REVIEW



Landscape Connectivity For Wildlife and Water: The State of the Literature

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Accepted: 3 August 2023 / Published online: 9 August 2023 © The Author(s) 2023

Abstract

Purpose of Review The science of landscape connectivity is widely applied to identify corridors for wildlife movement through unprotected areas. Where corridors coincide with forested or vegetated headwater catchments, they can contribute to blue water security for downstream users and recycle precipitation through green water flux to the larger region. This review examines the extent to which hydrology is recognized within studies on wildlife corridors. We illustrate the synergy between wildlife corridors and water security in the Central Indian Highlands, a globally important region for tiger (*Panthera tigris*) conservation and the water tower for five major rivers.

Recent Findings We find that a growing but still minor component of the literature on landscape connectivity addresses hydrology. Out of 127 publications on landscape connectivity that address both hydrology and wildlife, 50% were published after 2015 and hydrology-related words appear more frequently in abstracts over time (27% in 1993–2003 and 45% in 2014–2023 of most frequently used words) The case study illustrates potential synergies for water security and conservation, with areas for wildlife connectivity twice as rugged, three times more forested, and about 1.8 times denser with small streams than other areas in the landscape. About half of the area identified for landscape connectivity overlaps with catchment areas for five major dams. **Summary** Freshwater resources and water security are vital in human-dominated landscapes such as central India. A holistic view of landscape connectivity beyond wildlife provides practitioners with additional rationale for conserving these areas to maintain water resources that are directly relevant to people living in the landscape.

Keywords Central India \cdot Wildlife corridors \cdot Landscape connectivity \cdot Water security \cdot Hydrologic connectivity \cdot Human-dominated landscape \cdot Tigers

This article is part of the Topical Collection on *Landscape Ecological Science from India*

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Introduction

Connectivity arose as a key concept in landscape ecology in the 1990s, originally defined as "the degree to which the landscape facilitates or impedes movement among resource patches" [1]. The concept is now embedded in conservation practice to counterbalance negative effects of habitat fragmentation as people convert land for agriculture, urban areas, mines, and other uses, leaving higher quality patches within a matrix of lower quality habitat. Wildlife corridors are an established approach to maintain movement of plants and animals between patches. Corridors, such as Yellowstone to Yukon and the Terai Arc, facilitate movement of grizzly bears (*Ursus arctos horribilis*) and tigers (*Panthera tigris*), respectively, enable gene flow to retain health of populations and provide migration options in the face of climate change (see [2] for many examples of corridors). In addition to the importance of landscape connectivity for wildlife, corridors also control many other types of biotic and abiotic flows including seed dispersal, fire spread, water flows, pests, and diseases. Some of these flows can be harmful for people such as the spread of fires and disease, while some are beneficial such as surface and groundwater for downstream irrigation, urban water supplies, and other uses. Landscapes that protect high-quality wildlife habitat also protect streams in the watershed against high sediment loads from erosion, contamination from intensive human use, flooding due to rapid runoff from impervious surfaces, and impeded hydrological connectivity [3, 4]. Large forest patches in corridors also recycle evapotranspiration (green water flux) that contributes to precipitation over large regions [5–9].

Water security, particularly in light of increasingly variable and extreme precipitation and unsustainable water withdrawals, is a critical problem in many parts of the world [10]. The Ministerial Conference at the Second World Water Forum, held at The Hague in 2000, defined water security as "ensuring...that every person has access to enough safe water at an affordable cost to lead a healthy and productive life and that the vulnerable are protected from the risks of water-related hazards" [11]. The 2023 Global Commission on the Economics of Water notes that the adequate water provides a "stable foundation for human well-being and ecosystem health, and hence is a necessity for socio-economic and ecological prosperity" [12]. Although economic and political forces are critical to achieve all aspects of water security, healthy vegetation in headwater catchments contributes to water security by promoting hydrologic connectivity, maintaining water quality, reducing sediment generation, cycling precipitation, and enhancing infiltration. In this paper, we adopt the definition of hydrologic connectivity as "the internal linkages between runoff and sediment generation in upper parts of the catchments and the receiving waters" including two types of connectivity: "direct connectivity via new channels or gullies, and diffuse connectivity as surface runoff reaches the stream network via overland flow [13]."

