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River interlinking and biodiversity risks in Indian freshwater ecosystems

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Abstract

India's National River Linking Project (NRLP) is a large-scale inter-basin water transfer scheme designed to address water scarcity and excesses by connecting surplus basins to deficit ones across the country. However, such large-scale hydrological alterations pose serious ecological risks. This study examines the potential role of river interlinking on the distribution and dynamics of freshwater invasive alien species and their interactions with native biodiversity across Indian river basins. We modelled the distribution of 15 naturalised freshwater IAS using species distribution models based on bioclimatic variables. These maps were then overlaid with basin-level freshwater biodiversity and threatened-species data, as well as the proposed river-linking network. The results reveal strong positive correlations between IAS richness and overall as well as threatened freshwater biodiversity, with biodiversity hotspots such as the Krishna, Godavari, Mahanadi, Brahmaputra, and Western Ghats basins being most at risk. The proposed interlinking routes are expected to act as ecological corridors, enabling biotic exchange among previously isolated basins. Such increased connectivity could accelerate biological invasions, disrupt migratory routes, alter hydrological regimes, and undermine ecosystem resilience. The findings emphasise the urgent need to incorporate invasion ecology and biodiversity safeguards into NRLP plans to prevent irreversible ecological damage.

Keywords: Inter-basin water transfer, freshwater biodiversity, invasive alien species, species distribution modelling, national river linking project, Indian rivers

Introduction

Freshwater ecosystems cover only 2.4% of Earth's surface but support nearly 10% of all known species, including half of all fishes and one-third of vertebrates^{1,2,3}. Yet, freshwater habitats are among the most threatened ecosystems globally and are disappearing at three times the rate of global forest loss^{2,4}. Nearly 50% of countries now report at least one degraded aquatic or near-aquatic ecosystem, and over 37% of rivers longer than 1,000 km have lost their natural flow regimes². Despite this, freshwater systems remain critical for nutrient cycling, climate regulation, food security, livelihoods, and water supply for millions of people⁵.

Degradation of freshwater ecosystems results from multiple interacting stressors. Direct drivers include water pollution, dam construction, diversion, invasive alien species (IAS), and overharvesting, while indirect drivers such as land-use change, climate change, and population growth intensify these impacts^{6,7,8}. Among these, IAS and river interlinking or inter-basin water transfer projects (IBWTs) represent two interrelated threats often studied in isolation⁹. Both threaten freshwater biodiversity individually, but their combined effects remain largely unexplored¹⁰.

After naturalisation, IAS significantly disrupt freshwater systems, competing with or displacing native species, altering trophic structures, degrading habitats, depleting oxygen, and causing socio-economic losses^{11,12}. Similarly, river linking, the transfer of untreated water between basins through canals, tunnels, or pipelines, reshapes hydrological connectivity and facilitates IAS spread between previously isolated systems^{9,10,13,14}. Despite its ecological implications, this dispersal pathway remains overlooked in environmental policy and research^{9,13}.

Globally, several large-scale IBWT projects have accelerated biological invasions. In the United Kingdom, linking the Severn and Thames rivers facilitated the invasion of quagga mussels, altering sediment and alkalinity regimes¹⁰. In China, the South-to-North water diversion enabled northward spread of *Alternanthera philoxeroides*, *Pontederia crassipes*, and *Pistia stratiotes*⁹, while in South Africa, the Orange-Great Fish River link expanded the range of *Clarias gariepinus*. The Columbia Basin Project in the U.S. similarly altered zooplankton assemblages¹⁴. These

examples illustrate how engineered hydrological connectivity can act as ecological "highways" for IAS.

India's National River Linking Project (NRLP), among the world's most ambitious hydrological schemes, proposes connecting 37 major rivers through 30 planned links, spanning ~15,000 km of canals and over 3,000 reservoirs^{15, 16, 17}. The project aims to redistribute ~174 billion m³ of water from surplus to deficit basins and generate 34,000 MW of hydroelectric power¹⁸. The main vision behind NRLP is to enhance agricultural productivity, reduce flood and drought risks in surplus and arid regions¹⁹. However, despite these well-intended socio-economic benefits, it poses serious ecological concerns, particularly regarding the spread of freshwater IAS.

India's river basins are ancient, topographically isolated evolutionary units that promote high endemism^{20, 21}. Basin-level barriers have historically limited dispersal and facilitated speciation^{22, 23}. Large-scale canal linkages could therefore homogenise biotas, eroding these evolutionary boundaries²⁴. Even a single canal may have a limited impact, but sequential links can cumulatively drive biotic mixing (homogenization), species replacement, and the loss of local endemics, such as the golden mahseer (*Tor putitora*), which depends on specific temperature and flow regimes for reproduction²⁵.

Previous studies have warned of multiple risks associated with river linking in India, including the spread of invasive alien fishes²⁶, altered monsoon dynamics²⁷, sediment loss²⁸, mass displacement, and economic inefficiency²⁹. Yet, biological invasions remain poorly represented in Indian Environmental Impact Assessments, which primarily assess hydrological parameters while neglecting biodiversity. This oversight could have profound implications for fisheries, irrigation, and water quality, as IAS such as *Oreochromis mossambicus* and *Salvinia molesta* disrupt aquatic habitats and reduce native fish abundance^{30, 31, 32}.

In this context, the present study investigates how river linking may influence the distribution and dynamics of IAS and their potential impacts on freshwater biodiversity across India, under the hypothesis that inter-basin water transfers under NRLP will facilitate the spread of freshwater IAS and increase biotic homogenization across Indian river basins. Specifically, we aim to: (i) model

the predicted distributions of key freshwater IAS across Indian river basins; (ii) assess whether proposed NRLP links connect basins with differing invasion levels, potentially facilitating the spread of IAS; (iii) analyse relationships between IAS distribution, native species richness, and threatened taxa; and (iv) identify high-, moderate-, and low-risk basins for targeted intervention.

