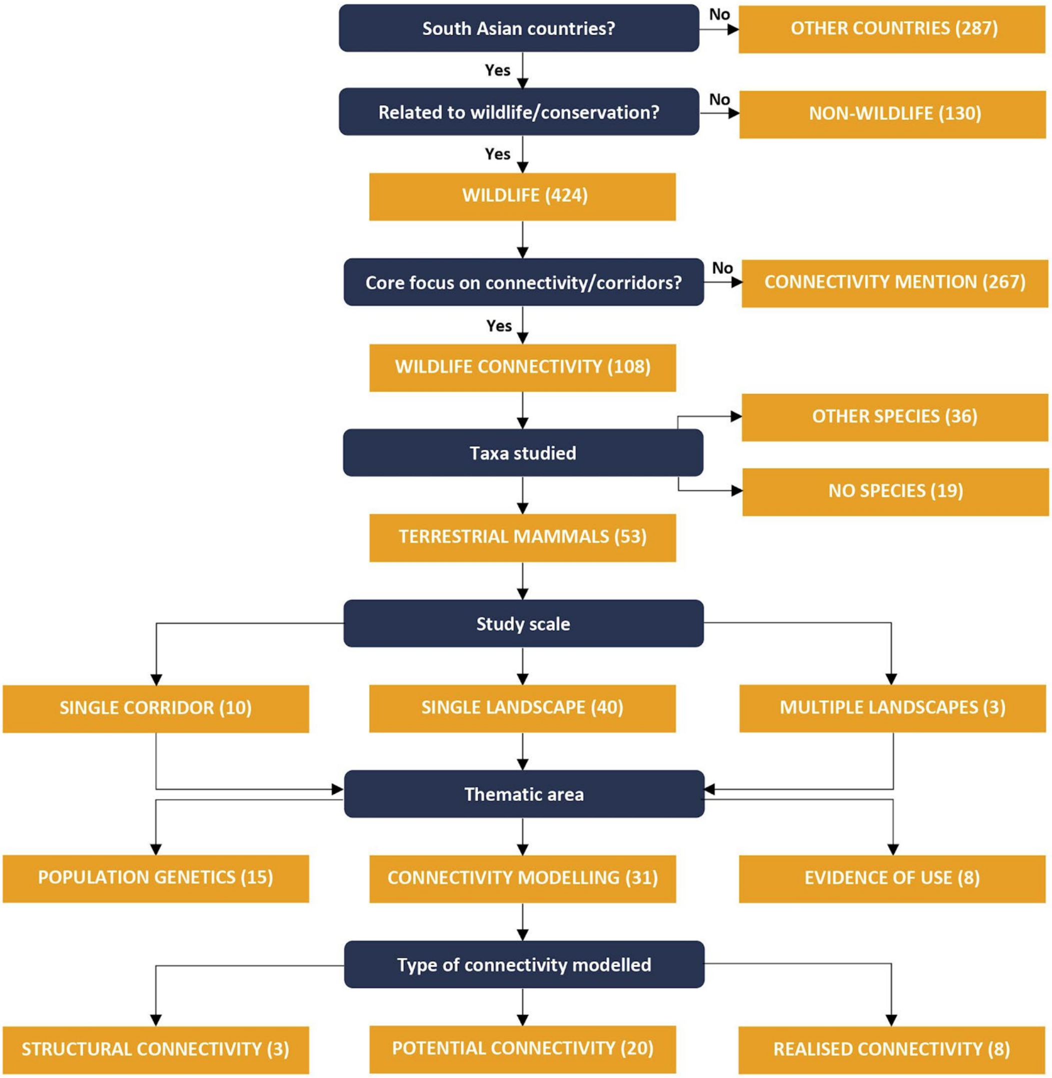

Figure 1: Flowchart followed for the tagging process for all studies in our search ($n = 841$), criteria for tag in blue box and ensuring logical tag given in yellow. Numbers in brackets signify the total number of studies given the respective tag.

surface in these studies is vital, but was invariably not based on real-world movement data. In our dataset, ten of sixteen studies assigned resistance values based on habitat suitability modelling, while others used expert opinion, movement behaviour, habitat use and occupancy, and one study did not specify the basis for assigning resistance values. Habitat suitability modelling (HSM) is usually carried out using animals' presence locations within their home range and often unmodified habitat. It is used for parameterizing a resistance surface based on the assumption that suitable habitat approximates conditions suitable for successful dispersal. However, several studies show that dispersing individuals move through the landscape very differently, compared to movement within their home range[14,92,93]. A study on brown bears in the Carpathians, for example, found habitat suitability models underestimated bear connectivity, as they predicted substantially higher resistance values for most non-habitat areas[33].

Based on the resistance surface, corridors were identified using various approaches such as circuit theory-based modeling[94] ($n = 8$), least cost path (LCP) algorithms ($n = 6$), least cost resistant kernel approach ($n = 3$) and individual-based movement model ($n = 1$). Least cost methods (LCM) evaluate a resistance surface to determine the lowest cumulative resistance to travel between