"Water towers"—a symbolic term that underscores the importance of mountain regions in providing freshwater for adjacent areas downstream [14]—are particularly critical in Asia to provide water for lowland agriculture and major population centers [15]. Headwater streams constitute a large proportion of overall stream length in a hydrologic system and can act as the conduit for water flows to lowlands. Vegetation in catchment areas for small streams can curtail soil erosion and provide many other ecosystem services that maintain water supply, aquatic biodiversity, and water quality [16, 17]. Protection of watersheds in the Catskills region, for example, provides clean, unfiltered water for millions of downstream consumers in New York City [18]. In Kenya, the government established the Waters Towers Agency in 2012 to oversee sustainable management of the country's critical water towers in the face of rampant deforestation and declining water resources [17]. In Mumbai, the forests of the Borivali in the Sanjay Gandhi National Park protect water catchments and reservoirs that supply clean drinking water to the mega-city [19].

Wildlife corridors are located where land cover and low human population densities offer low resistance to animal movements. Many wildlife corridors are located in remaining forested areas, which in turn tend to be located in hilly areas, particularly in India (the focus of this special issue) [20]. These upper reaches also serve as water towers that are vital for water security. Consequently, headwaters and wildlife corridors potentially overlap to provide critical services to society.

In this paper, we address the confluence of these two aspects of landscape connectivity—conservation of iconic wildlife and water security. Both relate to the management of landscapes to provide societal needs into the future. If such a synergy holds up to scientific scrutiny, a holistic view of corridors provides policy makers additional rationale for conserving and managing wildlife corridors as hydrologically and hydro-climatologically important for downstream water users.

First, we assess the literature to determine the degree to which hydrologic function is incorporated into research and practice related to wildlife corridors. We then provide a case study from the Central Indian Highlands to assess the utility of wildlife corridors for protecting headwaters for critical rivers and catchment areas for major dams. The Central Indian Highlands and their forests serve as the water tower for five major rivers and 268 reservoirs [21] and recycle moisture to delay the withdrawal of the summer monsoon as well as to support precipitation regionally [22]. The region is also a globally recognized area for tiger conservation [23].

Data and Methods

Bibliometric Analysis

We used the Biblioshiny web interface version 4.0.0 of the bibliometrix library in R [24] to analyze the extent to which the literature addresses overlaps between landscape connectivity for wildlife corridors and for watershed protection. The bibliometrix analysis is used in many publications to assess trends in research fields, e.g., [25, 26] for sustainability-related topics. We accessed the ISI Web of Science database on February 7, 2023 to retrieve metadata for publications in all possible years (1990–2023) for search terms in the category "abstract" [27]. Search terms were "(landscape connectivity OR corridor) AND (wildlife OR biodiversity)," and "("landscape connectivity" OR corridor) AND (hydrology OR watershed)". To identify the publications that address both wildlife/biodiversity and hydrology/ watershed we conducted a search on the term "("landscape connectivity" OR corridor) AND (wildlife OR biodiversity) AND (hydrology OR watershed)." We also checked results from a search with the same criteria in SCOPUS, which produced similar results but fewer and overlapping papers as Web of Science.

For the publications identified through the search that pertain to both wildlife/biodiversity and hydrology/watershed, we utilized Biblioshiny to calculate annual scientific production and to track the focus of these papers over time based on frequency of words in the abstracts. We used Biblioshiny software to identify the top ten words based on frequency in abstracts, then grouped these words depending on whether they pertain to wildlife/biodiversity conservation or watersheds. We report the frequency of these words by decade beginning with the earliest paper identified in the search.

Case Study of Landscape Connectivity in Central Indian Highlands

The Central Indian Highlands exemplifies multiple potential benefits from landscape connectivity for water security and wildlife conservation. As in other parts of India, tiger populations have increased with improved protection over the last decade [28], but mines, roads, urbanization, and other development activities are advancing at a rapid pace to impede connectivity [29]. With the small size of India's protected areas relative to home range sizes of many wildlife species, the habitat matrix outside protected areas plays a major role in the ability of animals to disperse [30]. Wildlife corridors are paramount to the health of the endangered tiger (*Panthera tigris*) and other iconic wildlife populations.