By addressing these objectives, we provide a spatially explicit framework for integrating invasion ecology into national water planning and conservation policy, ensuring that biodiversity risks are accounted for in the design and implementation of India's river interlinking initiatives.

Results

Distribution patterns of freshwater IAS

A total of 15 freshwater IAS that have naturalised in Indian freshwater habitats were used to assess their distribution patterns. Of these, eight are fish species (five families and seven genera, including two congeneric taxa), four are plants (four families and four genera), two are molluscs (two families and two genera), and one is a reptile (see Table 1; Supplementary Fig. S1). We used river basin boundaries derived from hydrological modelling of Digital Elevation Model (DEM) data to map IAS distributions (Fig. 1a). All 15 IAS were intentionally introduced as ornamental, biocontrol, pet, or for aquaculture purposes. Ten of these IAS originate from North and South America; the rest are from Europe, Central Asia, China, and Africa. Three of the four freshwater invasive alien plants (*Pontederia crassipes*, *Pistia stratiotes*, and *Salvinia molesta*) are floating, while only one is rooted and emergent (*Ipomoea carnea*). The modelled distribution of IAS across hydrosheds in India reveals high species richness in all basins of Northeast India, with the Brahmaputra sub-basin, Ganga and lower Ganga sub-basins, and the Krishna river basin showing the highest invasion rates (13-15 species; Fig. 1b). The proposed river linking between water-surplus and water-deficient basins, such as the Ganges to rivers on the east coast and the Krishna to the lower Kaveri via the Kaveri, will facilitate the movement of invasives towards the southern parts of India, from Krishna (13-15 species) to Kaveri-Krishna (10-12 species) and to Godavari river basins (10-12 species), and from Krishna (13-15 species) to lower Kaveri (7-9 species). A total of 610,446.96 km² of basin area is low risk, 1,286,409.19 km² is moderate risk, and 1,533,480.99 km² is at high risk of IAS invasion.

Basin-level biodiversity patterns

For overall freshwater species richness, the Lower Ganga (1270 species), Left Bank Brahmaputra (1329 species), Kaveri (1352 species), and South-Western Ghats (1533 species) basins were highly diverse. This is followed by all other Peninsular Indian river basins (Fig. 2a). For Threatened species (CR, EN, and VU), the Krishna (151 species), Left Bank Brahmaputra (143 species), Kanyakumari to Kaveri (141 species), Right Bank Brahmaputra (110 species), lower Ganges (101 species), and Kaveri (222 species and South-Western Ghats (318 species) showed the highest richness (Table 2; Fig. 2b). Comparable patterns were also evident when examined across individual freshwater taxa (Table 2; Supplementary Fig. S2).

Relationship between IAS and freshwater biodiversity

The correlation analysis (Fig. 3) shows clear patterns across major freshwater taxa: mammals, reptiles, amphibians, fishes, crustaceans, molluscs, odonates, other invertebrates, and plants. In most groups, IAS richness exhibits a strong positive association with native species richness, with high R^2 values (often >0.8). These relationships indicate that basins supporting more native species also tend to harbour more IAS. Although the correlation remains positive for amphibians and crustaceans, it is weak for molluscs and plants. Most taxa show strong and statistically significant correlations ($p < 0.01$), indicating reliable relationships between IAS richness and both total and threatened species richness (Table 3). In contrast, plants show non-significant results ($p > 0.05$). Meanwhile the regression analysis indicates that the total species richness shows a moderate positive correlation with IAS richness ($R^2 = 0.475$; Fig. 4), reinforcing the pattern observed across individual taxa: species-rich basins tend to accumulate more invasives (Fig. 3) but the relationship between IAS richness and threatened species richness is weaker ($R^2 = 0.181$), but still positive, suggesting that basins facing more invasions often also contain more threatened taxa.

Priority river basins

The weighted-average analysis shows that all Northeast Indian and Peninsular Indian basins are highly vulnerable (priority score: 374-664) compared to the central and North Indian west-flowing river basins (Table 2). All North and Northwestern river basins have very low priority scores (priority score: 89-193). Also, these regions have low invasive species and biodiversity.

Discussion

India supports some of the world's most diverse freshwater biota, with many species both endemic and threatened³³. However, this biodiversity faces increasing pressures from IAS, developmental activities, land-use change, and habitat degradation³⁴, which will be compounded by large-scale river modifications³⁵. The IBWT projects, though intended to enhance irrigation efficiency and water availability, pose significant ecological risks^{36,37}. They alter the natural flow regime, sediment transport, and nutrient deposition; reduce groundwater recharge; disrupt migratory routes (e.g., *Hilsa* and *Mahseer*); and alter spawning habitats by changing temperature, dissolved oxygen, salinity, and turbidity. Most importantly, they facilitate biological invasions by removing hydrological barriers and creating dispersal corridors^{10,38,39,40}.

Among India's major sub-basins, the Lower Ganga (299,000 km²) and the Krishna (279,000 km²) are the largest, supporting exceptionally high freshwater diversity (>1200 species) and populations exceeding 440 million and 66 million people⁴¹. In contrast, smaller sub-basins, such as the Beas (14,000 km²) and the drainage flowing into Burma (26,000 km²), also contain notable biodiversity (Table 2). The South-Western Ghats and the Kaveri basins are hotspots, with 1533 and >1352 species, respectively, and many threatened taxa. Biological invasions threaten livelihoods from inland fisheries⁴², biodiversity, and ecosystem stability through competition, food-web disruption, and local extinctions⁴³.

