

Prioritizing India's landscapes for biodiversity, ecosystem services and human well-being

Received: 25 July 2022

Accepted: 12 January 2023

Published online: 6 February 2023


 Check for updates

Arjun Srivathsa ^{1,2,16} , Divya Vasudev^{3,16}, Tanaya Nair ^{1,4,16},
Stotra Chakrabarti⁵, Pranav Chanchani⁶, Ruth DeFries ⁷, Arpit Deomurari ^{6,8},
Sutirtha Dutta⁹, Dipankar Ghose⁶, Varun R. Goswami³, Rajat Nayak¹⁰,
Amrita Neelakantan¹¹, Prachi Thatte⁶, Srinivas Vaidyanathan ¹⁰,
Madhu Verma ¹², Jagdish Krishnaswamy ^{13,14,15,16}, Mahesh Sankaran ^{1,15} &
Uma Ramakrishnan ^{1,15,16} 

Biodiversity conservation and human well-being are tightly interlinked. Yet, mismatches in the scale at which these two priority issues are planned and implemented have exacerbated biodiversity loss, erosion of ecosystem services and declining human quality of life. India houses the second largest human population on the planet, while < 5% of the country's land area is effectively protected for conservation. This warrants landscape-level conservation planning through a judicious mix of land-sharing and land-sparing approaches combined with the co-production of ecosystem services. Through a multifaceted assessment, we prioritize spatial extents of land parcels that, in the face of anthropogenic threats, can safeguard conservation landscapes across India's biogeographic zones. We found that only a fraction (~15%) of the priority areas identified here are encompassed under India's extant Protected Area network, and furthermore, that several landscapes of high importance were omitted from all previous global-scale assessments. We then examined the spatial congruence of priority areas with administrative units earmarked for economic development by the Indian government and propose management zoning through state-driven and participatory approaches. Our spatially explicit insights can help meet the twin goals of biodiversity conservation and sustainable development in India and other countries across the Global South.

The concomitant impacts of biodiversity decline, climate change, unsustainable land use and inequitable extraction of natural resources have degraded the quality of human life^{1–3}. Biodiversity underpins several provisioning, regulatory and cultural or aesthetic ecosystem services. Ecosystem services linked to biodiversity, in turn, are crucial for ensuring long-term human well-being⁴. Recent discourse on nature-based solutions acknowledges nature's contribution as

humanity's 'safety net'^{5,6} and that ecological processes are shaped by a complex interplay between ecological and social systems^{7,8}. A sustainable future can only be ensured by adopting an ecosystem approach to conservation that emphasizes the links between human and natural systems to address global-, regional- and biome-scale threats to their functioning⁹. Siloed management approaches to meet conservation targets that ignore this interplay have failed to yield equitable and

A full list of affiliations appears at the end of the paper.  e-mail: arjuns@ncbs.res.in; uramakri@ncbs.res.in

sustainable progress^{10,11}. A renewed global resolve will need to consider nature in the Anthropocene and explicitly reconcile land-use planning for economic development with ecosystem functioning, biodiversity conservation and long-term human well-being.

For nearly two decades, several priority-setting tools have been proposed the world over to identify and rank species, habitats and locations based on their relative importance, vulnerability or ease of management intervention¹². These approaches generally adopt systematic spatial conservation planning—a set of decision-making tools that help determine the spatial locations where resources and actions need to be directed to optimize conservation gains^{13,14}. Earlier iterations of these tools largely involved identifying locations to demarcate Protected Areas (PAs), determine optimal reserve design or propose conservation corridors¹⁵. However, human interests such as economic aspirations, infrastructure development and agricultural expansion to ensure food security must be integrated with conservation goals to enhance traction with policymakers¹⁶. This necessitates the adoption of ‘landscape approaches’ to conservation¹⁷ so as to offer pragmatic solutions in the Anthropocene. Such considerations led to the idea of ‘zoning’ landscapes, whereby assessors not only identify priority locations, but also stratify them into various zones and determine appropriate management interventions^{18,19}. This combination of prioritization and zoning therefore holds promise to guide a better management of landscapes in an increasingly human-modified world.

Since its conception, the idea of prioritizing areas for conservation at the global level has seen wide application in scientific studies. While these investigations can offer important insights at the macroscale, their real-world applications have been limited²⁰. One reason for this is perhaps the lack of alignment between scientific ‘boundaries’ (sampling units) and administrative jurisdictions; yet, it is within these jurisdictions that implementation typically occurs⁴. Aligning ecological findings with administrative boundaries, or existing policy, may thus increase the utility of prioritization exercises. A second reason may be that making assessments at global scales potentially compromises the spatial resolution of analyses, hampered by the lack of availability and comparability of data at scale, or miss out on local socio-political nuances^{21,22}. Finally, macro-scale analyses could entail intrinsic biases in the representation of key features or attributes. For example, certain historically overlooked biomes may continue to remain ignored²³, habitats presumed to be ‘unproductive’ may not be prioritized (for example, grasslands²⁴), indices such as species richness, which ignore community composition, may discount rarity or endemism²⁵, PAs or ‘intact’ wilderness areas may take precedence over heterogeneous multi-use conservation landscapes^{26,27} and important dimensions, such as human populations, may be excluded altogether²⁸.

Achieving conservation goals, sustaining ecosystem services and ensuring human well-being while balancing economic development present formidable challenges in implementation³. India exemplifies this premise for the following reasons: (1) it is a large, diverse country with ten distinct biogeographic zones and four biodiversity hotspots, (2) its PA network, conservation landscapes and riverscapes support several ecologically important and evolutionarily distinct species assemblages, (3) it has the second largest human population in the world, with a large proportion of the people directly dependent on resources drawn from natural ecosystems and (4) with rapid infrastructure development and liberal investment policies, India is currently among the fastest-growing economies in Asia. In this study we (1) identified spatial scale(s), resolutions and thematic dimensions for a priority-setting exercise across the country (Fig. 1), (2) used a systematic spatial prioritization approach to optimize landscapes for habitat protection, biodiversity conservation and ecosystem service gains while penalizing locations facing negative anthropogenic impacts, and (3) aligned our results with global biodiversity

targets (Post-2020 Global Biodiversity Framework²⁹, COP15) and the Indian government’s development initiative to identify ‘aspirational’ economic districts. We provide insights that can guide future environmental planning and policy to help meet the twin goals of biodiversity conservation and sustainable development in a strategically important country for Asia. More broadly, our framework can be adapted and applied to conservation planning in ecoregions of other developing countries.

Overlap in priority sites across themes

Priority maps generated independently for the three themes of Habitats, Ecosystem Services and Biodiversity (Fig. 2a) represented sites of high value in isolation, that is, sites that are (1) representative of important and rare natural habitats, (2) responsible for the provision of key ecosystem services, namely, water and carbon, and (3) important solely from the perspective of threatened species diversity and turnover. We found moderate overlap between these three layers, which varied across biogeographic zones (hereafter, ‘zones’; Fig. 2). The overlap of priority sites for biodiversity (defined as the top 30% rankings) and habitats was 37% across the country, ranging from 30% in deserts to 48% in the Western Ghats (Supplementary Fig. 1). There was a substantial increase in overlap sites when ecosystem services were included as a criterion in addition to biodiversity and habitats. Around 38% of priority sites for ecosystem services were not covered by either biodiversity or habitat priority sites; these locations collectively contain a population of 2.3 million people (based on spatial overlap alone) who are directly dependent on these watersheds (Supplementary Fig. 1).