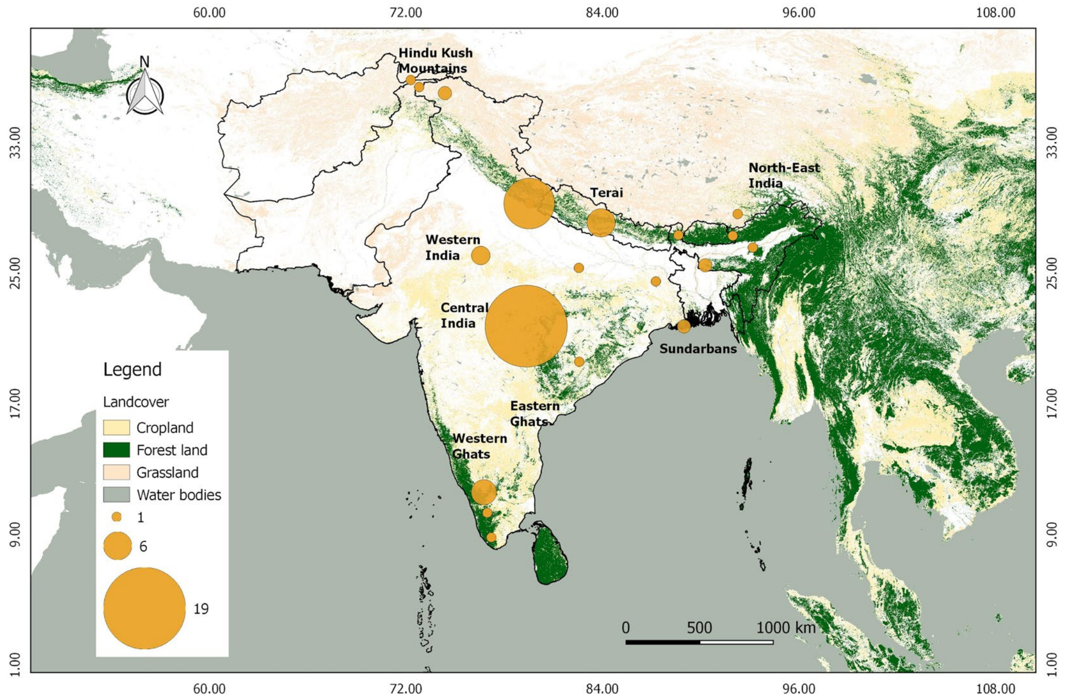

Figure 2: Map showing the distribution of the 53 studies reviewed across different sub-regions in South Asia (created using QGIS v2.18.25).

source and destination[30,95]. LCM assumes that an animal has complete knowledge of the landscape and is likely to follow the shortest path based on resistance through the landscape[91]. However, they have been criticized as they emphasize corridors as relatively simple paths by only representing a line between two points, whereas animals are highly unlikely to follow these exact trajectories[96]. This is especially pertinent because corridors sometimes exist in an extensive matrix of agriculture, and wildlife use these areas widely, relying on myriad pathways to disperse[12]. Least-cost-resistant kernel approach involves the identification of the least cost path with resistant kernel buffering. An advantage of this approach is that it includes dispersal thresholds that limit the calculation of paths between nodes to a specified threshold representing the dispersal ability of the species[15]. While circuit theory is a more holistic landscape-level analysis, it does not incorporate any data on dispersal ability and the output visualisations are not easily actionable in terms of conservation strategies to preserve connectivity since they lack explicit boundaries. However, Circuitscape output accounts for multiple movement pathways and varying degrees of corridor use across the landscape[97], and in combination with on-the-ground validation of use, circuit theory-based output can be used to define boundaries and even investigate multiple corridor routing options.

Four studies did not use a resistance-based modelling approach. Two of them identified corridors visually, based on habitat suitability modelling and a combination of visual evaluation of structural connectivity, expert opinion and some direct observations[39,56]. One used a game theory and graph theory-based modeling approach and provided a basic computational framework for designing corridors, though the approach needs further refinement for conservation application[38]. Another used a novel dynamic occupancy modelling approach to understand potential connectivity. While it does not incorporate actual movement data, it estimates the probability of persistence over space between habitat patches using animal space-use data and provides a robust way to measure potential connectivity[87].

Realised connectivity ($n=8$) studies were largely motivated by the need to understand how various landscape features impacted dispersal (6/8 studies), and advocated the use of rigorous/advanced methods[65,75]. These studies used animal movement data (genetic, radio-telemetry, etc.) to identify the degree of resistance offered by different land use features and then visualize this on a map to indicate areas of low to high resistance. All realised connectivity studies in our

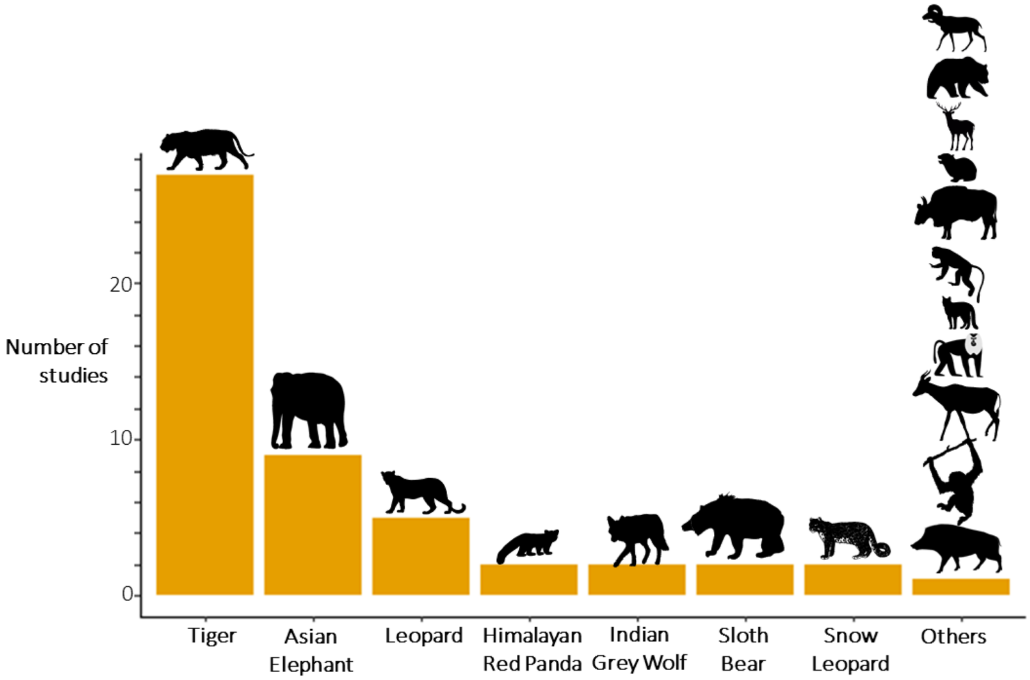

Figure 3: Histogram showing species-wise distribution of studies. All species encountered only once are indicated above the last bar—Argali (*Ovis ammon*), Brown bear (*Ursus arctos*), Chital (*Axis axis*), Fishing cat (*Prionailurus viverrinus*), Gaur (*Bos gaurus*), Himalayan langur (*Semnopithecus schistaceus*[80]), Jungle cat (*Felis chaus*), Lion-tailed macaque (*Macaca silenus*), Nilgai (*Boselaphus tragocamelus*), Western hoolock gibbon (*Hoolock hoolock*), and Wild boar (*Sus scrofa*), from top to bottom. One of the studies[72] does not specifically study any species and has, therefore, not been considered for this figure. Silhouettes are from phylopic.org.

dataset evaluated the impact of landscape features and generated resistance surfaces, but only two of them identified corridors. The other six had the relevant information and a basis to identify corridors/connectivity spaces, but their objective was to investigate the impact of landscape features like human settlements, agriculture, roads, etc. on connectivity. Overall, these studies that generate information on how human-made landscape features impede or facilitate the movement of animals have much greater conservation applicability.