Our results collectively show that the distribution of IAS in India's freshwater ecosystem can be negatively influenced by hydrological connectivity. Basins with high native species and high threatened species, such as the South-Western Ghats, Kaveri, Krishna, Lower Ganga, and the Brahmaputra systems, also contain the highest number of IAS. This co-occurrence pattern likely reflects stable water availability and the presence of diverse habitats and complex ecological niches that support both native and alien taxa⁴⁴. High human population density and hydrological modification may further increase the propagule pressure of IAS⁴⁵. Consistent with global findings, basins with high IAS richness also exhibit high overall biodiversity and concentrations of threatened taxa⁴⁶, suggesting that biodiversity hotspots may not be inherently resistant to invasion, and that the long-term persistence of native species may be severely compromised⁴⁷.

In the NRLP's peninsular India component, the links connecting Godavari, Krishna, Pennar, and Kaveri (Fig. 1b) fall into the high-risk category. These links increase the probability of IAS spreading from high-risk to medium-risk zones (Fig. 2b). Similarly, the Himalayan component link connecting Ganga-Damodar-Subernarekha-Mahanadi is among the most ecologically sensitive links. The Lower Ganga is already heavily invaded (13-15 IAS) and would become a major source of propagules into the Mahanadi, a basin with high threatened-species richness ($n=69$). This can increase the risk of extinction for threatened taxa such as odonates and crustaceans (Supplementary Fig. S3). The strong positive correlations ($R^2 > 0.9$) observed for all species indicate that basins rich in native biodiversity tend to simultaneously accumulate more IAS, suggesting that "biodiversity hotspots become invasion hotspots."

These freshwater taxa are likely to experience niche overlap, competition, or altered food-web dynamics when IAS proliferate. Plants show no significant correlation ($p > 0.05$), reflecting either lower data points or different drivers of establishment. The weaker correlations in amphibians and crustaceans may partly reflect data limitations; however, these groups remain highly vulnerable to indirect invasion impacts such as microhabitat alteration, pathogen transmission, and water-quality shifts^{48,49} (Supplementary Fig. S2). Threatened species richness showed a weaker positive relationship with IAS richness, highlighting coexistence and increased extinction risk through predation, competition, hybridisation, trophic alteration, habitat modification, nutrient shifts, ecosystem-service loss, and disease spread^{50,51,52,53,54,55,56}.

The weighted-average ranking analysis shows a few basins in the high-risk category, indicating simultaneous pressure from IAS, high biodiversity, and a large number of threatened species. In contrast, arid and ephemeral basins such as Jaisalmer, Bikaner, Barmer, the Indus, and the Sabarmati show low native and IAS richness. However, low richness does not necessarily imply low conservation concern; small basins may harbour rare, endemic and evolutionarily distinct taxa that are highly vulnerable to disturbance⁵⁷. Together, these patterns highlight priority basins; the South-Western Ghats has the highest weighted score (664.2), driven by high species richness (1533), exceptionally high threatened species (318), high IAS presence (11), and a moderate-to-large basin area. Krishna, Lower Ganga, and the Brahmaputra basin complex as regions also

require urgent attention, targeted monitoring, as the NRLP may further facilitate the downstream spread of IAS into high-value biodiversity areas.

Ecological impacts beyond biodiversity loss: Beyond biological invasions, inter-basin transfers alter ecological and hydrological systems by increasing connectivity, disrupting flow regimes, sediment transport, and geomorphological processes^{58,59} leading to habitat degradation⁶⁰, obstruction of fish migratory pathways⁶¹, heavy metal and industrial pollution⁶², genetic homogenisation and reduced ecosystem resilience^{63, 64,65} and spread of aquatic pathogens^{66, 67, 68,69}.

The transboundary nature of India's rivers means NRLP impacts may extend to downstream nations^{70, 71}. Also, global evidence suggests that climate change exacerbates biological invasions, as alterations in temperature, precipitation, and hydrological flow, sediment regimes and water quality can create new ecological niches and weaken the resilience of native species^{72,73,74,75,76}. Although future climate projections were not explicitly modelled in this study, the spatial patterns identified here provide insight into how climatic suitability may interact with hydrological connectivity.

Policy implications and the need for integrated management: The increasing threats from IAS and hydrological modification necessitate proactive, evidence-based management³⁵. Early detection, rapid response, and long-term biosecurity monitoring should be embedded in the design and implementation of river interlinking projects⁷⁷. Invasion ecology principles must be integrated into river basin management, climate adaptation strategies, and national infrastructure planning⁷⁸. Embedding these principles within the NRLP aligns with global sustainability goals, including SDG 6 (Clean Water and Sanitation), SDG 13 (Climate Action), SDG 15 (Life on Land), and SDG 11 (Sustainable Cities and Communities)⁷⁹. Incorporating ecological foresight into national water infrastructure is therefore not only a matter of environmental stewardship but also a socio-economic necessity that supports long-term sustainability in the Anthropocene.

This paper acknowledges several caveats in the current study. (i) Freshwater biodiversity data are incomplete, as many taxa remain unassessed or lack updated IUCN range maps, which are more than a decade old, (ii) Occurrence records from multiple sources may contain spatial biases despite

cleaning, (iii) SDMs were primarily climate-based and excluded anthropogenic and hydrological drivers (e.g., flow alteration, pollution, land use, species interactions), which may lead to overprediction. Future studies can further improve reliability by developing standardised data from long-term monitoring networks for freshwater invasive species, integrating high-resolution land-use and anthropogenic disturbance datasets, and incorporating hydrological and habitat-structure variables as they become available, which are currently unavailable in India. Model robustness could be improved through ensemble modelling, bias-correction techniques, and hierarchical modelling frameworks, which may also help account for data uncertainty and enhance predictive performance. Additionally, citizen-science programs and centralised national reporting platforms would substantially enhance data uniformity, coverage, and temporal spread, thereby strengthening future large-scale ecological modelling efforts, and (iv) Due to data deficiency, the Andaman and Nicobar Islands were not included in the analysis and discussion. Addressing these limitations will improve predictive robustness and support more management-relevant invasion risk forecasting under river interlinking scenarios.