Conservationists often highlight the mismatches in priority sites when different criteria are used to assign a ‘conservation value’^{30,31}. Our findings support this concern (Fig. 2) and point to the value of incorporating multiple contributors to conservation value. Of significance, our multicriterion approach selected for India’s Open Natural Ecosystems³² (prioritized on the basis of habitats, but not biodiversity), encompassing open grasslands, savannas, hot and cold deserts, ravines, rocky boulders and escarpments. These systems are extremely fragile, with unique endemic flora and fauna, but are inappropriately classified as ‘wastelands’ as per India’s land-use and conservation policy³³. Similarly, areas ranked high for habitat and biodiversity, but low in terms of ecosystem services represent some locations in the arid/semi-arid dry zones of western India, the cold deserts of the Trans-Himalayas and parts of the Terai grasslands along the India/Nepal border (Fig. 2a). Conversely, areas ranked high for ecosystem services, critical for water and carbon storage, did not rank high for biodiversity or habitats in some places (for example, parts of Northeast India). This, perhaps, is due to the low coverage of traditional PAs or insufficient data on biodiversity in the region.

Appraisal of anthropogenic pressures

Reconciling biodiversity conservation concerns with the demands of economic development is one of the greatest challenges of the twenty-first century. We explicitly incorporated Threats (Fig. 2b) as a factor that makes conservation more costly and also such that the final priority ranks represent such a reconciliation (Fig. 3). Across zones, we observed as a consistent pattern the compounding effects of agricultural expansion and urbanization, coupled with vegetation greening (indicative of increased year-round irrigation in agriculture areas) and linear infrastructure (Fig. 2b). Thus, urban hotspots, representing major cities and the agricultural belts of (1) the northern semi-arid zone, (2) the lowland plains of Northeast India and (3) the western and southern parts of the Deccan peninsula were ranked the highest in terms of anthropogenic pressures (Fig. 2b and Supplementary Fig. 1). Of these, the northern semi-arid zone and the western parts of the Deccan peninsula also had pronounced

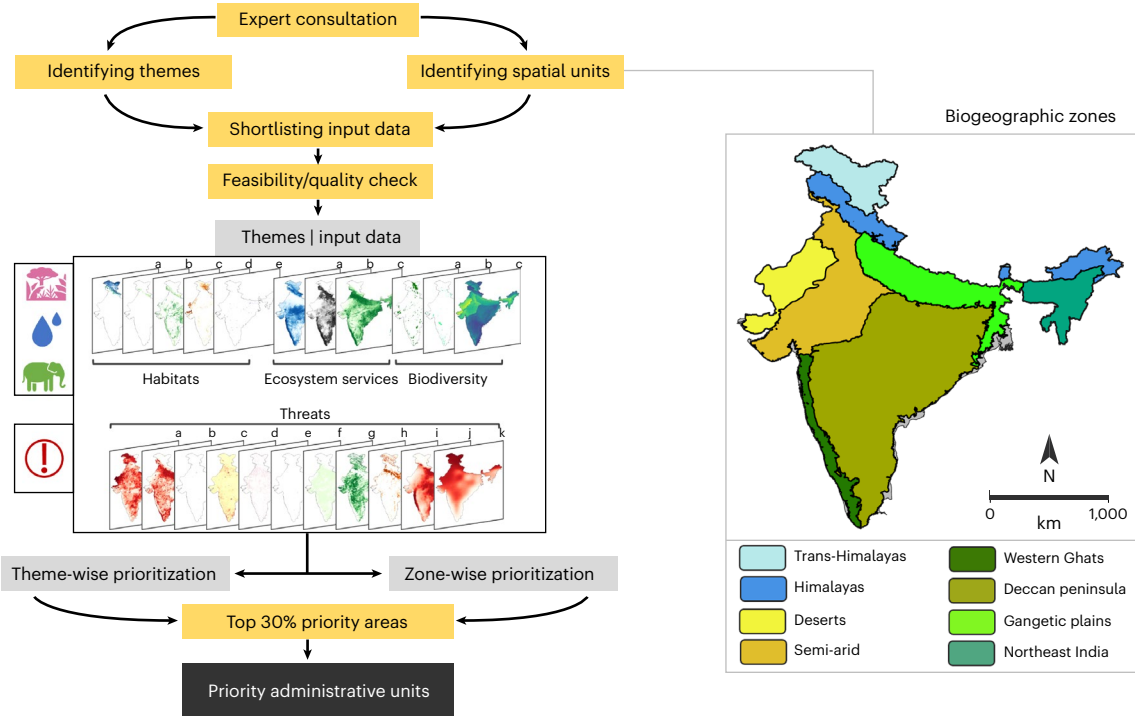


Fig. 1 | Schematic of the study framework and biogeographic zones of India. Themes and input layers identified for spatial prioritization: (1) Habitats (28 vegetation classes depicted as five composite panels), (2) Ecosystem services (blue water flux, above- and below-ground carbon and green water flux), (3) Biodiversity (PAs, key biodiversity areas and beta-diversity index of threatened

mammals, birds, reptiles and amphibians) and (4) Threats (human population density, livestock population density, urbanization, linear infrastructure, mines, river fragmentation, agricultural expansion, vegetation greening, vegetation browning, future climate warming and future rainfall anomaly).

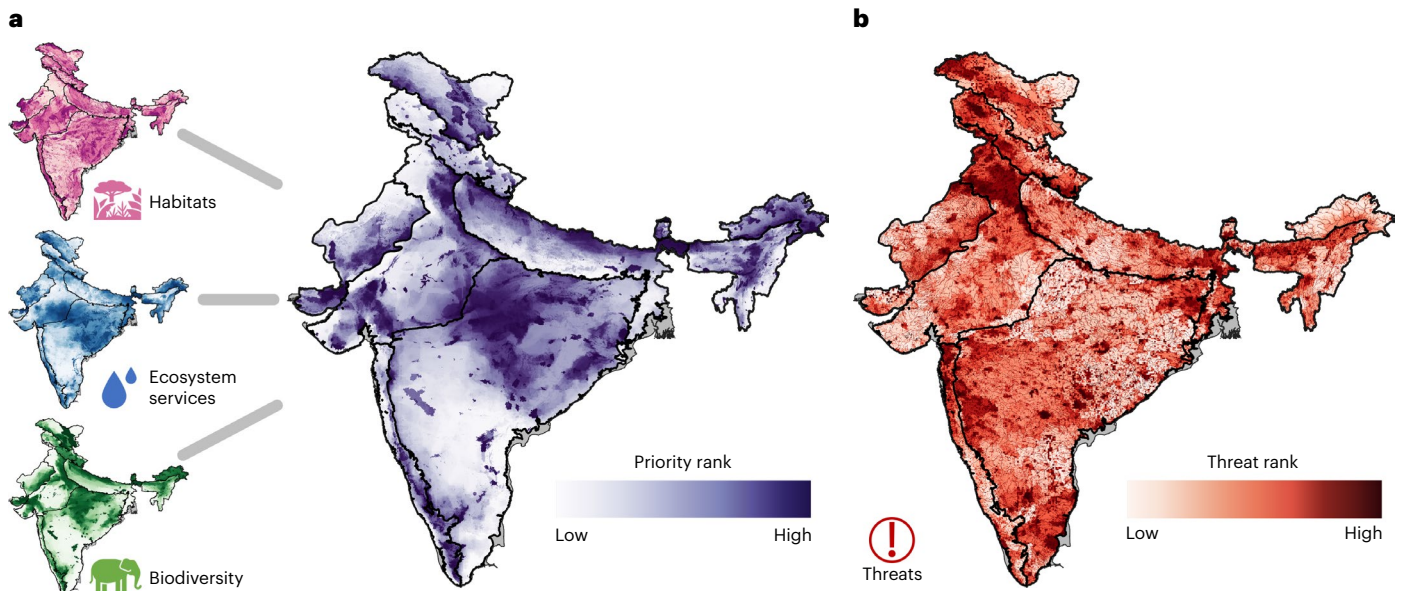


Fig. 2 | Theme-wise results from prioritization analyses. **a**, Priority maps based on Habitats (top left), Ecosystem Services (centre left), Biodiversity (bottom left) and the composite analysis of the three themes (right). **b**, Theme-specific results from the prioritization analysis of Threats.

signatures of vegetation browning and greening, respectively. Vegetation browning could arise from forest degradation, deforestation or forest fires, but it could also be due to natural shifts in woody vegetation to grass-dominated systems or the loss of green foliar biomass due to climate change impacts. Vegetation greening could be due to ecological restoration or natural regeneration of native species, but the more ubiquitous source is CO₂ fertilization and the proliferation of invasive alien species (for example, *Prosopis* and *Lantana*^{34–36}).