We observed a trend in the realised connectivity studies. Earlier studies tested the impact of landscape features by correlating genetic and resistance distance between populations. In these studies, resistance was parameterized based on knowledge of the species, occupancy data and habitat suitability modelling. Some recent studies have integrated telemetry data with connectivity modelling and lately, a few studies have used genetic data as a response variable to infer the resistance of landscape features using multivariate optimization approaches.

Connectivity research for terrestrial mammals has progressively increased in India over the past decade, largely represented by potential connectivity studies. Most potential connectivity studies, however, have used habitat suitability modelling, which unfortunately is unlikely to capture conditions suitable for successful dispersal. Effective planning for connectivity conservation needs a reliable understanding of the processes that shape connectivity patterns, how matrix or landscape features impact dispersal and use that information to identify areas between habitat patches that need to be conserved to maintain connectivity. With the lack of movement data in most potential connectivity studies and likely bias of the habitat suitability modelling towards underestimating connectivity, there is a risk of misleading inferences and inefficient connectivity planning.

3.3 Conservation Implications

One of the fundamental challenges associated with connectivity research is the translation of science-based connectivity research into conservation prioritization of regions or corridor

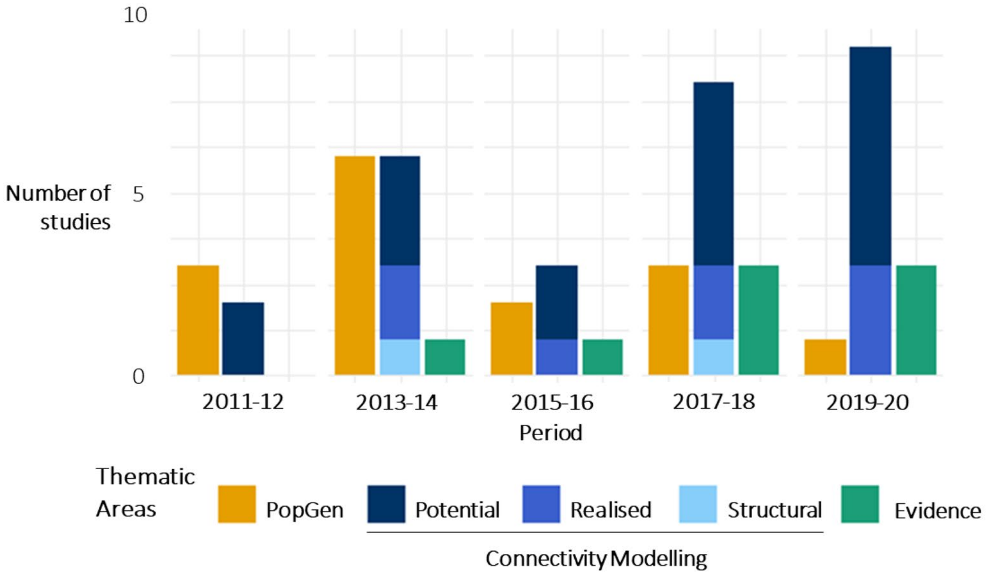

Figure 4: Histogram showing the distribution of studies in the five thematic areas across different time periods.

areas[98,99], often referred to as the research-implementation gap. Overall, the reviewed studies identified conservation implications arising from their results, ranging from broad guidelines to more specific suggestions. However, none of the reviewed studies went on to identify mechanisms for implementation of their recommendations. Although successful conservation action must integrate connectivity research with multiple other elements including land-use planning and zonation, mitigation of conflict, stakeholders' feedback, and other social and economic considerations, it was beyond the scope of the connectivity studies we surveyed. Only a small subset of studies dealt with specific conservation issues and identified specific measures to remedies, such as mitigating the impact of identified barriers or restoring connectivity[68,75]. We note, however, that the current study does not include grey literature such as conservation reports and policy documents, thus precluding us from comprehensively discussing conservation applications of the surveyed connectivity literature.

Mismatch in the scale of the research study and management targets further hinders the application of scientific recommendations. Connectivity studies are typically conducted at the landscape scale, sometimes even across multiple geographies, political boundaries and communities. But management remains largely at a very local scale, of one management unit/PA. Policy documents, such as the Indian National Wildlife Action Plan (2017–31) (https://wii.gov.in/nwap_2017_31), that emphasizes the need for landscape-scale planning (with a focus on mapping and monitoring of wildlife corridors between PAs), and the Bhutan Biological Conservation Complex, a landscape conservation initiative, along with Bhutan's national connectivity legislation[100], may pave the way for easier implementation of connectivity science. Another challenge is that research outcomes are often several steps away from implementation. For instance, connectivity modelling studies usually require rigorous on-ground validation to verify corridor use by the study species thus establishing functional connectivity. Yet, the majority of validation studies fall short in terms of design; they are carried out within "known" corridors, ignoring the movement of individuals in surrounding areas. We hope future studies are based on more robust study design, in ways that can inform management of policy decisions related to corridors.

4 Future Directions

The past few decades have seen a shift in the conceptual underpinnings of connectivity from a primarily landscape characteristics-focused approach (structural connectivity), to one incorporating species- and individual-specific responses to the landscape (functional connectivity)[25,101–103]. Effective dispersal is a complex interplay between the individual/species' dispersal ability and its interaction with the landscape[104,105]. However, predicting how dispersing individuals may move through a heterogeneous landscape remains a challenging task and studies often only partially account for species behaviour while studying functional connectivity[106,107]. Advancements in methods and incorporation of animal movement data increasingly enable the modelling of functional connectivity with more accurate predictions[87,102,108,109]. Adopting improved methods with better accuracy in identifying movement areas/corridors, or realised connectivity, must therefore be a priority.

Telemetry data clearly provides one of the best ways to estimate landscape resistance, since it is based on real-world animal movement paths. However, this data is still hard to obtain given the large number of field constraints, and only one study in our dataset used telemetry data, where it had six dispersal paths from four individuals[65]. High costs and frequent collar failures often result in insufficient sample sizes, poorer study design and weaker statistical inferences[110]. However, newer biotelemetry approaches and biologging devices, with enhanced spatial and temporal resolution in measurement of animal movement, are making it increasingly possible to investigate fine-scale space use by animals[111]. Biologging devices, with accelerometers and a variety of sensors (that can not only detect location but also measure heart rate, blood pressure, etc.), can provide fine resolution spatiotemporal data that can provide insights to understand behavioural and physiological response of species to the environment during dispersal[112–114]. Development of communication technology with high precision and transmission ability, miniaturization of digital sensors, improved data management tools and advances in analysing movement data are likely to make bio-logging and telemetry-based tools more accessible for connectivity studies in the near future[109].