Central India includes the Central Indian Highlands and spans multiple states without a clearly defined boundary, is a globally designated tiger conservation landscape (defined as "areas where there is sufficient habitat for at least five tigers, and tigers have been confirmed in the last ten years") [31]. Central India, which houses approximately 30% of India's tigers, contains four out of seventeen class 1 highest priority tiger conservation landscapes globally [32]. An estimated one-third of wild tigers in central India live outside protected areas [33] within a matrix of forest patches, smallscale farms, villages, and cities. Local livelihoods depend on small-scale agriculture, cattle rearing, and collection of forest products for people living near forested areas [34].

Schoen et al. [23] identified "consensus connectivity areas" in the Central Indian Highlands based on five independent, published studies that mapped corridors in central India based on varying data inputs and model parameters. Competition for land use is acute in the consensus connectivity areas (CCAs). Approximately 70% of the CCAs fall within village administrative boundaries, 16% within 1 km of linear infrastructure, and 78% of forest land diversions for infrastructure and mining in the state comprising the majority of the area (Madhya Pradesh) occurred in districts containing CCAs. All of the land in the CCAs fall within forest department management boundaries [23].

The Central Indian Highlands also serve as the water tower for five of India's major rivers (Ganga, Narmada, Godavari, Mahanadi, and Tapti). Average precipitation is 987 mm per year with nearly all precipitation falling within the monsoon season. Agriculture is the dominant land use and accounts for 95% of total water demand (Fig. 1). There are 17 urban centers with populations greater than 100,000 within the landscape, all of which experience water stress (demand greater than supply) at some time during the year [35]. As irrigation and urban water demand continue to increase, managing land use to maintain flows to reservoirs and to recharge groundwater is critical for water security.

The study extent—the common extent of the five studies on tiger connectivity in the Central Indian Highlands used to generate the CCAs [23]—includes fourteen protected areas (Fig. 1).

The vegetation of the central Indian region plays an important role in regulating and supplying rainfall to ecosystems and people due to the monsoon wind circulation patterns and through recycling of evapotranspiration or green-water. In the central Indian region, precipitation is a factor of at least two greater in air parcels with exposure to large vegetation patches than in air parcels with small exposure [5]. Precipitation from recycled evapotranspiration varies from approximately 20 to more than 200 mm per day during the southwest monsoon. The recycling delays the end or withdrawal of the summer monsoon in September [5–7, 9, 22].

Analysis of Overlap Between Wildlife Corridors and Headwaters in Central India Highlands

For the case study, we overlaid the wildlife corridors with topographic data and the stream network. The wildlife corridors, denoted as consensus connectivity areas (CCAs), were obtained from [23]. We further identified the domain for the case study by drawing a convex hull around the CCAs within the area covered by all five studies. The convex hull excludes parts of the landscapes around the edges that potentially are important for connectivity but are not within the CCAs merely because the studies did not include nodes beyond the boundaries of their study regions. We further clipped the case study domain to include entire watersheds to constrain the comparison of areas within and outside CCAs, using level 12 (highest available) watershed boundaries from HydroBASIN [36].





Fig. 1 Location of study extent (left), land use and land cover (LULC) (1) consensus connectivity (CCA) (2), and major rivers (3) (right)

Ruggedness was determined by R package for terrain ruggedness index based on 30-m resolution elevation data from the ALOS global digital surface model [37]. The stream network was obtained from [36]. Stream order represents Strahler orders in the HydroRivers data set. Land cover data at 10-m resolution was obtained from [38]. Major dams were located from data used in [35].