Conclusion

Our findings highlight that while NRLP is proposed to be carried out to improve agriculture productivity, hydropower, drought and flood mitigation, ambitious inland navigation, and improve employment, if implemented haphazardly without ecological safeguards, it could accelerate the spread of IAS in the freshwater ecosystems and homogenise the unique biotas of its river basins. Our study provides a spatially explicit framework for understanding and integrating invasion ecology into water resource planning and demonstrates the importance of balancing developmental ambitions with ecological integrity. Recognising that infrastructure development and biodiversity conservation need not be mutually exclusive, the future of India's river systems will depend on adaptive, science-based management that safeguards both ecosystem function and human well-being.

Methods

a) Selection of target IAS: This study focused on 15 major freshwater IAS that are naturalised in India and have been documented to impact native freshwater ecosystems (Table 1). These species were selected based on their widespread distribution, established invasion status, and evidence of ecological or economic damage, ensuring that the analysis captured taxa of greatest national concern. While additional alien species occur in Indian freshwater systems, those with insufficient or highly localised distribution data, or with uncertain ecological impacts, were excluded to maintain data reliability and analytical robustness. Occurrence data for invasive alien fish were derived from Nobinraja et al. (2023), and for the remaining taxa, occurrence records were taken from GBIF (www.gbif.org (30 Nov. 2025); Supplementary Table S2). Spatial thinning was performed for those other than those from Nobinraja et al. (2023)²⁶. The final georeferenced dataset was used to generate species distribution models (SDM). Model performance was evaluated using the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve, where values between 0.7–0.9 indicated good predictive accuracy and values <0.5 reflected poor performance. A jackknife test was conducted to assess the relative importance of environmental variables. Spatial overlap analyses with native and threatened freshwater taxa were subsequently performed.

b) Freshwater biodiversity data. Data on the distribution of freshwater biodiversity, including mammals, reptiles, amphibians, fishes, molluscs, crustaceans, aquatic plants, and other freshwater-associated taxa, were obtained from the IUCN Red List of Threatened Species spatial database (www.redlist.org). The data were downloaded as species-range polygons in .shp format and subsequently clipped to India's political boundaries to ensure national relevance. Given the extremely large dataset available for avifauna and the fact that birds are highly mobile taxa whose distributions are not strongly constrained by river basin boundaries, bird data were excluded from the present analysis⁸⁰. Moreover, the potential impact of river interlinking projects on birds is likely to be less direct compared to primarily aquatic or semi-aquatic groups. The processed species range polygons for all selected taxa were then spatially aggregated by river basin, following the basin delineations provided by HydroSHEDS (<https://www.hydrosheds.org/>). This basin-level analysis enabled an assessment of biodiversity patterns and overlap with proposed

inter-basin water transfer routes. All spatial analyses were performed in ArcGIS Pro ver. 2.1(ESRI Inc., USA).

Species distribution modelling: In the present study, SDM was primarily used for invasive species as a data normalisation and spatial synthesis tool rather than a predictive ecological forecasting framework. This approach was necessitated by the absence of standardised, fine-scale occurrence datasets for freshwater invasive species across India, where distribution records are highly fragmented and unevenly reported. At broad spatial scales, climatic variables are widely recognised as the primary constraints governing species establishment and potential range limits, and therefore provide a conservative basis for large-extent modelling.

We developed SDMs for all 15 IAS using occurrence records from both native and invaded ranges⁸¹. SDM provides the fundamental ecological niche of a species using mathematical approximations⁸². For the SDM analysis, 19 bioclimatic layers were downloaded from WorldClim (ver 2.1; <https://www.worldclim.org/data/bioclim.html>) for the current climatic scenario⁸³ (for the period 1950-2000), and elevation data were derived from the Shuttle Radar Topography Mission (SRTM). All 19 bioclimatic layers and DEM had a spatial resolution of 30 arc seconds (~1 km²). For each occurrence point, the values of bioclimatic layers were extracted using the point sampling tool in QGIS version 3.16 (www.qgis.org). Pearson's correlation was used to reduce multicollinearity and overparameterization between environmental variables⁸⁴. To minimise redundancy in the output, one of the two highly correlated bioclimatic variables with $|r| > 0.70$ was removed, and only one variable, which makes ecological sense, was retained⁸⁵. The SDM analysis was performed using MaxEnt ver 3.4.4^{86,87} a presence-only algorithm to predict habitat suitability for 15 freshwater IAS based on bioclimatic variables.

Model settings followed 10 replicates, 25 per cent random test data, subsampling as the replication type, and 1000 iterations. Model performance was evaluated using the Area Under the Curve (AUC), with higher values indicating better predictive accuracy^{86,87}. Values from 0.5 to 0.6 indicate poor performance, 0.6 to 0.7 signify average performance, 0.7 to 0.8 reflect good performance, 0.8 to 0.9 denote better performance, and 0.9 to 1.0 represent excellent performance^{88,89}. A Jackknife test was performed to estimate the variable's contribution to the model⁹⁰. The model performance and other matrices are given in the supplementary information.