Landscape genetics remains one of the best avenues for investigating functional connectivity and has progressed rapidly since its inception nearly two decades ago[37]. In our review, only seven studies effectively combined and correlated patterns of genetic variation with spatial or landscape data. Globally, however, over 500 landscape genetics studies have been reported between 2011 and 2015[115]. Genetic data provide an indirect way of inferring resistance by reflecting movement that results in successful breeding. Landscape genetics methods are especially useful for species whose movement is difficult to track, as genetic data can be easily generated from non-invasively collected (e.g. hair or scat) samples. With the development of high-throughput next-generation sequencing and reduction in processing costs per sample, generating large amounts of molecular data per individual is now possible and even feasible for non-model organisms. This transition to genome-scale data is helping uncover more fine-scale patterns and additional insights about adaptive genetic variation in wildlife populations and inform their conservation[116]. As this field continues to evolve, there are no 'best practices' yet—from choosing the right measure of genetic differentiation[117] to the selection of the most appropriate analytical approach[118] and the assignment of resistance values to landscape features[119]. With rapidly developing technology and analytical approaches, improved methods are likely to emerge in the near future to better understand landscape genetic pattern–process relationships.

While telemetry and landscape genetic methods may best identify realised functional connectivity, obtaining such data remains challenging, making it more feasible to study potential connectivity. Nonetheless, exploring alternative and innovative approaches to investigate potential connectivity should be favoured instead of the current heavy reliance on HSM + LCP/Circuitscape that we observe in the reviewed literature. Modifications to habitat suitability modelling to identify important habitat patches followed by dynamic occupancy modelling to quantify connectivity and identify corridors[87] or individual (or agent) based modeling[79] that integrates behaviour, dispersal range and movement decisions into modelling connectivity would bring more accuracy to connectivity modelling. Beyond implementing the best methods, it must also be an academic priority to test the validity of the predictions to ensure they are real—through replicated studies in other landscapes, multi-species studies and validation of predicted movement areas through observation data.

We find a significant "charismatic-species" bias in the connectivity literature, with tigers and elephants being the most-studied species. However, conservation strategies based on information from a single species may not effectively capture varied ecological requirements for dispersal of other sympatric species[120,121]. Several opinion pieces emphasize that conservation strategies for a landscape need to factor in the different requirements of multiple species when developing guidelines for landscape-level conservation and management[122,123]. But only three studies in our dataset do this[44,67,81] and relatively few studies globally have studied connectivity for multiple species[124–126]. While understanding multi-species connectivity is critical, using multi-species connectivity data for conservation planning is challenging. Any planning approach that aims to conserve multiple species is likely to be a compromise between what is best for each species individually and what is optimum and feasible when all species are considered together[127]. Only a few studies have tried to incorporate data on multiple species that differ in their connectivity pattern and dispersal ability into conservation planning exercises[124,127,128]. As generalization across species can be a challenge, there is growing interest in species-agnostic approaches for large-scale land-use and connectivity planning[129]. There are no studies in South Asia that have used a species-agnostic modelling approach. Although potentially useful, such approaches require careful consideration of how the impact of landscape features is defined and parameterized, and rigorous testing to estimate the uncertainty associated with the parametrization[129].

As landscapes and climate continue to change, it will become necessary to account for dynamic changes in connectivity into the future. A recent review examining connectivity studies in the context of climate and land-use change found that globally, studies included climate change in connectivity design more often than land-use change[130]. Our dataset had one study that investigated the impact of climate change on connectivity for brown bears. Such research is necessary to facilitate the development of adaptive planning and strategies in the context of future climate change. One study in our dataset investigated how connectivity might change in the face of future development[9], but did not factor in climate change. We found no studies that investigated the combined impacts of climate and land-use change in South Asia. In a rapidly changing landscape, such studies are important to develop adaptive conservation strategies and prevent isolation of habitat and accumulation of extinction debt in the future. Along with understanding how future change is likely to impact connectivity, an adaptive and dynamic planning approach is required, which in turn requires continuous monitoring and analysis of implementation actions and strategies[131,132]. Along with considering dynamic models for the seasonality and variation in the behaviour of dispersing animals[133], researchers are also recognizing that human activity in landscapes can also be modelled to better inform conservation practice or landscape modeling[134].

A starting point to include the human dimension of connectivity is to consider how the impact of human behaviour or activity could be assessed and how it can be assigned a resistance score in circuit theory-based modelling exercises[134] or an interaction rule for agent-based modelling exercises. In South Asian countries, understanding social resistance to animal movement will be important in human-dominated landscapes with high biodiversity and global conservation importance. Studying social resistance also supports the paradigm shift in connectivity science from predominantly structural preservation of habitats to managing functionally connected populations with many dynamic aspects to consider—human behaviour being one such aspect. In the landscapes of tomorrow, the perspective of viewing connectivity from a functional and dynamic lens will bode well for the conservation of endangered wildlife alongside multitudes of developing and vulnerable human communities. A vision that is already present across much of South Asia.

5 Conclusion

Connectivity is clearly a priority for wildlife conservation, and the literature on the subject is growing. In this review, we have analysed the trends in the literature, identified gaps and future directions.

In summarizing our key findings: first, in terms of an overview, there is a growing interest in connectivity as evident in the rate of publications, but only a fraction of studies that mention connectivity actually study this for terrestrial mammals (53 out of 375), with a significant bias towards charismatic megafauna and their habitats. Second, and perhaps most importantly, is that habitat suitability modelling is growing in popularity, but there is a dearth of animal movement data, without which studies significantly fall short of capturing functional connectivity. More data on how animals move through anthropogenic landscapes is vital in better understanding dispersal and connectivity. Genetic tools offer significant opportunities in the future, to non-invasively and cost-efficiently glean insights into animal movement. Third, there is a research-implementation gap, where the majority of studies do not aim to identify actionable conservation outcomes, resulting in a knowledge gap in managing regions outside of formal conservation zones to ensure long-term connectivity. Fourth is a gap in the human dimensions, to understand anthropogenic impacts on animal movement in terms of development trajectories[9], as well as human culture and tolerance to wildlife[135–137].