For this study, we follow [17] to define "headwater streams" as 1^{st} order streams, i.e., the smallest streams

with a defined channel. We define "small streams" as 1st and 2nd order streams together, with 2nd order streams resulting from the confluence of two 1st order streams. We assessed the number of headwater and small streams that overlap the consensus connectivity areas relative to the total number of stream reaches in the domain. For the five largest dams in the case study domain based on surface area, we identify the catchment area by using the HydroSheds raster Layers "HSdrainageUTM" and



Fig. 2 Venn diagram of publications on landscape connectivity identified through Web of Science for "wildlife OR biodiversity" search terms (red) and "hydrology OR watershed" search terms ("yellow") and overlap for search term "("landscape connectivity" OR corridor) AND (wildlife OR biodiversity) AND (hydrology OR watershed)." Searches were conducted on abstracts for all dates in the database

"HSstreamUTM." We then determined the outlet point of a dam that coincided with the stream layer and noted its coordinates. We used the 'r.water.outlet' tool and loaded HSdrainageUTM as input along with the coordinates of the identified outlet point to generate the catchment area for each dam. For each catchment area, we determine the proportion of the catchment that overlaps CCAs. The density of streams is the number of stream reaches per unit area within CCAs or in the case study domain.

Results

Bibliometric Analysis

3608 publications on landscape connectivity (78% of all publications identified in the three searches) pertain specifically to wildlife and biodiversity, while 856 (19%) publications pertain to hydrology and watersheds. Far fewer papers address the synergy between the two functions of landscape connectivity, with 127 (3%) publications identified when using all the search terms (Fig. 2). The search revealed that 3% and 13% of wildlife and hydrology-related publications on landscape connectivity, respectively, address synergies between the two landscape functions.

The number of publications per year that address this synergy has increased in recent years, from 1 in 1993 to 15 in 2022. Approximately 50% of all publications on landscape connectivity that address both wildlife/biodiversity and hydrology/watershed were published after 2015 (Fig. 3).

The frequency of words in the abstracts per decade revealed growing attention to water-related issues in the connectivity literature that addresses both wildlife and watersheds (Fig. 4). The top ten words with highest frequency in the abstracts (from greatest to least) were water, species, biodiversity, riparian, landscape, ecological, habitat, connectivity, conservation, and river. The words related to water ("water," "riparian," and "river") are less frequent (27%) in the early decades compared to words related to wildlife ("species," "biodiversity," "habitat," and "conservation"). In later decades, frequencies of water-related words (45%) increase relative to wildlife-related words. This trend indicates increasing attention to water in the connectivity literature. Notably, words related to landscape connectivity for

20 140 CUMULATIVE PUBLICATIONS 120 PUBLICATIONS PER YEAR 15 100 80 10 60 40 5 20 0 0 1990 1995 2000 2005 2010 2015 2020 2025 YEAR Publications Cumulative

Fig. 3 Number of publications per year and cumulative from search in Web of Science search for words in abstracts for "landscape connectivity OR corridor AND (wildlife OR biodiversity) AND (hydrology OR watershed)"

Fig. 4 Frequency of words in abstracts by decade for 127 publications from search in Web of Science search for words in abstracts for "landscape connectivity OR corridor AND (wildlife OR biodiversity) AND (hydrology OR watershed)



water security and water supply to downstream users, such as "agriculture," "cities," "dams," or "reservoirs," do not appear in the words that are used most frequently.

Within the 127 papers, the most highly cited papers focus on hydrologic connectivity in wetland, riparian, and river systems and the implications for aquatic ecosystems and biodiversity [39–42] and biosphere reserves [43]. Within these most five highly cited papers, none focused on potential synergies between landscape connectivity for wildlife and downstream water flows and green water flux.

Synergies Between Consensus Connectivity Areas For Tigers and Hydrologic Function in Central India Highlands

The connectivity consensus areas (CCAs) cover approximately 13% of the total area of the case study domain (study extent clipped to the convex hull around the CCAs and watershed boundaries). The CCAs are approximately twice as rugged and have three times more forest cover and five times less cropland than the areas outside of the CCAs. Although the CCAs contain only approximately 25% of headwater and small streams in the total case study domain, the density of these streams in the CCAs is almost twice the density outside the CCAs for both headwater and small streams (Table 1).

The total catchment area for the five largest dams in the case study domain comprises 46% (79,320 km² out of 171,649 km²) of the total case study domain (Fig. 5). The proportion of catchment areas that overlap CCAs range from 2 for Pench Totladoh to 20% for Bargi, with 15% for the total catchment areas for the five dams (Table 2). Protected areas cover between 3 (Bansagar) and 24% (Tawa) of the catchment areas, which by definition are not included in CCAs and provide additional protection of the catchment areas. Relative to total CCA area, over 50% (11,748 km² out of 23,134 km²) of CCA overlaps the catchment areas of these five major dams.