Our results pertaining to threats, when viewed in the context of projected human population growth and the demands of meeting future food security concerns, are representative of areas that either have or will soon surpass thresholds beyond which interventions for sustainable land-use practices may not be feasible³⁷. However, our analyses could not fully elicit the broader deleterious impacts of certain human activities. These include threats that are (1) rapidly evolving in terms of scale, extent and impacts, for example, hydropower dams and road networks^{38,39}, (2) peculiar to certain regions of the country

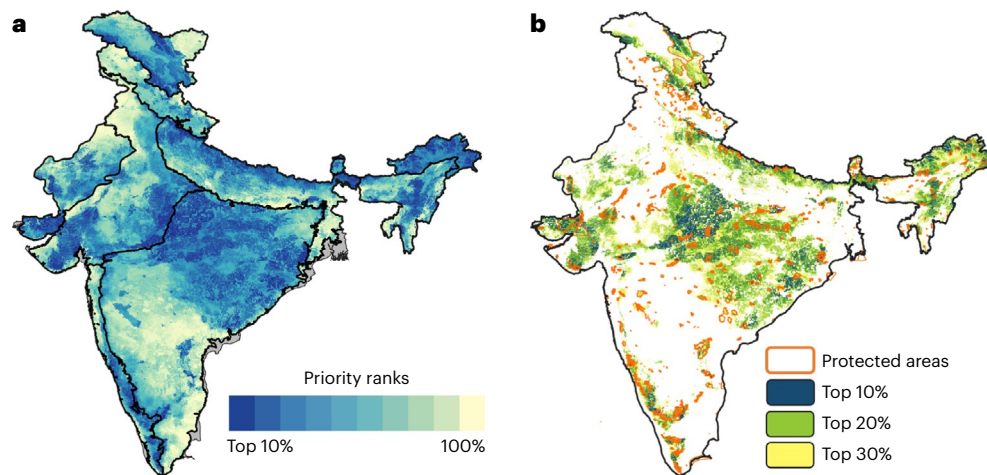


Fig. 3 | Composite spatial priority maps and overlap with extant Protected Area network. **a**, Conservation priority ranks for India, computed zone-wise and combined. **b**, Top 30% priority areas in each zone demarcated as a set of three

10% blocks. Designated PAs are overlaid to show the extent of overlap and spatial congruence with high priority locations.

(for example, the expansion of oil palm plantations⁴⁰) or (3) difficult to quantify in terms of their long-term consequences (for example, loss of connectivity⁴¹). While we did incorporate projected temperature increases and future rainfall anomalies to account for climate change impacts, zones that are likely to be the most vulnerable to these threats, that is, coastal areas and island systems, were not part of our assessment. Nevertheless, climate change is still projected to impact various ecosystems considered in our analysis in significant ways. For example, predicted increases in the magnitude and frequency of major floods can shape the distribution of biodiversity on the floodplains of Northeast India⁴². Such influences underscore the importance of spatial conservation planning based on prioritization efforts of the kind we undertook in this study. We also note that climatic influences on terrestrial systems are extremely dynamic and are pivotally linked to future national and global policy changes.

Landscape-level approach to conservation

Recent conservation literature has highlighted the importance of viewing shared habitats as coupled human–natural systems that are encompassed within ‘conservation landscapes’^{41,43}. Across zones, we found that most designated PAs, which constitute ~5% of India’s land area and span an average area of ~300 km² (ref. ⁴⁴), were included as priority sites. But these were embedded within larger landscapes that also included high priority non-PA locations. Contrary to our expectation that PAs would be over-represented in our results, 85% of the top 30% priority sites were outside PAs (Fig. 3). This finding was reinforced by the specific inclusion of ecosystems (such as the Open Natural Ecosystems referred to above) that are not part of India’s PA network and sites critical for the supply of ecosystem services. Interestingly, locations that constituted the top 30% priority ranks in our study were largely connected (Fig. 3), even when we did not explicitly impose connectivity parameters via the prioritization model. To examine this further, we generated the ‘clumpiness’ index, which compares priority adjacencies with what would be expected at random⁴⁵. The index ranges from –1 (disaggregated) to +1 (clumped). When examined at the countrywide level, the index value was 0.80; within-zone analyses produced index values ranging from 0.77 to 0.88, indicating the high aggregation of priority sites at both spatial scales. Although our zone-wise analyses allowed for better geographic representation of sites, they still indicated a lack of contiguity across some zone boundaries (Fig. 3a). These aspects together emphasize that functional connectivity is an important consideration when implementing landscape-scale conservation interventions within our priority sites⁴⁶.

Traditional PAs, which typify a land-sparing approach to conservation, are mostly focused on forested habitats in the country. A substantially large proportion of biodiversity continues to inhabit unprotected, human-use landscapes, warranting a land-sharing approach. Realizing conservation and human well-being goals in the landscapes that encompass the 30% priority areas will therefore necessitate invoking other effective area-based conservation measures (OECMs). The core tenets of these approaches hinge fundamentally on effective and equitable models of governance that are fully cognizant of the complexities of socio-ecological systems, which are only beginning to be recognized in environmental and conservation policy⁴⁷. In India, this may be achieved through the implementation of existing frameworks, for instance, in locations where communities are granted Community Forest Rights, and by declaring areas as Critical Wildlife Habitats under the Forest Rights Act, provisions that, at present, remain extremely underused. Our spatially explicit landscape approach that considers that linked biodiversity–ecosystem service dimensions can only succeed if the beneficiaries of ecological restoration, and those who may be otherwise impacted (typically the marginalized sections of society), are addressed in policies and implementation.

Synergies and trade-offs within and between themes

In the final prioritization assessment, we assigned equal weighting to all input themes (equal but negative weight for Threats). We ascertained the synergies and trade-offs between themes by examining alternative scenarios in which (1) areas with high human impacts were prioritized rather than penalized, that is, Threats-focused assessment, and (2) Habitats, Ecosystem Services and Biodiversity were each iteratively afforded higher weighting than the others (see the Methods section for details). While there was reasonable concordance between the results from our balanced scenario (themes with equal weights) and those from individual theme-focused scenarios, some locations showed stark mismatches indicative of trade-offs (Supplementary Figs. 3–5). These trade-offs may reflect regional peculiarities: biodiversity conservation could constrain provisioning services such as non-timber forest products or livestock grazing in certain locations (such as PAs), and an increase in tree cover through habitat (mis)management could alter hydrological services⁴⁸. Such trade-offs could also be spatially asynchronous: upstream water abstraction from rivers and disruption of sediment transport by dams can have deleterious impacts on aquatic biodiversity and ecosystem services downstream. All these cases collectively highlight the problems of prioritizing areas based on

single themes or biasing prioritization on one theme over the other(s). Of course, there is also a trade-off in choosing locations that are of high conservation value and relatively secure (avoiding regions of high Threats) or those that are vulnerable (prioritizing Threats). Ideally, the former are suited to interventions involving preservation (for example, reserve design and OECMs), and the latter, to interventions involving mitigation or restoration (for example, mitigation of linear infrastructure impacts).