The average raster file obtained after MaxEnt analysis was used to create binary maps for each species using the 10th-percentile Cloglog threshold⁹¹. All 15 binary maps were combined into a single species richness map for all invasive species. This map was later masked and clipped for each river basin, to calculate the number of invasives per river basin, which corresponds to the layers used for aquatic biodiversity.

Statistical analysis: For each river basin (Fig. 1a), the number of species for each taxon and the number of threatened species were calculated. Correlation analysis was performed in PAST5⁹² to assess the relationships among freshwater IAS richness, total species richness, and the number of threatened species. The weighted average for each sub-basin was calculated using specific weights (Supplementary Table S1). To do this, the values in each column were ranked and assigned weights from 1 to 5. The lowest 20% of values were assigned a weight of 1, and the highest 20% were assigned a weight of 5.

The formula used for calculating the weighted average per river basin is as follows:

$$\text{Weighted Average} = ((NI \times WNI) + (TS \times WTS) + (NTh \times WTh)) / (WNI + WTS + WTh)$$

Where,

NI is the number of IAS, WNI is the weight for the number of IAS, TS is the total species richness, WTS is the weight for total species richness, NTh is the number of Threatened species, WTh is the weight of Threatened species.

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Data availability. The data used in the analysis were downloaded from GBIF, iNaturalist and the India Biodiversity Portal.

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Author contributions: NAA conceived the idea, secured funding, and wrote and reviewed the MS. GPriya performed GIS and ENM analyses for non-fish species. NR did ENM for fish, and wrote the first draft of the MS. GR secured funding and reviewed the MS.

Figures

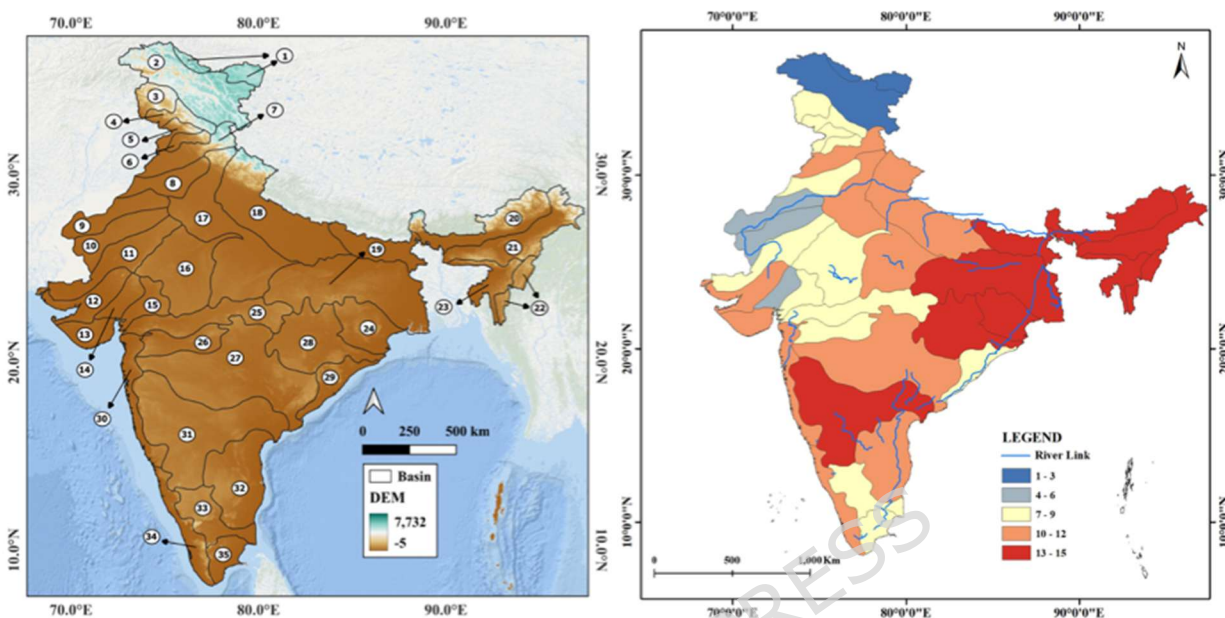


Fig. 1. (Left) Major river basins and subbasins of India, shaded by elevation derived from a Digital Elevation Model. Basin and subbasin boundaries correspond to the 35 classified hydrological units - 1. Ephemeral incipient drainage not flowing into Indus, 2. Indus, 3. Jhelum, 4. Chenab, 5. Ravi, 6. Beas, 7. Sutlej, 8. Ghaghar (old Saraswati), 9. Ephemeral (Jaisalmer–Bikaner), 10. Ephemeral (Barmer–Jaisalmer), 11. Rivers of Rann of Kutch & Luni, 12. Drainage of Gulf of Kutch, 13. Southern Kathiawar, 14. Sabarmati, 15. Mahi, 16. Chambal, 17. Yamuna, 18. Upper Ganga, 19. Lower Ganga, 20. Right Bank Brahmaputra, 21. Left Bank Brahmaputra, 22. Drainage Flowing into Burma, 23. Drainage Flowing into Bangladesh, 24. Mandhali to Ganga WR Region, 25. Narmada, 26. Tapti, 27. Godavari, 28. Mahanadi, 29. Godavari to Mahanadi, 30. Rivers of North-Western Ghats, 31. Krishna, 32. Kaveri to Krishna, 33. Kaveri, 34. South-Western Ghats, 35. Cape Comorin to Kaveri. (Right) Number of freshwater invasive alien species (IAS) per subbasin, represented by colour-coded categories, with the NRLP-proposed river linking map overlaid. (The maps were generated by Gokulapriya R., using Arc GIS 10.4, using DEM <https://earthexplorer.usgs.gov/>) and river basins of India (<https://www.hydrosheds.org/>), superimposed on OpenStreetMap (open-source maps) and river-linking map (generated in-house).