The number of headwater streams (first order) and small streams (first and second order) in these catchment areas is disproportionately high in the CCAs relative to the proportion of total catchment area (Fig. 6). CCAs in the catchment areas for the five dams combined contain 27% of all first-order streams and 19% of small streams compared with 15% of total area in CCAs. The disproportionately high representation of headwater and small streams in CCAs

| Table 1 | Comparison | of ruggedness | (mean a | and star | ndard d | leviation | of |
|----------|----------------|------------------|----------|----------|----------|-------------|----|
| differen | ce in elevatio | n (m) between | pixels), | forest c | cover, a | and numb | er |
| of heady | water and sma | all streams betw | veen con | sensus | connec | ctivity are | as |

(CCAs) and outside CCAs within the case study domain. Headwater streams are 1st order and small streams are 1st and 2nd order. See text for data sources

| | Area (km ²) | Mean ruggedness (m) | Cropland cover (%) | Forest cover (%) | Headwater streams | | Small streams | |
|-------------------------|-------------------------|---------------------|--------------------------|---------------------|-------------------|--|---------------|--|
| | | | | | Number | Density (n/100 km ²) | Number | Density (n/100 km ²) |
| Within CCAs | 23,134 | 3.55 ± 3.14 | 11.4 | 59.7 | 1541 | 6.67 | 2162 | 9.35 |
| Total case study domain | 171,649 | 1.92 ± 2.29 | 50.0 | 20.6 | 6001 | 3.50 | 8741 | 5.09 |
| Proportion within CCAs | 0.13 | | | | 0.26 | | 0.25 | |





varies among the catchment areas, with Bargi containing 32% and 23% of headwater and small streams, respectively, compared with 20% of area. At 8% and 6%, respectively, the disproportionately high representation in the number of streams occurs for Pench Totladoh as well, which only has 2% of the catchment area as CCA. The high relative number of headwater and small streams suggests that maintaining CCAs with vegetation cover and free from disturbances,

such as large mines and transport infrastructure, would contribute to hydrologic function and sediment control as well as landscape connectivity for wildlife.

| Dam Storage Surface capacity (km ³) (km ²) | | Surface area (km ²) | Total catchment area (km ²) | Catchment area within CCA (km ²) | Proportion of area within CCA | Proportion of area within protected area | |
|---|-------|---------------------------------|--|---|-------------------------------|--|--|
| Bansagar | 5.43 | 430 | 18563 | 2243 | 0.12 | 0.03 | |
| Bargi | 3.92 | 248 | 14604 | 2934 | 0.20 | 0.14 | |
| Gosekhurd | 3.83 | 40 | 35843 | 5360 | 0.15 | 0.08 | |
| Tawa | 1.24 | 174 | 6009 | 1106 | 0.18 | 0.24 | |
| Pench Totladoh | 0.79 | 65 | 4301 | 105 | 0.02 | 0.14 | |
| Total five dams | 15.21 | 958 | 79320 | 11748 | 0.15 | 0.09 | |

Table 2 Catchment area and overlap with consensus connectivity areas (CCAs) for the five largest dams in the case study area

Discussion and Conclusions

The bibliometric analysis of literature on landscape connectivity/corridors, wildlife/biodiversity, and hydrology/watershed indicates that the research field of landscape connectivity for wildlife movement is well-established. On the other hand, literature on landscape connectivity that incorporates hydrologic function and water security is an emerging but less mature research area. Within the papers produced from the search on the overlap between landscape connectivity for wildlife and water security, there is a paucity of papers that examine the potential for corridors to maintain landscape connectivity to address these two objectives. In general, these results indicate a need for the scientific community to examine possible synergies that landscape connectivity can provide for water security and wildlife conservation.