Besides the differences between the themes described above, we acknowledge that there could be trade-offs even within the thematic dimensions considered here. For instance, we found very low spatial concordance between carbon and blue water flux, and a marginally higher correlation between carbon and green water flux; the spatial mismatch was more pronounced at locations where values of above- and below-ground carbon reached very high levels (Supplementary Fig. 6). This relationship is not unique to our study area, with a previous report indicating that carbon sequestration and hydrological services do not necessarily work in synergy⁴⁹. Regulatory services, such as hydrological or water services, can be generated only for a certain size of catchment, depending on factors such as climate, soil, geology and vegetation type. And while there could be synergy between carbon and water services to people at a local or regional scale⁵⁰, transpiration from a large patch of forest can increase rainfall in other regions and benefit agriculture and communities elsewhere⁵¹. These considerations of synergies and trade-offs are particularly relevant when viewed in the context of the drastic biodiversity declines documented in the recent Living Planet Report⁵². This report reiterates the important links between biodiversity loss, climate change, ecosystem services (water) and food security— aspects addressed in this study through our multicriteria assessment and by allocating equal importance (weights) to the constituent input attributes.

Linking landscape prioritization and administration

Overlaying administrative (district) boundaries, we highlight 338 districts that play a key role in maintaining India's biodiversity and ecosystem services (Fig. 4a,b). Of these, 169 are 'high priority' districts, where natural habitats, biodiversity and ecosystem services are currently at optimal levels and span a large spatial extent. The next 169 are 'potential priority' districts (Fig. 4b), where the three aspects are currently at suboptimal levels in terms of the extent of coverage. At this point, our aim was also to link our results with India's aspirational districts, identified by the Indian government for economic development (that is, the National Institute for Transforming India (NITI) Aayog aspirational districts; see Methods for details).

Considered in conjunction with our results, we recommend that for locations where the NITI aspirational districts overlap with 'high priority' districts (Fig. 4c), the management focus needs to be on the retention of habitats, ecosystem services and biodiversity through both state-driven and participatory approaches. This will require deprioritizing mega-infrastructure projects while promoting equitable models of nature protection in addition to the demarcation of PAs. Such approaches may entail community stewardship for biodiversity protection, co-management of habitats outside PAs and nature-friendly livelihood development within larger conservation landscapes. In locations where aspirational districts overlap with 'potential priority' districts, the management focus, in addition to the retention of important sites, should also aim for proactive rewilding and ecological restoration efforts. Here, targeted actions are essential to mitigate the negative impacts of infrastructure development through economically incentivized instruments, such as paying for ecosystem services, promoting agroforestry and, where appropriate, demarcating conservation and/or community reserves (PA categories that are not exclusionary but mandate sustainable use of resources by local communities). These localized efforts and interventions need to be synergistically integrated

into district- and state-level plans to ensure tangible impacts. For further deliberation, we provide maps showing the spatial overlaps between NITI aspirational districts and (1) the top 30% priority areas and (2) threat ranks across the country in Supplementary Fig. 7.

Practical considerations for on-ground implementation

This study represents a country-level assessment that attempts to link eco-socio-administrative dimensions for landscape-level prioritization in India. We submit, however, that the spatial scale and resolution at which we carried out this assessment were constrained by several limitations associated with data availability that are commonplace across developing countries as well as for global-level datasets alike. Our metric of species diversity, for instance, relied on range maps derived from the International Union for Conservation of Nature (IUCN) that do not have uniform accuracy across species⁵³. In fact, range maps for many rare, endemic and data-deficient species in India were either unavailable or excluded from our assessment because they were completely inaccurate. We also used only a subset of ecosystem services deemed important for human well-being; services such as pollination, forest produce extraction, rangeland services or freshwater dependence could not be included due to the unavailability of spatially explicit data. Incorporating these features (when such information becomes available) may yield a more accurate and comprehensive assessment of priority locations and landscapes.

The relationship between ecosystem services and poverty alleviation (especially in the aspirational and poorer districts of India, as defined by the NITI Aayog discussed above) is also driven by the political economy of negotiations between stakeholders and those who manage or regulate ecosystem services⁵⁴. A detailed understanding of the associated vulnerabilities is important to enable ecosystem services to benefit the poor. If not internalized, an ecosystem services approach to conservation planning may fail because of resistance from those who are excluded or those who stand to lose most from such undertakings. The actions discussed above will also be critical in other countries of the Global South, where a large proportion of the people are directly dependent on forests and other natural ecosystems for their livelihoods. The nuances and location-based differences in prescriptive actions that we have discussed here reiterate the importance of (1) spatially explicit prioritization assessments incorporating regional expertise on biodiversity and threats, and (2) mainstreaming biodiversity and ecosystem service goals into district and state management plans for socio-economic development. In this context, India's ambitious endeavours on climate change mitigation through the reversal of land degradation (26 million ha), the Green India Mission⁵⁵ and renewable energy projects initiated under the intended Nationally Determined Contribution (NDC) will require a degree of reorientation to include biodiversity and ecosystem service considerations.

The recognition of links between ecosystem integrity and human health has led to broad and ambitious goals under global targets such as the Post-2020 Global Biodiversity Framework. However, repercussions of the COVID-19 pandemic have underscored the wide geographical imbalance in the capacities, resources and vulnerabilities of different countries to achieve such goals. The Global South, in particular, aims to conserve biodiversity and meet climate change goals under scenarios in which people have high dependency on natural resources⁵⁶, coupled with aspirations of economic progress and better standards of human life. To address these expectations, national-scale prioritization exercises such as ours, which combine conservation priorities, human well-being indices, economic development and infrastructure considerations, can guide countries and governments towards meeting international targets set for the next decade (for example, see ref. ⁵⁷); linkages between prioritization exercises and existing government schemes and administrative boundaries are crucial in this regard^{53,58}.