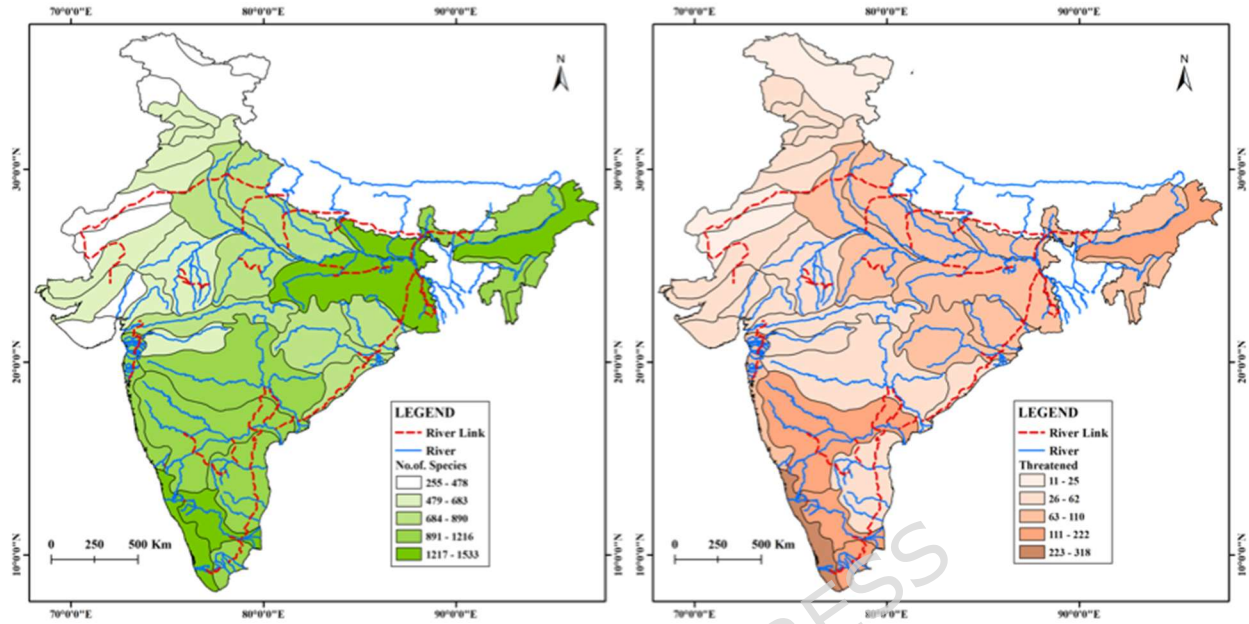


Fig. 2. (Left) Freshwater species richness per basin and (Right) Threatened freshwater species per basin shown using a colour gradient indicating increasing species counts, overlaid with proposed NRLP links and major river systems. (The maps were generated by Gokulapriya R., using Arc GIS 10.4, using river basins of India and rivers (<https://www.hydrosheds.org/>), superimposed on the India political boundary, river-linking map (generated in-house) and freshwater biodiversity (www.redlist.org).

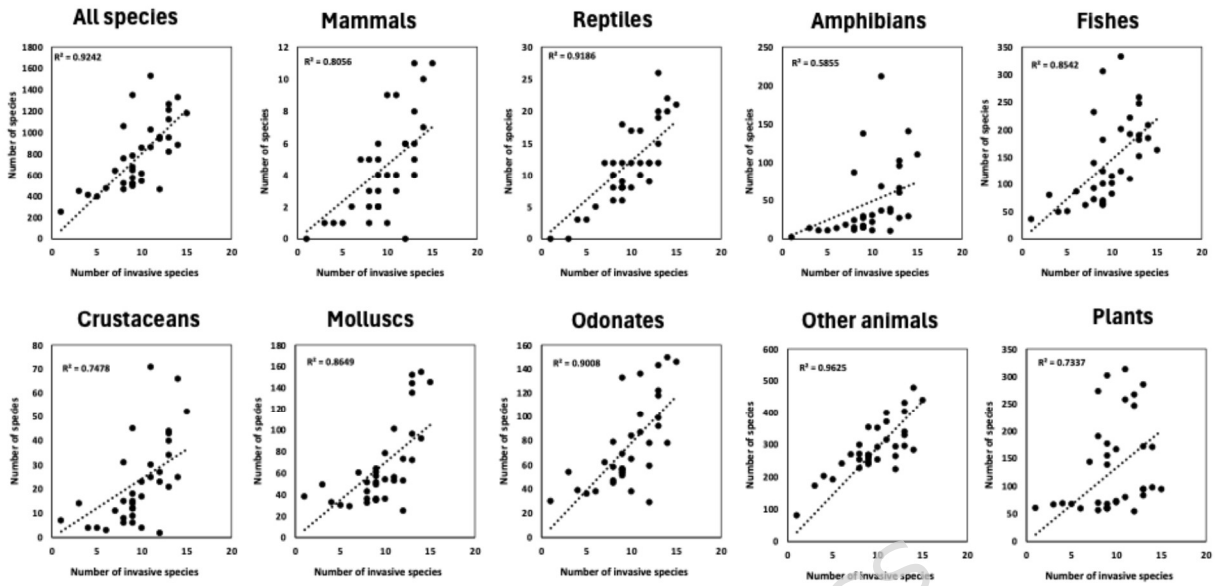


Fig. 3. The scatter plot shows the relationship between the number of IAS (x-axis) and the total number of species (y-axis) for different taxonomic groups across subbasins. The dashed line represents a linear regression, with the corresponding R^2 values indicating the strength of the correlation for each group.