South Asia is comparable to other biodiverse regions in the world but is unique in the extent and intensity of human pressures on these conservation landscapes. This context of shared human–wildlife spaces has allowed research from South Asia to offer key insights into bridging the nature–society dichotomy by bringing human dimensions into ecology[138] and "re-imagining wilderness" to be more human-inclusive[139]. Co-adaptation is a key to successful coexistence[140], where research from South Asia highlights that animals are adapting to living in modified landscapes in multiple ways[141,142], which are vital for long-term connectivity. The literature is evolving, land-use changes are being included in connectivity science, with emerging work in not just individual animal behaviour but also human behaviour. The pressure and focus on shared human–wildlife spaces is also an opportunity to explore this frontier further, to provide insights for connectivity and conservation outside PAs as similar contexts emerge in other parts of the world in the future.

Publisher's Note

Acknowledgements

We would like to thank Pranav Chanchani and Jared Margulies for their informal comments, as well as two anonymous reviewers whose extensive feedback significantly improved the manuscript. We also thank Mansi Monga for data management work during this review to classify a subset of the papers with appropriate tags. Finally, the Coalition for Wildlife Corridors for playing a key role in bringing some of us together to work on this review.

Declarations

Conflict of interest

We declare that we do not have any conflict of interest.

Supplementary Information

Below is the link to the electronic supplementary material.Supplementary file1 (XLSX 14 kb).

Received: 25 February 2021 Accepted: 5 May 2021

References

1. Keeley ATH, et al (2019) Thirty years of connectivity conservation planning: an assessment of factors influencing plan implementation. Environ Res Lett 14(10):103001
2. Steffen W, Grinevald J, Crutzen P, McNeill J (2011) The anthropocene: conceptual and historical perspectives. Philos Trans R Soc Math Phys Eng Sci 369:842–867
3. Dirzo R et al (2014) Defaunation in the Anthropocene. Science 345:401–406
4. Brodie JF et al (2016) Connecting science, policy, and implementation for landscape-scale habitat connectivity: corridor science and policy. Conserv Biol 30:950–961
5. Brooks TM et al (2004) Coverage provided by the global protected-area system: is it enough? Bioscience 54:1081
6. Nayak R, et al (2020) Bits and pieces: forest fragmentation by linear intrusions in India. Land Use Policy 99(C):104619
7. Dutta T, Sharma S, Maldonado JE, Panwar HS, Seidensticker J (2015) Genetic variation, structure, and gene flow in a sloth bear (Melursus ursinus) meta-population in the satpura-maikal landscape of Central India. PloS One 10(5):e0123384
8. Sharma S et al (2013) Forest corridors maintain historical gene flow in a tiger metapopulation in the highlands of central India. Proc R Soc B Biol Sci 280:14
9. Thatte P, Joshi A, Vaidyanathan S, Landguth E, Ramakrishnan U (2018) Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations. Biol Conserv 218:181–191
10. Díaz S et al (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES secretariat, Bonn, Germany
11. Chapron G et al (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346:1517–1519
12. Warrier R, Noon BR, Bailey L (2020) Agricultural lands offer seasonal habitats to tigers in a human-dominated and fragmented landscape in India. Ecosphere 11:e03080
13. Moritz C (2002) Strategies to Protect Biological Diversity and the Evolutionary Processes That Sustain It. Syst Biol 51:238–254
14. Keeley ATH, Beier P, Keeley BW, Fagan ME (2017) Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. Landsc Urban Plan 161:90–102
15. Diniz MF, Cushman SA, Machado RB, Júnior PDM (2020) Landscape connectivity modeling from the perspective of animal dispersal. Landsc Ecol 35:41–58

16. Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landsc Ecol 27:777–797
17. Fletcher RJ, Burrell NS, Reichert BE, Vasudev D, Austin JD (2016) Divergent perspectives on landscape connectivity reveal consistent effects from genes to communities. Curr Landsc Ecol Rep 1:67–79
18. Kumar D, Scheiter S (2019) Biome diversity in South Asia - How can we improve vegetation models to understand global change impact at regional level? Sci Total Environ 671:1001–1016
19. Nagendra H (2009) Reforestation and regrowth in the human dominated landscapes of South Asia. In: Nagendra H, Southworth J (eds) Reforesting Landscapes. Springer, New York, pp 149–174
20. DeFries R, Pandey D (2010) Urbanization, the energy ladder and forest transitions in India's emerging economy. Land Use Policy 27:130–138
21. Nagendra H, Sudhira H S, Katti M, Tengo M, Schewenius M (2014) Urbanization and its impacts on land use, biodiversity and ecosystems in India. INTERdisciplina 2:169–178
22. Narain V, Vij S (2016) Where have all the commons gone? Geoforum 68:21–24
23. Donaldson MR, et al (2017) Taxonomic bias and international biodiversity conservation research. FACETS 1:105–113
24. Di Marco M et al (2017) Changing trends and persisting biases in three decades of conservation science. Glob Ecol Conserv 10:32–42
25. Tischendorf L, Fahrig L (2000) On the usage and measurement of landscape connectivity. Oikos 90:7–19
26. Taylor P, Fahrig L, With K (2006) Landscape connectivity: a return to the basics. Conserv Biol 14:29–43
27. Calabrese JM, Fagan WF (2004) A comparison-shopper's guide to connectivity metrics. Front Ecol Environ 2:529–536
28. McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724
29. Spear SF, Cushman SA, McRae BH (2016) Resistance surface modeling in landscape genetics. In: Balkenhol N, Cushman S, Storfer A, Waits L (eds) Landscape genetics: concepts, methods, applications. Wiley, New York, pp 129–148
30. Beier P, Majka DR, Newell SL (2009) Uncertainty analysis of least-cost modeling for designing wildlife linkages. Ecol Appl 19:2067–2077
31. Alexander JL, Olimb SK, Bly KL, Restani M (2016) Use of least-cost path analysis to identify potential movement corridors of swift foxes in Montana. J Mammal 97:891–898
32. Hirzel AH, Le Lay G (2008) Habitat suitability modelling and niche theory. J Appl Ecol 45:1372–1381
33. Ziółkowska E et al (2016) Assessing differences in connectivity based on habitat versus movement models for brown bears in the Carpathians. Landsc Ecol 31:1863–1882
34. Bunn AG, Urban DL, Keitt TH (2000) Landscape connectivity: a conservation application of graph theory. J Environ Manage 59:265–278
35. Kindlmann P, Burel F (2008) Connectivity measures: a review. Landsc Ecol 23:879–890
36. Godet C, Clauzel C (2021) Comparison of landscape graph modelling methods for analysing pond network connectivity. Landsc Ecol 36:735–748
37. Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol 18:189–197
38. Shanu S et al (2019) A graph theoretic approach for modelling tiger corridor network in Central India-Eastern Ghats landscape complex, India. Ecol Inform 50:76–85
39. Baskaran N, Kannan G, Anbarasan U, Thapa A, Sukumar R (2013) A landscape-level assessment of Asian elephant habitat, its population and elephant-human conflict in the Anamalai hill ranges of southern Western Ghats India. Mamm Biol 78:470–481
40. Mukherjee T, et al (2021) Adaptive spatial planning of protected area network for conserving the Himalayan brown bear. Sci Total Environ 754:142416
41. Wegge P, Yadav SK, Lamichhane BR (2018) Are corridors good for tigers Panthera tigris but bad for people? An assessment of the Khata corridor in lowland Nepal. Oryx 52:35–45
42. Thapa K, et al (2018) Assessment of genetic diversity, population structure, and gene flow of tigers (Panthera tigris tigris) across Nepal's Terai Arc Landscape. PloS One 13(3):e0193495
43. Borah J, Jena J, Yumnam B, Puia L (2016) Carnivores in corridors: estimating tiger occupancy in Kanha-Pench corridor, Madhya Pradesh India. Reg Environ Change 16:43–52
44. Thapa A, et al (2017) Combined land cover changes and habitat occupancy to understand corridor status of Laljhadi-Mohana wildlife corridor, Nepal. Eur J Wildl Res 63:83
45. Dutta T, Sharma S, McRae BH, Roy PS, DeFries R (2016) Connecting the dots: mapping habitat connectivity for tigers in central India. Reg Environ Change 16:53–67
46. Joshi A, Vaidyanathan S, Mondol S, Edgaonkar A, Ramakrishnan U (2013) Connectivity of tiger (*Panthera tigris*) populations in the human-influenced forest Mosaic of Central India. PloS One 8(11):e77980
47. Natesh M, et al (2017) Conservation priorities for endangered Indian tigers through a genomic lens. Sci Rep 7:9614
48. Mondol S, Bruford MW, Ramakrishnan U (2013) Demographic loss, genetic structure and the