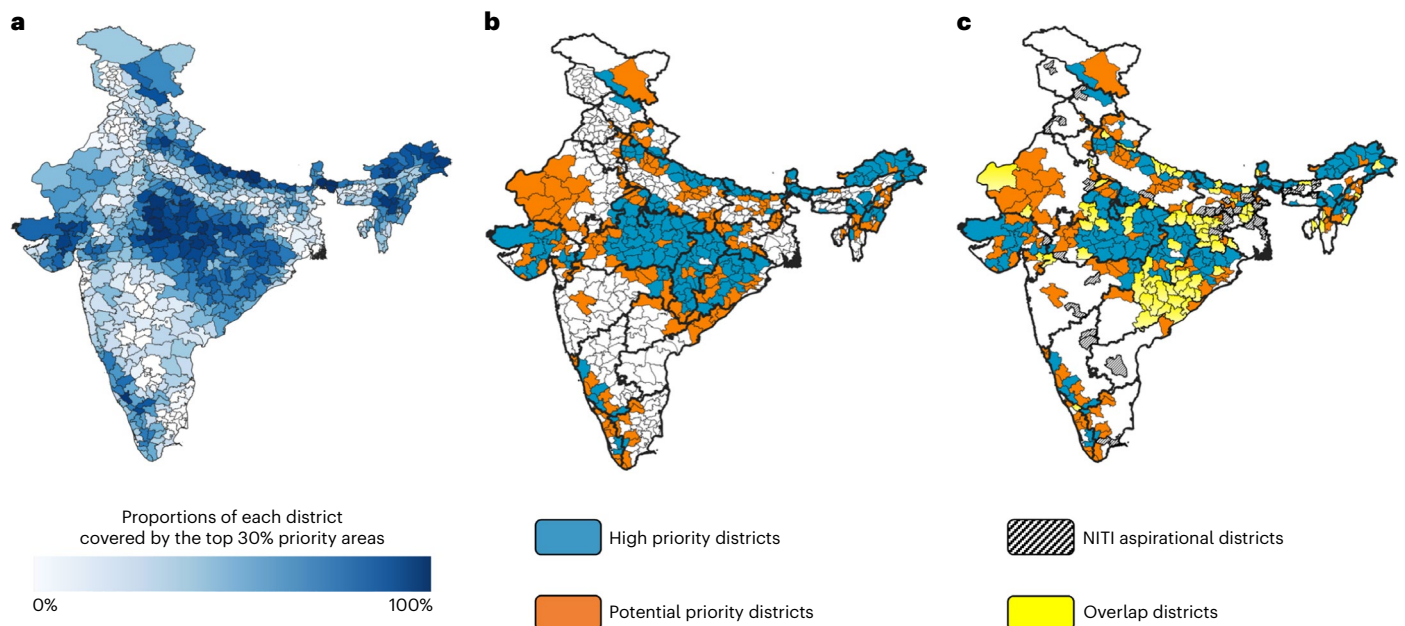


Fig. 4 | Priority areas and India's administrative units. **a**, Proportions of each district covered by areas identified as the top 30% priority locations. **b**, Districts in the top quantile (25%) identified as 'high priority' districts (169) and the next 25% quantile identified as 169 'potential priority' districts (169). **c**, NITI Aayog

aspirational districts (112) earmarked by the Government of India and their overlap with the 338 priority districts identified in this study (72 districts overlap). The darker lines in **b** and **c** denote state boundaries.

In the context of elevated competition for scarce land and water, exacerbated by climate change, the importance of our framework lies in its ability to objectively and effectively address trade-offs at the intersection of sustainable development goals, conservation of biodiversity and ecosystem services.

Methods

Framework for prioritization

The main goal of our study was to prioritize representative landscapes for biodiversity conservation, securing ecosystem services and human well-being targets, while balancing these with the economic aspirations of 1.4 billion people. Our prioritization exercise is part of a larger programme aimed at mainstreaming biodiversity conservation into the discourse on development and human well-being—the Government of India's National Mission for Biodiversity and Human Well-Being (NMB-HWB)⁵⁹. Recognizing the importance of delineating, characterizing and evaluating functional landscapes, the NMBHWB set up a working group in 2020 that was tasked with deliberating on and determining landscape-level approaches to biodiversity conservation, keeping nature's benefits to human well-being as the central theme. Through consultations with 42 experts from across the country, the working group first outlined the need for, salient features of and prerequisites for a priority-setting exercise. Subsequently, the working group engaged with 18 field and domain experts (the authors of the present study) to undertake the prioritization exercise in India.

Prioritization approach

We used a two-step prioritization approach (Fig. 1) to ensure representation of geographies and ecoregions across India. We first chose biogeographic zones ('zones') as described by Rodgers and Panwar⁶⁰ as an appropriate level of primary spatial classification. This level of classification splits the country into zones that have some similarity in biogeography, while across zones, they capture diversity of species, ecosystems and human–nature relationships. The country has ten zones: (1) Trans-Himalayas, (2) Himalayas, (3) deserts, (4) semi-arid, (5) Western Ghats, (6) Deccan plateau, (7) Gangetic plains, (8) Northeast

India, (9) coasts and (10) islands. We excluded coasts and islands from our analyses as we deemed them to be unique and requiring a separate treatment of biodiversity, ecosystem services and threats. The eight selected zones are shown in Fig. 1 (additional descriptions are provided in Supplementary Table 1). We then identified three broad focus themes, each of which encompassed a set of criteria for prioritization.

- (1) We considered natural habitats that require inclusion in priority landscapes. These layers, with zone-specific sets of priority ecosystems, represented our Habitats theme.
- (2) Recognizing the increasing emphasis on human–nature links and the joint well-being of biodiversity and people, we considered Ecosystem Services as the second theme.
- (3) Species diversity, biodiversity hotspots and locations of species population sources collectively formed the Biodiversity theme.

Lastly, we included a Threats theme to recalibrate conservation priorities based on spatial variation of anthropogenic pressures and impacts on natural ecosystems and biodiverse areas that provision essential ecosystem services. The full list of input layers is presented in Fig. 1 and detailed in Supplementary Table 2.

Spatial prioritization

There are several approaches to conducting spatial prioritization analyses, depending on the objectives of the study, type(s) of spatial data available and the optimization functions of interest, along with the corresponding software programs, of which MARXAN and Zonation are the most widely used^{18,61–64}. Zonation takes information on multiple input features to produce conservation ranks across the entire area of interest. Depending on the metrics used and the analytical specifications, it is possible to use either program to yield comparable results⁶⁵. We found Zonation to be well-suited for our analysis because it allowed us to seamlessly combine feature data (0/1) with quantitative data on ecosystem services across large regions at a relatively fine spatial resolution. The program is also robust to differences in scale (range of values) across different input layers. The program's algorithm follows an iterative process to rank cells (in our case, 1 km² pixels) within

the area of interest by excluding cells one at a time and measuring the collective conservation value of retained cells. In other words, cells with the lowest values are removed first and those with the highest values are retained until the end. The final output thus generated is an optimized map whose pixels are ranked according to relative priority values. For additional details, see Moilanen et al.⁶². For each zone, we conducted a set of six prioritization analyses (four theme-wise runs and two composite runs) as explained below.

Habitats. We used data from Roy et al.⁶⁶ with 156 land-cover classes across the country. We first reduced the data into 28 habitat classes by grouping together similar land-cover classes, broadly following the forest-type classification of Champion and Seth⁶⁷. For instance, the land-cover types labelled 'Grassland', 'Human-made grassland', '*Lasiurus-Panicum* grassland', '*Cenchrus-Dactyloctenium* grassland', '*Aristida-Oropetium* grassland' and '*Sehima-Dichanthium* grassland' were reclassified collectively as 'Grasslands'. Data from 25 m² pixels of the original dataset were resampled at a 1 km² resolution; the value assigned to each 1 km² pixel for each of the 28 habitat classes reflected the proportion of 25 m² pixels of the corresponding class. For each zone, we further subselected habitat classes to retain (1) the dominant vegetation classes (covering > 1% of the total zone area) and (2) select, rare, vulnerable habitats, determined on the basis of our experience and knowledge of the landscape(s). For example, we included wet grasslands in the Northeast India zone due to their importance for ecology and livelihood, even though this habitat class covers only 0.25% of the zone. The final number of habitat types chosen for each zone thus varied between three (deserts zone) and ten (Western Ghats zone; Supplementary Table 2). All habitats were assigned equal weights for prioritization. We chose the 'core-area zonation' cell removal rule as it prioritizes pixels with the most important yet rare features; this way, pixels that contained high proportions of rare habitats were retained even if the other zone-wide dominant habitats within these pixels were low.

Ecosystem services. We identified and used three layers that collectively reflect key ecosystem services, for which we were able to obtain or generate spatially explicit metrics across the country. These were (1) blue water flux, the amount of flowing water or ground water available to help meet utilitarian needs and for ecological flows in rivers, (2) green water flux, the amount of water lost through surface evapo-transpiration, which contributes to multiple ecosystem services, from flood control in very wet regions to recycling as rainfall in other regions, and (3) carbon stock, a harmonized metric of above- and below-ground biomass carbon density calculated using woody plant, grassland and cropland biomass (Supplementary Table 2). While these do not represent a comprehensive set of ecosystem services, we believe that they capture two critical policy mandates for India: water security and climate change mitigation. We assigned equal weights to all three layers and chose the 'additive benefit function' (ABF) cell removal rule in Zonation to ensure that locations with relatively high values of all three features are prioritized higher than areas where individual features or subsets of the three features had high values.