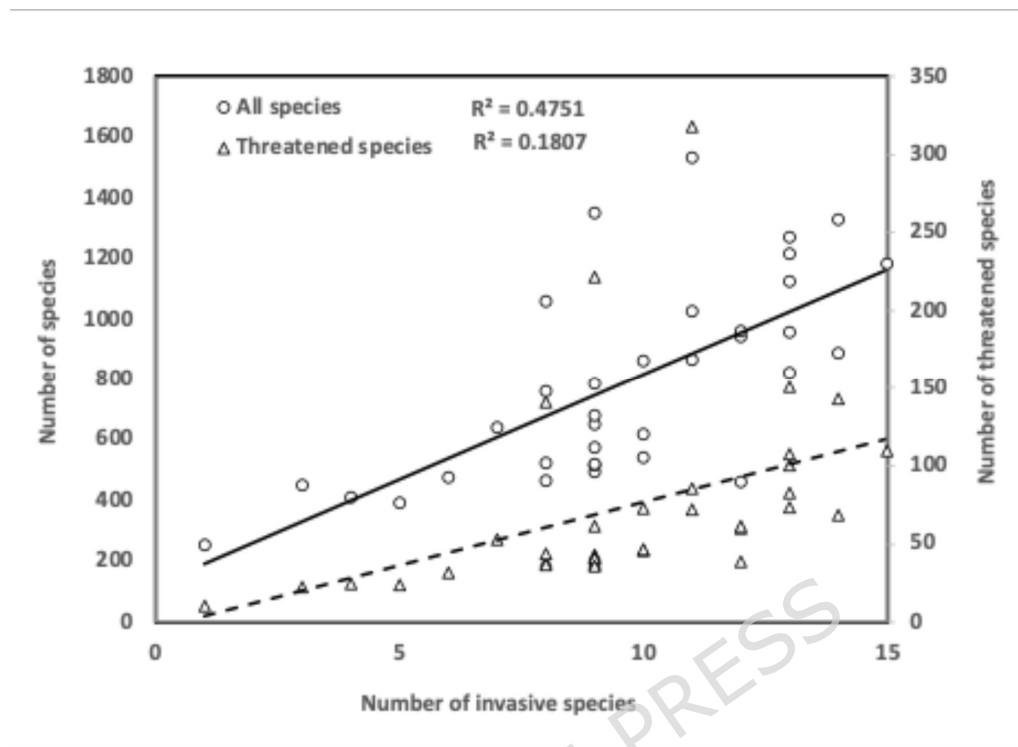


Fig. 4. Scatter plot showing the regression analysis between the number of IAS (x-axis) and the total number of species (circles, left y-axis) and the number of threatened species (triangles, right y-axis) across subbasins. The solid line shows a linear fit for all species ($R^2 = 0.475$) and the dashed line for threatened species ($R^2 = 0.181$). Symbols and trend lines indicate positive correlations.

Tables

Table 1. List of 15 freshwater invasive alien species (IAS) recorded in India, including taxonomic details, native regions, introduction pathways, and key references.

Sl no	Group	Family	Species	Common name	Native region	Reason of Introduction	References
1	Plants	Pontederiaceae	<i>Pontederia crassipes</i>	Water hyacinth	South America	Ornamental	Narayanan et al. 2007; Shah et al. 2025
2	Plants	Araceae	<i>Pistia stratiotes</i>	Water lettuce	Americas (unclear)	Ornamental	U.S. Fish & Wildlife Service, January 2015; Neuenschwander et al. 2009
3	Plants	Salviniaceae	<i>Salvinia molesta</i>	Giant Salvinia	South America	Ornamental	McFarland et al. 2004
4	Plants	Convolvulaceae	<i>Ipomoea carnea</i>	Bush morning glory	South America	Ornamental	Shaltout et al. 2010
5	Molluscs	Physidae	<i>Physella acuta</i>	Acute bladder snail	North America	Aquarium trade	Dumidae et al. 2024; Paul & Aditya 2021
6	Molluscs	Ampullariidae	<i>Pomacea diffusa</i>	Spike-topped apple snail	South America	Aquarium trade	Benson 2025;
7	Reptile	Emydidae	<i>Trachemys scripta elegans</i>	Red-eared slider	North America	Pet trade	Aravind et al. 2023
8	Fishes	Clariidae	<i>Clarias gariepinus</i>	African catfish	Africa	Aquaculture	Nobinraja et al. 2023; Neilson, M.E., 2025
9	Fishes	Cyprinidae	<i>Cyprinus carpio</i>	Common carp	Europe and Central Asia	Aquaculture	Nobinraja et al. 2023; Kohlmann & Kersten, 2013
10	Fishes	Poeciliidae	<i>Gambusia</i> spp.*	Mosquitofish	North America	Biocontrol	Nobinraja et al. 2023
11	Fishes	Cyprinidae	<i>Hypophthalmichthys nobilis</i>	Bighead carp	China	Aquaculture	Nobinraja et al. 2023; Zhu et al. 2022

12	Fishes	Cichlidae	<i>Oreochromis mossambicus</i>	Mozambique tilapia	South Africa	Aquaculture	Nobinraja et al. 2023; Hassan et al. 2019
13	Fishes	Cichlidae	<i>Oreochromis niloticus</i>	Nile tilapia	Africa	Aquaculture	Nobinraja et al. 2023; Kour et al. 2014
14	Fishes	Poeciliidae	<i>Poecilia reticulata</i>	Guppies	South America	Aquarium trade / biocontrol	Nobinraja et al. 2023
15	Fishes	Loricariidae	<i>Pterygoplichthys</i> spp.*	Tank cleaner	South America	Aquarium trade	Nobinraja et al. 2023

Species marked with an asterisk () indicate grouped (congeneric) taxa, combined because of taxonomic uncertainty and similar ecological characteristics.