The case study in the Central Indian Highlands, where areas of importance for wildlife movement also serve as headwaters for multiple rivers that provide essential water to downstream users, illustrates the potential for increased synergy to address multiple goals through management of these headwaters. The CCAs comprise 13% of the total land area but contain approximately 25% of headwater and small streams in the case study domain. Forest cover in the CCAs (approximately three times the forest cover outside of CCAs) reduces soil erosion through maintaining vegetative cover, slowing runoff, and enhancing infiltration. The ruggedness of the CCAs (approximately twice as rugged as areas outside the CCAs) makes conservation of forests within CCAs particularly crucial to control soil erosion and downstream water quality flowing from these headwater and small streams.

The extensive overlap between the CCAs and the catchment areas for the five largest dams (more than 50% overlap of all CCAs and 15% overlap of total catchment area) in the case study area illustrate the potential relevance of management of the CCAs to downstream water quality and flow. CCAs in the catchment areas contain 27% of the headwater and 19% of small streams on 15% of the total area. Consequently, management of the CCAs to maintain healthy vegetation cover and pervious surfaces contributes disproportionately to the water security for downstream users. The degree of potential co-benefit between water security and landscape connectivity for wildlife depends on the amount of overlap in



Fig. 6 Proportion of headwater streams, small streams, and area in the consensus connectivity area (CCA) within the catchment areas of five major dams

land area between the catchment area and wildlife corridor for any particular dam. In the case study, this overlap ranges from 2 to 20% across the five largest dams.

Despite the potential for synergies between management for wildlife movement and watershed protection, the practicality of management for multiple objectives is limited. The mandate for wildlife managers is to manage habitat for wildlife, the mandate for water managers is to manage water flows, and the mandate of the development sector is to expand infrastructure, mines, and other activities. Increased attention from the research community on the potential for landscape connectivity to synergistically contribute to hydrologic function as well as wildlife movement could help foster a useful dialogue. Such a dialogue could nudge managers and decision-makers towards overcoming silo-ed management and achieving more holistic management of these critical parts of the landscape. For example, efforts that protect both wildlife corridors and watersheds such as reducing pressure on forests for construction, fuelwood, and other forest products would address both objectives [44].

The imperative to holistically manage remaining semiwild areas for landscape connectivity is particularly acute in India. Water security is a primary concern in its own right for over a billion people. While tiger conservation is highly valued by many and a success story in the country, water is a daily, immediate need recognized by every citizen and manager. Headwaters with healthy vegetation to reduce sedimentation, filter contaminants, recharge groundwater, maintain streamflow into the dry season, and recycle and redistribute precipitation through green water flux potentially serve a dual purpose of wildlife corridors—for tigers and for reducing water stress for people and ecosystems across the landscape. This aspect of landscape connectivity has been underappreciated in the literature.

The scarcity of land for multiple uses leads to competition between agriculture, commercial forestry, habitations, energy and transport infrastructure, and other human uses in the region. Most often, forest lands are diverted for infrastructure and mining in the region [23]. In central India, conserving remaining semi-wild areas for hydrologic function can add much-needed rationale to the conservationists' calls for landscape connectivity for wildlife movement. Similar situations are likely to exist around the world, particularly in areas facing water insecurity from overuse and climate change. Our results conclude that research into the synergies between landscape connectivity and ecosystem services, in specific hydrologic function that contributes to water security, can lead to less-silo-ed management decisions to meet multiple wildlife and human development goals.

Author Contributions R.D. wrote the manuscript text and conceived of the analysis. S.P. carried out geospatial analysis and prepared Figs. 1, 5, and 6. A.N. carried out bibliometric analysis and prepared Figs. 2 and 3. B.C. and J.K. provided input and data for the analysis of hydrologic function. All authors reviewed the manuscript.

Funding Funds from the DeFries Bajpai Foundation for the Network for Conserving Central India supported Amrita Neelakantan and Satvik Parashar for this analysis.

Data Availability Shape files with consensus connectivity areas for tigers for the case study region are publicly available at https://www.centralindia-datacollab.org/. All other data sets used in this analysis are publicly available.

Compliance with Ethical Standards

Conflict of Interest Ruth DeFries, Satvik Parashar, Amrita Neelakantan, Benjamin Clark, and Jagdish Krishnaswamy have no conflicts of interests to declare.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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