Biodiversity. India supports an extremely high diversity of wildlife (inside and outside designated PAs); most of these species are found in higher densities here than elsewhere across their range. In considering attributes that best represent biodiversity, our goal was twofold. First, we wanted to include areas that support high populations of species and, second, those areas that support and adequately represent the wide diversity of species outside PAs. We therefore used PAs, reasonably assuming that these locations currently harbour source populations of many species. In addition, we also used Key Biodiversity Areas (KBAs)⁶⁸ to include locations outside designated PAs with a high diversity of species that are of ecological or conservation importance (that is, PAs and KBAs did not spatially overlap in our analysis and were 0/1 data).

Next, we collated distribution ranges of imperilled mammals, birds, amphibians and reptiles—species categorized as Critically Endangered, Endangered, Vulnerable or Threatened as per the IUCN Red List (IUCN 2020). We limited our criteria to only include species for which the range distribution data were reliable; for a subset of species, we also corrected and modified the IUCN maps (based on expert consultation) before inclusion in our analyses. For each zone, we stacked the species maps and generated a beta-diversity index, calculated as the Bray–Curtis distance between a focal cell and a hypothetical reference cell that had all threatened species of the corresponding zone. This gave us an index of zone-wise species turnover. We assigned equal weights to all three layers (treating PAs and KBAs with high population densities with the same importance as the layer characterizing species turnover) and chose the ABF cell removal rule in Zonation to prioritize areas based on this theme.

Threats. We identified 11 attributes that negatively impact biodiversity, ecosystem services and habitats to varying degrees and that are likely to reduce the ease of implementing conservation actions. These were human population density, livestock population density, urbanization, linear infrastructure, mines, river fragmentation, agricultural expansion, vegetation greening and vegetation browning (both of which can have positive or negative impacts on ecosystem services and biodiversity), future climate warming and future rainfall anomaly (see Supplementary Table 2 for details). We assigned zone-specific weights to these layers following a consensus approach based on the collective field knowledge of the assessors. The weights assigned to the threats varied across zones, reflecting the relative severity of impacts in each zone (see Supplementary Table 3 for zone-wise threat ranks). We chose the ABF cell removal rule again so that locations under more severe threat and those under multiple threats were ranked high. This ranking thus combines information on the presence and intensity of threats across space.

Composite. In addition to the four sets of theme-wise analyses described above, we also undertook two composite analyses. First, we used the outputs from the theme-wise analyses of Habitats, Ecosystem Services and Biodiversity. All input layers were assigned equal weights and the ABF cell removal rule was specified. Second, we used the aforementioned three layers along with the rank output from the Threats analysis. In this case, we assigned equal positive weights to Habitats, Ecosystem Services and Biodiversity and an equal but negative weight to Threats (that is, 1, 1, 1 and -1; see ref.⁶⁹ for the justification of using equal weights for input attributes). The first analysis thus gave us an assessment of conservation importance, while the second incorporated feasibility. To assess the sensitivity of our weighting scheme, we performed similar composite analyses to consider alternate scenarios in which (1) the Threats layer was assigned a weight of +1, such that areas with high human impacts are also prioritized rather than penalized, and (2) the Threats layer was weighted -1, but the Habitats, Ecosystem Services and Biodiversity were each iteratively assigned higher weights than the other two, that is, 1, 0.5 and 0.5. These outputs are presented in Supplementary Figs. 2–5.

Alignment with global and national policy

We collated results across zones post-prioritization to demarcate the top 30% priority areas in the country so as to align our results with the Post-2020 Global Biodiversity Framework targets. The areas were selected on the basis of the pixel ranks in each zone; these covered 30% of the area in every zone and therefore collectively included 30% of the country (excluding the coasts and islands). This approach ensured representation of unique features from each zone, encompassing a more diverse set of habitats, ecosystem services, biodiversity and associated threats. We then overlaid administrative units (districts) and calculated the proportion of each district covered by pixels with the top 30% ranks. We chose two sets of districts: (1) those in the top

25% quantile, which we term ‘high priority’ districts, and (2) those in the subsequent 25% quantile, which we term ‘potential priority’ districts. We juxtaposed these results with districts earmarked by the Government of India’s flagship Aspirational Districts Programme for economic development. India’s Aspirational Districts Programme was launched in 2018 by the Government of India through the think tank, the NITI Aayog. The NITI Aayog replaced the erstwhile Planning Commission with the aim of achieving sustainable development goals for the country. The programme has earmarked over 100 of India’s most economically backward districts as ‘aspirational’ districts to help reduce regional imbalances in development. The programme aims to reduce disparity across regions and improve baseline rankings of district-level development using real-time data on 49 indicators across five thematic sectors, namely health and nutrition, education, infrastructure, financial inclusion and skill development. Of particular relevance to our assessment is the programme’s thrust towards increasing road connectivity and intensification of agriculture⁷⁰ (additional details are available at www.niti.gov.in/aspirational-districts-programme). Our maps were generated with the goal of directly offering prescriptive management actions for the governments of the corresponding administrative units.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All the analyses were based on open source datasets; details are provided in Supplementary Table 2. The input data used in the analyses can be accessed from <https://doi.org/10.6084/m9.figshare.21678518>.