conservation implications for Indian tigers. Proc R Soc B Biol Sci 280:20130496

49. Dalui S. et al (2020) Fine-scale landscape genetics unveiling contemporary asymmetric movement of red panda (*Ailurus fulgens*) in Kangchenjunga landscape, India. Sci Rep 10:15446
50. Dutta T et al (2013) Fine-scale population genetic structure in a wide-ranging carnivore, the leopard (*Panthera pardus fusca*) in central India. Divers Distrib 19:760–771
51. Singh SK, et al (2017) Fine-scale population genetic structure of the Bengal tiger (*Panthera tigris tigris*) in a human-dominated western Terai Arc Landscape, India. PloS One 12(4):e0174371
52. Anwar M, Borah J (2019) Functional status of a wildlife corridor with reference to tiger in Terai Arc Landscape of India. Trop Ecol 60:525–531
53. Dutta T et al (2013) Gene flow and demographic history of leopards (*Panthera pardus*) in the central Indian highlands. Evol Appl 6:949–959
54. Reddy PA, et al (2012) Genetic evidence of tiger population structure and migration within an isolated and fragmented landscape in Northwest India. PloS One 7(1):e29827
55. Sharma R et al (2011) Genetically distinct population of Bengal tiger (*Panthera tigris tigris*) in Terai Arc Landscape (TAL) of India. Mamm Biol 76:484–490
56. Areendran G et al (2011) Geospatial modeling to assess elephant habitat suitability and corridors in northern Chhattisgarh India. Trop Ecol 52:275–283
57. Kabir M, et al (2017) Habitat suitability and movement corridors of grey wolf (*Canis lupus*) in Northern Pakistan. PloS One 12(11):e0187027
58. Luikart G et al (2011) High connectivity among argali sheep from Afghanistan and adjacent countries: inferences from neutral and candidate gene microsatellites. Conserv Genet 12:921–931
59. Kenney J, Allendorf FW, McDougal C, Smith JLD (2014) How much gene flow is needed to avoid inbreeding depression in wild tiger populations? Proc R Soc B Biol Sci 281:20133337
60. Talukdar NR, Choudhury P, Ahmad F, Al-Razi H, Ahmed R (2020) Mapping and assessing the transboundary elephant corridor in the Patharia Hills reserve forest of Assam India. Rangel Ecol Manag 73:694–702
61. Sharma LK, Mukherjee T, Saren PC, Chandra K (2019) Identifying suitable habitat and corridors for Indian Grey Wolf (*Canis lupus pallipes*) in Chotta Nagpur Plateau and Lower Gangetic Planes: a species with differential management needs. PloS One 14(4):e0215019
62. Sarkar MS et al (2018) Multiscale statistical approach to assess habitat suitability and connectivity of common leopard (*Panthera pardus*) in Kailash Sacred Landscape India. Spat Stat 28:304–318
63. Rathore CS, Dubey Y, Shrivastava A, Pathak P, Patil V (2012) Opportunities of habitat connectivity for tiger (*Panthera tigris*) between Kanha and Pench National Parks in Madhya Pradesh, India. PloS One 7(7):e39996
64. Rameshan M, Roy A, Ramasamy EV (2014) Identification of potential elephant corridor between Anamalai landscape and Periyar tiger reserve, southern western Ghats: a geospatial approach. Int J Geoinform 10:41–52
65. Krishnamurthy R et al (2016) Multi-scale prediction of landscape resistance for tiger dispersal in central India. Landsc Ecol 31:1355–1368
66. Hameed S, et al (2020) Identifying priority landscapes for conservation of snow leopards in Pakistan. PloS One 15(11):e0228832
67. Gangadharan A, Vaidyanathan S, St. Clair CC (2017) Planning connectivity at multiple scales for large mammals in a human-dominated biodiversity hotspot. J Nat Conserv 36: 38–47
68. Anitha K et al (2013) Identifying habitat connectivity for isolated populations of lion-Tailed Macaque (*Macaca silenus*) in Valparai Plateau, Western Ghats India. Primate Conserv 27:91–97
69. Tobgay S, Mahavik N (2020) Potential habitat distribution of Himalayan red panda and their connectivity in Sakteng Wildlife Sanctuary Bhutan. Ecol Evol. https://doi.org/10.1002/ece3.6874
70. Puyravaud J-P, Cushman SA, Davidar P, Madappa D (2017) Predicting landscape connectivity for the Asian elephant in its largest remaining subpopulation. Anim Conserv 20:225–234
71. Yumnam B, et al (2014) Prioritizing tiger conservation through landscape genetics and habitat linkages. PloS One 9(11):e111207
72. Goparaju L, Ahmad F, Sinha D (2018) Spatial analysis of wildlife habitat around Madihan forests of Mirzapur district, Uttar Pradesh in India, using geospatial technology. Folia For Pol Ser A 60:73–79
73. Sharma S et al (2013) Spatial genetic analysis reveals high connectivity of tiger (*Panthera tigris*) populations in the Satpura-Maikal landscape of Central India. Ecol Evol 3:48–60
74. Reddy PA, Puyravaud J-P, Cushman SA, Segu H (2019) Spatial variation in the response of tiger gene flow to landscape features and limiting factors. Anim Conserv 22:472–480
75. Dutta T, Sharma S, DeFries R (2018) Targeting restoration sites to improve connectivity in a tiger conservation landscape in India. PeerJ 6:e5587
76. Reddy PA, Cushman SA, Srivastava A, Sarkar MS, Shivaji S (2017) Tiger abundance and gene flow in Central India are driven by disparate combinations of topography and land cover. Divers Distrib 23:863–874
77. Thapa K, et al (2017) Tigers in the Terai: strong evidence for meta-population dynamics contributing to tiger recovery and conservation in the Terai Arc Landscape. PloS One 12(6):e0177548

78. Singh R, Qureshi Q, Sankar K, Krausman PR, Goyal SP (2013) Use of camera traps to determine dispersal of tigers in semi-arid landscape, western India. J Arid Environ 98:105–108
79. Kanagaraj R, Wiegand T, Kramer-Schadt S, Goyal SP (2013) Using individual-based movement models to assess inter-patch connectivity for large carnivores in fragmented landscapes. Biol Conserv 167:298–309
80. Bagaria P, et al (2020) West to east shift in range predicted for Himalayan Langur in climate change scenario. Glob Ecol Conserv 22:e00926
81. Thatte P et al (2020) Human footprint differentially impacts genetic connectivity of four wide-ranging mammals in a fragmented landscape. Divers Distrib 26:299–314
82. Vasudev D, Fletcher RJ (2015) Incorporating movement behavior into conservation prioritization in fragmented landscapes: an example of western hoolock gibbons in Garo Hills India. Biol Conserv 181:124–132
83. Yadav BP, Appel A, Shrestha BP, Dahal BR, Dhaka M (2020) The fishing cat *Prionailurus viverrinus* (Bennet, 1833) (Mammalia: Carnivora: Felidae) in Shuklaphanta National Park Nepal. J Threat Taxa 12:17203–17212
84. Singh SK et al (2015) Tigers of Sundarbans in India: is the population a separate conservation unit? PloS One 10(4):e0118846
85. Shrestha B, Kindlmann P (2020) Implications of landscape genetics and connectivity of snow leopard in the Nepalese Himalayas for its conservation. Sci Rep 10:19853
86. Kachhwaha TS (1993) Temporal and multisensor approach in forest/vegetation mapping and corridor identification for effective management of Rajaji National Park, Uttar Pradesh India. Int J Remote Sens 14:3105–3114
87. Vasudev D, Goswami VR, Oli MK (2021) Detecting dispersal: a spatial dynamic occupancy model to reliably quantify connectivity across heterogeneous conservation landscapes. Biol Conserv 253:108874
88. Yapa A, Ratnavira G (2015) The mammals of Sri Lanka. Field ornithology group of Sri Lanka, Department of Zoology, Colombo
89. Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858
90. Srinivasulu C, Srinivasulu B (2012) South Asian mammals: their diversity, distribution, and status. Springer, New York
91. Adriaensen F et al (2003) The application of 'least-cost' modelling as a functional landscape model. Landsc Urban Plan 64:233–247
92. Selonen V, Hanski IK (2006) Habitat exploration and use in dispersing juvenile flying squirrels. J Anim Ecol 75:1440–1449
93. Mateo-Sánchez MC et al (2015) Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data. Ecosphere 6:1–16
94. McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. Proc Natl Acad Sci 104:19885–19890
95. Cushman SA, McKelvey KS, Schwartz MK (2009) Use of empirically derived source-destination models to map regional conservation corridors. Conserv Biol 23:368–376
96. Rudnick D, et al. (2012) The role of landscape connectivity in planning and implementing conservation and restoration priorities. Issues in Ecology. Report No. 16. Ecological Society of America, Washington, D.C.
97. Kool JT, Moilanen A, Treml EA (2013) Population connectivity: recent advances and new perspectives. Landsc Ecol 28:165–185
98. Keeley ATH et al (2018) Making habitat connectivity a reality: habitat Connectivity. Conserv Biol 32:1221–1232
99. Arlettaz R et al (2010) From publications to public actions: when conservation biologists bridge the gap between research and implementation. Bioscience 60:835–842
100. Wangchuk S (2007) Maintaining ecological resilience by linking protected areas through biological corridors in Bhutan. Trop Ecol 48:177
101. Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. Oikos 68:571–573
102. Naidoo R et al (2018) Evaluating the effectiveness of local- and regional-scale wildlife corridors using quantitative metrics of functional connectivity. Biol Conserv 217:96–103
103. Day CC, Zollner PA, Gilbert JH, McCann NP (2020) Individual-based modeling highlights the importance of mortality and landscape structure in measures of functional connectivity. Landsc Ecol 35:2191–2208
104. Baguette M, Van Dyck H (2007) Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landsc Ecol 22:1117–1129
105. Knowlton JL, Graham CH (2010) Using behavioral landscape ecology to predict species' responses to land-use and climate change. Biol Conserv 143:1342–1354
106. Abrahms B et al (2017) Does wildlife resource selection accurately inform corridor conservation? J Appl Ecol 54:412–422
107. Vasudev D, Fletcher RJ Jr, Goswami VR, Krishnadas M (2015) From dispersal constraints to landscape connectivity: lessons from species distribution modeling. Ecography 38:967–978
108. Allen AM, Singh NJ (2016) Linking movement ecology with wildlife management and conservation. Front Ecol Evol 3:155
109. Katzner TE, Arlettaz R (2020) Evaluating contributions of recent tracking-based animal movement ecology to conservation management. Front Ecol Evol 7:519
110. Hebblewhite M, Haydon DT (2010) Distinguishing technology from biology: a critical review of the use of