Table 2. Number of invasive alien species (IAS), freshwater species richness, threatened freshwater biodiversity and weighted average for each subbasin of India. Values are presented for all 35 subbasins, including total basin area and the weighted average risk score used to derive the final invasion-risk category for each subbasin. Basins are listed in order based on threat category (low to high).

SI No	Region	Basin	Subbasin name	Basin area	No. of IAS	Total no. of recorded species	No of. threatened species	Weighted Average	Risk category
1	N	Area of North Ladakh Not draining into Indus	Ephemeral incipient drainage not flowing into Indus	28969.70	1	255	11	89	Low
2	N-W	Area of inland drainage in Rajasthan	Ephemeral (Jaisalmer, Bikaner)	59728.29	5	395	24	140.2	Low
3	N-W	Area of inland drainage in Rajasthan	Ephemeral (Barmer-Jaisalmer)	66315.99	4	412	25	145.8	Low
4	N-W	Indus	Indus	142232.24	3	451	23	158	Low
5	W	West flowing rivers of Kutch and Saurashtra including Luni	Southern Kathiawar	39102.00	12	463	39	163.4	Low
6	N-W	Indus	Jhelum	30111.64	8	465	39	163.6	Low
7	W	Sabarmati	Sabarmati	31243.12	6	478	32	170.8	Low
8	N-W	Indus	Chenab	26860.58	9	497	37	172.9	Low
9	N-W	Indus	Beas	14196.68	9	516	39	180.2	Low
10	N-W	Indus	Ravi	16253.91	9	520	43	184.8	Low
11	N-W	West flowing rivers of Kutch and Saurashtra including Luni	Rivers of Rann of Kutch & Luni	92373.23	8	525	37	185	Low

12	W	West flowing rivers of Kutch and Saurashtra including Luni	Drainage of Gulf of Kutch	63059.58	10	542	46	193.3	Low
13	N-W	Indus	Ghaghar (old Saraswati)	49714.46	9	576	42	206.1	Medium
14	N-W	Indus	Sutlej	53809.67	10	618	47	217.4	Medium
15	C	Ganga	Chambal	143884.37	7	643	53	226.3	Medium
16	W	Mahi	Mahi	40182.59	9	652	41	226.8	Medium
17	W	Tapti	Tapti	57231.95	9	683	36	238.4	Medium
18	W/C	Narmada	Narmada	106673.75	8	763	44	264.4	Medium
19	C-E	East flowing rivers between Mahanadi and Pennar	Godavari to Mahanadi	47812.23	9	789	62	307.2	Medium
20	N-C	Subernarekha & Brahmani and Baitarni	Mandhali to Ganga WR Region	77976.98	13	824	74	354.8	Medium
21	N	Ganga	Yamuna	227076.29	10	863	73	333.6	Medium
22	N	Ganga	Upper Ganga	195835.14	11	867	72	349.5	Medium
23	S	Pennar, East flowing rivers between Mahanadi and Pennar and East flowing rivers between Pennar and Kanyakumari	Kaveri to Krishna	147249.21	12	945	60	371.4	Medium
24	E	Mahanadi	Mahanadi	138962.55	14	890	69	374	High
25	N-E	Minor rivers draining into Myanmar	Drainage Flowing into Burma	25789.28	13	958	83	414	High

		(Burma and Bangladesh)							
26	S-C	Godavari	Godavari	302943.40	12	963	62	386.9	High
27	S-W	West flowing rivers from Tapi to Tadri	Rivers of North-Western Ghats	58363.84	11	1029	86	447.8	High
28	S	East flowing rivers between Pennar and Kanyakumari	Kanyakumari to Kaveri	40286.60	8	1062	141	507	High
29	E/N-E	Barak and others	Drainage Flow into Bangladesh	47850.39	13	1127	108	511	High
30	N-E	Brahmaputra	Right Bank Brahmaputra	100633.14	15	1184	110	551.2	High
31	S	Krishna	Krishna	279378.93	13	1216	151	607.4	High
32	N	Ganga	Lower Ganga	299322.92	13	1270	101	557	High
33	N-E	Brahmaputra	Left Bank Brahmaputra	107259.91	14	1329	143	623.8	High
34	S	Kaveri	Kaveri	75249.64	9	1352	222	653.2	High
35	S-W	West flowing rivers from Tadri to Kanyakumari	South-Western Ghats	57440.39	11	1533	318	664.2	High

C – Central; E - East; W - West; S - South; N – North; S-W - South West; S-C - South Central; N-C - North Central; N-W - North West; N-E - North East; C-E - Central East

Table 3. Correlation between invasive alien species richness and total native freshwater species richness and threatened freshwater biodiversity across India's river basins. Values represent R² and significance levels (P-values) from linear regressions for each taxonomic group.

Taxa	Species Richness		Threatened Species	
	R ²	P=	R ²	P=
Mammals	0.681	P<0.01	0.692	P<0.01
Reptiles	0.825	P<0.01	0.817	P<0.01
Amphibians	0.474	P<0.01	0.160	P>0.05
Fishes	0.594	P<0.01	0.285	P>0.05
Crustacean	0.611	P<0.01	0.423	P<0.01
Molluscs	0.678	P<0.01	0.364	P<0.05
Odonates	0.668	P<0.01	0.193	P>0.05
Others	0.786	P<0.01	0.615	P<0.01
Plants	0.286	P>0.05	0.141	P>0.05
All taxa	0.689	P<0.01	0.425	P<0.01

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