References

- Levett, R. Sustainability indicators—integrating quality of life and environmental protection. *J. R. Stat. Soc. A* **161**, 291–302 (1998).
- Harrison, P. A. Ecosystem services and biodiversity conservation: an introduction to the RUBICODE project. *Biodivers. Conserv.* **19**, 2767–2772 (2010).
- Otero, I. et al. Biodiversity policy beyond economic growth. *Conserv. Lett.* **13**, e12713 (2020).
- Seppelt, R., Lautenbach, S. & Volk, M. Identifying trade-offs between ecosystem services, land use, and biodiversity: a plea for combining scenario analysis and optimization on different spatial scales. *Curr. Opin. Environ. Sustain.* **5**, 458–463 (2013).
- 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, 2019); accessed from <https://ipbes.net/document-library-categories>
- Dinerstein, E. et al. A “Global Safety Net” to reverse biodiversity loss and stabilize Earth’s climate. *Sci. Adv.* **6**, eabb2824 (2020).
- Ostrom, E. A general framework for analyzing sustainability of social-ecological systems. *Science* **325**, 419–422 (2009).
- Bennett, E. M. et al. Linking biodiversity, ecosystem services, and human well-being: three challenges for designing research for sustainability. *Curr. Opin. Environ. Sustain.* **14**, 76–85 (2015).
- Haines-Young, R & Potschin, M. in *Ecosystem Ecology: A New Synthesis* (eds Raffaelli, D. & Frid, C.) 110–139 (Cambridge Univ. Press, 2010).
- Tallis, H. M. & Kareiva, P. Shaping global environmental decisions using socio-ecological models. *Trends Ecol. Evol.* **21**, 562–568 (2006).
- Steffen, W. et al. Trajectories of the Earth System in the Anthropocene. *Proc. Natl Acad. Sci. USA* **115**, 8252–8259 (2018).
- Wilson, K. A. et al. Conserving biodiversity efficiently: what to do, where, and when. *PLoS Biol.* **5**, e223 (2007).
- Moilanen, A. et al. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. *Proc. R. Soc. B* **272**, 1885–1891 (2005).
- Moilanen, A. et al. Balancing alternative land uses in conservation prioritization. *Ecol. Appl.* **21**, 1419–1426 (2011).
- Kremen, C. et al. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* **320**, 222–226 (2008).
- Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M. & Wilson, K. A. Conservation planning in a changing world. *Trends Ecol. Evol.* **22**, 583–592 (2007).
- Sayer, J. et al. Ten principles for a landscape approach to reconciling agriculture, conservation, and other competing land uses. *Proc. Natl Acad. Sci. USA* **110**, 8349–8356 (2013).
- Watts, M. E. et al. Marxan with Zones: software for optimal conservation based land- and sea-use zoning. *Environ. Model. Softw.* **24**, 1513–1521 (2009).
- Arkema, K. K. et al. Embedding ecosystem services in coastal planning leads to better outcomes for people and nature. *Proc. Natl Acad. Sci. USA* **112**, 7390–7395 (2015).
- Wyborn, C. & Evans, M. C. Conservation needs to break free from global priority mapping. *Nat. Ecol. Evol.* **5**, 1322–1324 (2021).
- Jenkins, C. N., Pimm, S. L. & Joppa, L. N. Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl Acad. Sci. USA* **110**, e2602–e2610 (2013).
- Brum, F. T. et al. Global priorities for conservation across multiple dimensions of mammalian diversity. *Proc. Natl Acad. Sci. USA* **114**, 7641–7646 (2017).
- Silveira, F. A. et al. Biome Awareness Disparity is BAD for tropical ecosystem conservation and restoration. *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2664.14060> (2021).
- Bond, W. J. & Parr, C. L. Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biol. Conserv.* **143**, 2395–2404 (2010).
- Veach, V., Di Minin, E., Pouzols, F. M. & Moilanen, A. Species richness as criterion for global conservation area placement leads to large losses in coverage of biodiversity. *Divers. Distrib.* **23**, 715–726 (2017).
- Venter, O. et al. Targeting global protected area expansion for imperiled biodiversity. *PLoS Biol.* **12**, e1001891 (2014).
- Potapov, P. et al. The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013. *Sci. Adv.* **3**, e1600821 (2017).
- Jung, M. et al. Areas of global importance for conserving terrestrial biodiversity, carbon and water. *Nat. Ecol. Evol.* **5**, 1499–1509 (2021).
- First Draft of the Post-2020 Global Biodiversity Framework (CBD, 2021); accessed from www.cbd.int/conferences/post2020
- Westgate, M. J., Barton, P. S., Lane, P. W. & Lindenmayer, D. B. Global meta-analysis reveals low consistency of biodiversity congruence relationships. *Nat. Commun.* **5**, 3899 (2014).
- Cadotte, M. W. & Tucker, C. M. Difficult decisions: strategies for conservation prioritization when taxonomic, phylogenetic and functional diversity are not spatially congruent. *Biol. Conserv.* **225**, 128–133 (2018).
- Madhusudhan, M. D. & Vanak, A. T. (2022). Mapping the distribution and extent of India’s semi-arid open natural ecosystems. *Journal of Biogeography* **00**, 1–11; <https://doi.org/10.1111/jbi.14471>
- Wastelands Atlas of India 2019 (Department of Land Resources, Ministry of Rural Development and the National Remote Sensing Centre, Indian Space Research Organisation, Department of Space, Government of India, 2019); www.dolr.gov.in/documents/wasteland-atlas-of-india

34. Krishnaswamy, J., John, R. & Joseph, S. Consistent response of vegetation dynamics to recent climate change in tropical mountain regions. *Glob. Change Biol.* **20**, 203–215 (2014).
35. Parida, B. R., Pandey, A. C. & Patel, N. R. Greening and browning trends of vegetation in India and their responses to climatic and non-climatic drivers. *Climate* **8**, 92 (2020).
36. Piao, S. et al. Characteristics, drivers and feedbacks of global greening. *Nat. Rev. Earth Environ.* **1**, 14–27 (2020).
37. Martin, D. A. et al. Land-use trajectories for sustainable land system transformations: identifying leverage points in a global biodiversity hotspot. *Proc. Natl Acad. Sci. USA* **119**, e2107747119 (2022).
38. Pandit, M. K. & Grumbine, R. E. Potential effects of ongoing and proposed hydropower development on terrestrial biological diversity in the Indian Himalaya. *Conserv. Biol.* **26**, 1061–1071 (2012).
39. Nayak, R. et al. Bits and pieces: forest fragmentation by linear intrusions in India. *Land Use Policy* **99**, 104619 (2020).
40. Srinivasan, U. et al. Oil palm cultivation can be expanded while sparing biodiversity in India. *Nat. Food* **2**, 442–447 (2021).
41. Vasudev, D., Goswami, V. R., Srinivas, N., Syiem, B. L. N. & Sarma, A. Identifying important connectivity areas for the wide-ranging Asian elephant across conservation landscapes of Northeast India. *Divers. Distrib.* **27**, 2510–2526 (2021).
42. Goswami, V. R., Vasudev, D., Joshi, B., Hait, P. & Sharma, P. Coupled effects of climatic forcing and the human footprint on wildlife movement and space use in a dynamic floodplain landscape. *Sci. Total Environ.* **758**, 144000 (2021).
43. Rodrigues, R. G., Srivathsa, A. & Vasudev, D. Dog in the matrix: envisioning countrywide connectivity conservation for an endangered carnivore. *J. Appl. Ecol.* **59**, 223–237 (2022).
44. Ghosh-Harihar, M. et al. Protected areas and biodiversity conservation in India. *Biol. Conserv.* **237**, 114–124 (2019).
45. Hesselbarth, M. H., Sciaiani, M., With, K. A., Wiegand, K. & Nowosad, J. Landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* **42**, 1648–1657 (2019).
46. Brennan, A. et al. Functional connectivity of the world's protected areas. *Science* **376**, 1101–1104 (2022).
47. Alves-Pinto, H. et al. Opportunities and challenges of other effective area-based conservation measures (OECMs) for biodiversity conservation. *Perspect. Ecol. Conserv.* **19**, 115–120 (2021).
48. Joshi, A. A., Sankaran, M. & Ratnam, J. 'Foresteering' the grassland: historical management legacies in forest-grassland mosaics in southern India, and lessons for the conservation of tropical grassy biomes. *Biol. Conserv.* **224**, 144–152 (2018).
49. Chisholm, R. A. Trade-offs between ecosystem services: water and carbon in a biodiversity hotspot. *Ecol. Econ.* **69**, 1973–1987 (2010).
50. Clark, B., DeFries, R. & Krishnaswamy, J. India's commitments to increase tree and forest cover: consequences for water supply and agriculture production within the Central Indian Highlands. *Water* **13**, 959 (2021).
51. Paul, S., Ghosh, S., Rajendran, K. & Murtugudde, R. Moisture supply from the Western Ghats forests to water deficit east coast of India. *Geophys. Res. Lett.* **45**, 4337–4344 (2018).
52. Almond, R. E. A., Grooten, M., Juffe Bignoli, D. & Petersen, T. (eds) *Living Planet Report 2022—Building a Nature-Positive Society* (WWF, 2022).
53. Srivathsa, A. et al. Opportunities for prioritizing and expanding conservation enterprise in India using a guild of carnivores as flagships. *Environ. Res. Lett.* **15**, 064009 (2020).
54. Vira, B. et al., Negotiating trade-offs: choices about ecosystem services for poverty alleviation. *Econ. Polit. Wkly* 67–75 (2012).
55. Ravindranath, N. H. & Murthy, I. K. Greening India mission. *Curr. Sci.* **99**, 444–449 (2010).
56. Fedele, G., Donatti, C. I., Bornacelly, I. & Hole, D. G. Nature-dependent people: mapping human direct use of nature for basic needs across the tropics. *Glob. Environ. Change* **71**, 102368 (2021).
57. Strassburg, B. B. et al. Global priority areas for ecosystem restoration. *Nature* **586**, 724–729 (2020).
58. Belote, R. T. et al. Beyond priority pixels: delineating and evaluating landscapes for conservation in the contiguous United States. *Landsc. Urban Plan.* **209**, 104059 (2021).
59. Bawa, K. S. et al. Securing biodiversity, securing our future: a national mission on biodiversity and human well-being for India. *Biol. Conserv.* **253**, 108867 (2021).
60. Rodgers, W. A. & Panwar, H. S. *Planning a Wildlife Protected Area Network in India. Vol. 1. A Report* (Wildlife Institute of India, 1988).
61. Watts, M., Klein, C. J., Tulloch, V. J., Carvalho, S. B. & Possingham, H. P. Software for prioritizing conservation actions based on probabilistic information. *Conserv. Biol.* **35**, 1299–1308 (2021).
62. Moilanen, A. et al. Zonation: spatial conservation planning methods and software. Version 4. User Manual. *C-BIG*; <https://core.ac.uk/download/pdf/33733621.pdf> (2014).
63. Sierra-Altamiranda, A. et al. Spatial conservation planning under uncertainty using modern portfolio theory and Nash bargaining solution. *Ecol. Model.* **423**, 109016 (2020).
64. Silvestro, D., Gorla, S., Sterner, T. & Antonelli, A. Improving biodiversity protection through artificial intelligence. *Nat. Sustain.* **5**, 415–424 (2022).
65. Delavenne, J. et al. Systematic conservation planning in the eastern English Channel: comparing the Marxan and Zonation decision-support tools. *ICES J. Mar. Sci.* **69**, 75–83 (2012).
66. Roy, P. S. et al. Development of decadal (1985–1995–2005) land use and land cover database for India. *Remote Sens.* **7**, 2401–2430 (2015).
67. Champion, H. G. & Seth, S. K. *A Revised Survey of the Forest Types of India* (Government of India, 1968).
68. BirdLife International *World Database of Key Biodiversity Areas* (KBA Partnership, version March 2021); accessed from www.keybiodiversityareas.org/kba-data/request
69. Koschke, L., Fürst, C., Frank, S. & Makeschin, F. A multi-criteria approach for an integrated land-cover-based assessment of ecosystem services provision to support landscape planning. *Ecol. Indic.* **21**, 54–66 (2012).
70. Sarkar, T., Mishra, M. & Singh, R. B. in *Regional Development Planning and Practice* (eds Mishra, M. et al.) 205–232 (Springer, 2022).