GPS telemetry data in ecology. Philos Trans R Soc Lond B Biol Sci 365:2303–2312

111. Stewart FE, Darlington S, Volpe JP, McAdie M, Fisher JT (2019) Corridors best facilitate functional connectivity across a protected area network. Sci Rep 9:1–9
112. Wilmers CC et al (2015) The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. Ecology 96:1741–1753
113. McClune DW (2018) Joining the dots: reconstructing 3D environments and movement paths using animal-borne devices. Anim Biotele 6:1–9
114. Fraser KC et al (2018) Tracking the conservation promise of movement ecology. Front Ecol Evol 6:150
115. DiLeo MF, Wagner HH (2016) A landscape ecologist's agenda for landscape genetics. Curr Landsc Ecol Rep 1:115–126
116. Manel S, Holderegger RT (2013) 10 years of landscape genetics. Trends Ecol Evol 28:614–621
117. Shirk AJ, Landguth EL, Cushman SA (2017) A comparison of individual-based genetic distance metrics for landscape genetics. Mol Ecol Resour 17:1308–1317
118. Zeller KA et al (2018) Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. Divers Distrib 24:868–879
119. Peterman WE et al (2019) A comparison of popular approaches to optimize landscape resistance surfaces. Landsc Ecol 34:2197–2208
120. Brodie JF et al (2015) Evaluating multispecies landscape connectivity in a threatened tropical mammal community. Conserv Biol 29:122–132
121. Gangadharan A, Vaidyanathan S, Clair CCS (2016) Categorizing species by niche characteristics can clarify conservation planning in rapidly-developing landscapes. Anim Conserv 19(5):451–461
122. Keller D, Holderegger R, van Strien MJ, Bolliger J (2015) How to make landscape genetics beneficial for conservation management? Conserv Genet 16:503–512
123. Richardson JL, Brady SP, Wang IJ, Spear SF (2016) Navigating the pitfalls and promise of landscape genetics. Mol Ecol 25:849–863
124. Dudaniec RY et al (2016) Dealing with uncertainty in landscape genetic resistance models: a case of three co-occurring marsupials. Mol Ecol 25:470–486
125. Engler JO, Balkenhol N, Filz KJ, Habel JC, Rödder D (2014) Comparative landscape genetics of three closely related sympatric hesperid butterflies with diverging ecological traits. PloS One 9(9):e106526
126. Marrotte RR et al (2017) Multi-species genetic connectivity in a terrestrial habitat network. Mov Ecol 5:1–11
127. Early R, Thomas CD (2007) Multispecies conservation planning: identifying landscapes for the conservation of viable populations using local and continental species priorities. J Appl Ecol 44:253–262
128. Magris RA, Treml EA, Pressey RL, Weeks R (2016) Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. Ecography 39:649–664
129. Marrec R et al (2020) Conceptual framework and uncertainty analysis for large-scale, species-agnostic modelling of landscape connectivity across Alberta, Canada. Sci Rep 10:1–14
130. Costanza JK, Terando AJ (2019) Landscape connectivity planning for adaptation to future climate and land-use change. Curr Landsc Ecol Rep 4:1–13
131. Gregory R, Failing L, Higgins P (2006) Adaptive management and environmental decision making: a case study application to water use planning. Ecol Econ 58:434–447
132. Zeller KA, Lewsion R, Fletcher RJ, Tulbure MG, Jennings MK (2020) Understanding the importance of dynamic landscape connectivity. Land 9:303
133. Osipova L et al (2019) Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons. Anim Conserv 22:35–48
134. Ghoddousi A et al (2021) Anthropogenic resistance: accounting for human behavior in wildlife connectivity planning. One Earth 4:39–48
135. Thekaekara T, Thornton TF (2016) Ethnic diversity and human-elephant conflict in South India. In: Locke P, Buckingham J (eds) Conflict, negotiation, and coexistence: rethinking human-elephant relations in South Asia, 1st edn. Oxford University Press, New Delhi, pp 300–330
136. Inskip C, Carter N, Riley S, Roberts T, MacMillan D (2016) Toward human-carnivore coexistence: understanding tolerance for tigers in Bangladesh. PloS One 11(1):e0145913
137. Bhatia S, Redpath SM, Suryawanshi K, Mishra C (2020) Beyond conflict: exploring the spectrum of human–wildlife interactions and their underlying mechanisms. Oryx 54:621–628
138. Lewis M (2003) Inventing global ecology: tracking the biodiversity ideal in India, 1945–1997. vol. 5. Orient Longman, Hyderabad
139. Bhagwat S (ed) (2018) Conservation and development in India: reimagining wilderness. Routledge, Abingdon
140. Carter NH, Linnell JD (2016) Co-adaptation is key to coexisting with large carnivores. Trends Ecol Evol 31:575–578
141. Srinivasaiah N, Kumar V, Vaidyanathan S, Sukumar R, Sinha A (2019) All-Male groups in Asian elephants: a novel, adaptive social strategy in increasingly anthropogenic landscapes of southern India. Sci Rep 9:1–11
142. Majgaonkar I, et al (2019) Land-sharing potential of large carnivores in human-modified landscapes of western India. Conserv Sci Practi 1(5):e34

Prachi Thatte works on connectivity conservation with WWF-India and also coordinates the Coalition for Wildlife Corridors.

Abhinav Tyagi is a molecular ecologist and PhD scholar at National Centre for Biological Sciences, Bangalore. He is investigating anthropogenic impacts on the connectivity of multiple species of herbivores and carnivores in central India. He is interested in understanding species-specific responses towards habitat fragmentation and also keen on developing novel methods for conservation genomics that enables the use of non-invasive samples for wildlife research.

Amrita Neelakantan coordinates the Network for Conserving Central India. She studies interactions between people and forests in central India.

Meghana Natesh is currently a post-doctoral researcher at the Indian Institute of Science Education and Research (Tirupati) and works on population genomics.

Mihika Sen is a project assistant at The Shola Trust, India. Her research is focused on the mitigation of human–elephant conflict in different parts of India.

Tarsh Thekaekara is a researcher–conservationist interested in conservation beyond protected areas and studies how elephants and people share space. He is a postdoctoral fellow at the National Centre for Biological Sciences and a Trustee of The Shola Trust.