Acknowledgements

This work was catalysed and supported by the Office of the Principal Scientific Adviser to the Government of India as part of the National Mission for Biodiversity and Human Well-Being. A.S. was supported by the Department of Science and Technology–Government of India's Innovation in Science Pursuit for Inspired Research Faculty Award. M.S. was supported by the Science and Engineering Research Board (SERB), Department of Science and Technology, Government of India (SERB DIA/2018/000038). We are grateful to J. Zacharias, V. Athreya, P. Bindra, A. Harihar, U. Ganguly, A. Kumar, M. Manuel, S. Babu, A. Kshetry, S. Nijhawan, M. Muralidharan, N. Namboothiri, Y. Jhala, K. S. Subin, S. Datta, M. Sen, S. Madhulkar, T. Thekaekara, V. Vasudevan, I. Anwardeen, S. Sahu, S. Reddy, V. Varadhan, K. T. Subramaniam, C. Madegowda, C. Meenakshi, K. Karanth, P. G. Krishnan, T. Dash, A. Chanchani and A. Bijoor for partaking in discussions on landscape-scale conservation in India. We thank K. Bawa and R. Chellam for their guidance, R.

G. Rodrigues, A. Samrat and N. Srinivas for assistance with data processing and compilation, and the National Centre for Biological Sciences–TIFR and Ashoka Trust for Research in Ecology and the Environment (part of the Biodiversity Collaborative) for facilitating this study. The authors received no specific funding for this work.

Author contributions

All the authors were involved in the conceptualization of the study. A.S., D.V. and T.N. led the analysis. A.S., D.V., T.N., A.D., R.N. and S.V. processed and analysed the data. A.S., D.V., V.R.G., A.N., J.K. and U.R. prepared the first draft. All authors provided critical feedback and approved the final version of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41893-023-01063-2>.

Correspondence and requests for materials should be addressed to Arjun Srivathsa or Uma Ramakrishnan.

Peer review information *Nature Sustainability* thanks Daniele Silvestro, Kayo Murakami and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

© The Author(s), under exclusive licence to Springer Nature Limited 2023, corrected publication 2023

¹National Centre for Biological Science, TIFR, Bengaluru, India. ²Wildlife Conservation Society-India, Bengaluru, India. ³Conservation Initiatives, Guwahati, India. ⁴Division of Biosciences, University College London, London, UK. ⁵Departments of Biology and Environmental Studies, Macalester College, Saint Paul, MN, USA. ⁶World Wildlife Fund, Delhi, India. ⁷Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, USA. ⁸Amity Institute of Forestry and Wildlife, Amity University, Noida, India. ⁹Wildlife Institute of India, Dehradun, India. ¹⁰Foundation for Ecological Research, Advocacy and Learning, Bengaluru, India. ¹¹Network for Conserving Central India, Gurgaon, India. ¹²World Resources Institute, New Delhi, India. ¹³School of Environment and Sustainability, Indian Institute for Human Settlements, Bengaluru, India. ¹⁴Ashoka Trust for Research in Ecology and the Environment, Bengaluru, India. ¹⁵Biodiversity Collaborative, Bengaluru, India. ¹⁶These authors contributed equally: Arjun Srivathsa, Divya Vasudev, Tanaya Nair, Jagdish Krishnaswamy, Uma Ramakrishnan. ✉e-mail: arjuns@ncbs.res.in; uramakri@ncbs.res.in

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

- | | |
|-----|-----------|
| n/a | Confirmed |
|-----|-----------|
- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
 - A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
 - The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
 - A description of all covariates tested
 - A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
 - A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
 - For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
 - For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
 - For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
 - Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection All the data used in this study are sourced from published literature or open-source databases. The Supplementary file(s) include all the data sources, citations, weblinks and detailed descriptions of the input variables used in the study.

Data analysis All the analyses were performed on software Zonation 4.0 (Moilanen 2014).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

We have uploaded all the input files on FigShare. We have provided the link to the repository in the Data availability statement (<https://doi.org/10.6084/m9.figshare.21678518>)

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We used countrywide data on habitats, biodiversity, ecosystem services and anthropogenic pressures in India to prioritize landscapes across India's biogeographic zones to target actions in meeting national and international conservation targets
Research sample	We used 45 variables sourced from published literature, open-data sets and governmental data portals as input data to conduct spatial prioritization analyses.
Sampling strategy	The input variables were selected based on a consensus approach with all co-authors partaking in discussions, providing justifications for their use (described in detail in the main MS as well as associated supplementary files. We only used those datasets for which spatially explicit information was available at the countrywide scale in India.
Data collection	The lead author was involved in data compilation with assistance from select co-authors, as acknowledged in the author contributions section.
Timing and spatial scale	Data used in the analyses correspond to papers/databases compiled over the last ~15 years.
Data exclusions	We focus on 8 of India's 10 biogeographic zones. We excluded (1) coasts and (2) islands, because they require a separate set of considerations (ecosystems services, biodiversity, human dependence, etc.) which were beyond the scope of this paper-- which focuses on landscape/riverscape prioritization.
Reproducibility	The datasets used are described in detail in the supplementary files, with the corresponding papers/datasets/website links/portals cited within the document. The software we used (Zonation) is also open-source and free to download.
Randomization	NA
Blinding	NA; we used published or open source data.
Did the study involve field work?	<input type="checkbox"/> Yes <input checked="" type="checkbox"/> No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology and archaeology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data
<input checked="" type="checkbox"/>	<input type="checkbox"/> Dual use research of concern

Methods

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging