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**35** PUBLICATIONS **323** CITATIONS

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
nature sustainability

Analysis

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

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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.

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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-being[4]. 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 functioning[9]. Siloed management approaches to meet conservation targets that ignore this interplay have failed to yield equitable and 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 intervention[12]. 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 corridors[15]. 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 policymakers[16]. This necessitates the adoption of 'landscape approaches' to conservation[17] 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 macro-scale, their real-world applications have been limited[20]. 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 occurs[4]. 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 ignored[23], habitats presumed to be 'unproductive' may not be prioritized (for example, grasslands[24]), indices such as species richness, which ignore community composition, may discount rarity or endemism[25], 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 altogether[28].

Achieving conservation goals, sustaining ecosystem services and ensuring human well-being while balancing economic development present formidable challenges in implementation[3]. 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 Framework[29], 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 Ecosystems[32] (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 policy[33]. 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
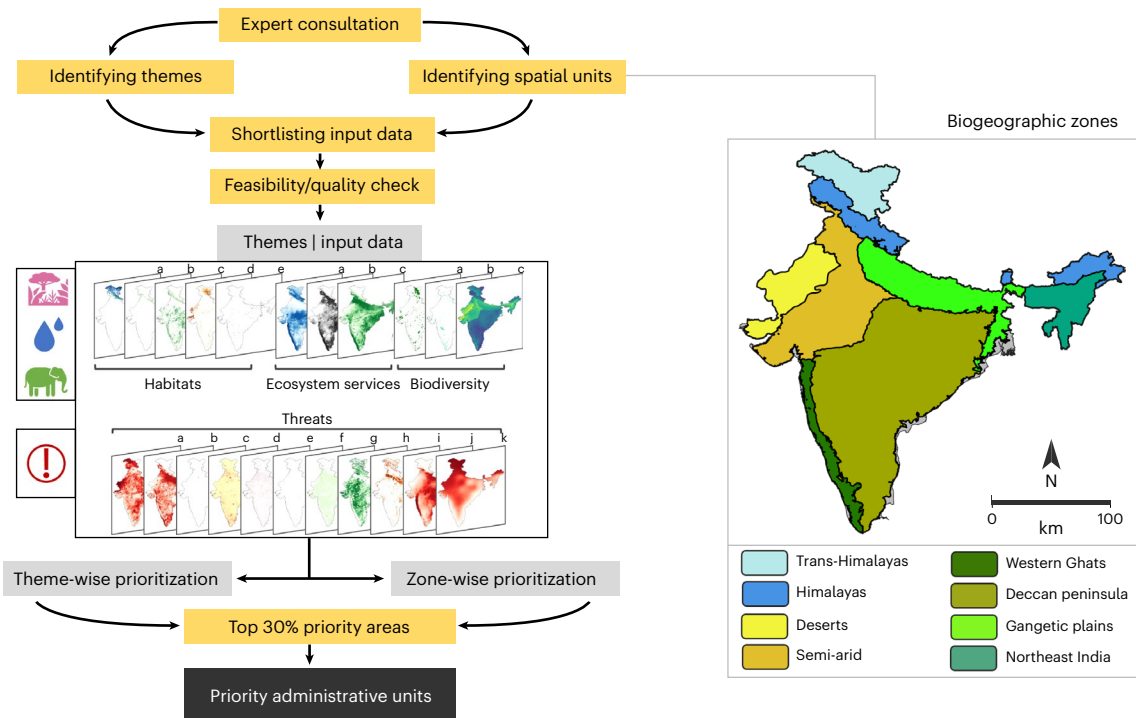
Fig. 1 | Schematic of the study framework and biogeographic zones of India. Themes and input layers identified for spatial prioritization: (1) Habitats (28 vegetation classes depicted as five composite panels), (2) Ecosystem services (blue water flux, above- and below-ground carbon and green water flux), (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).
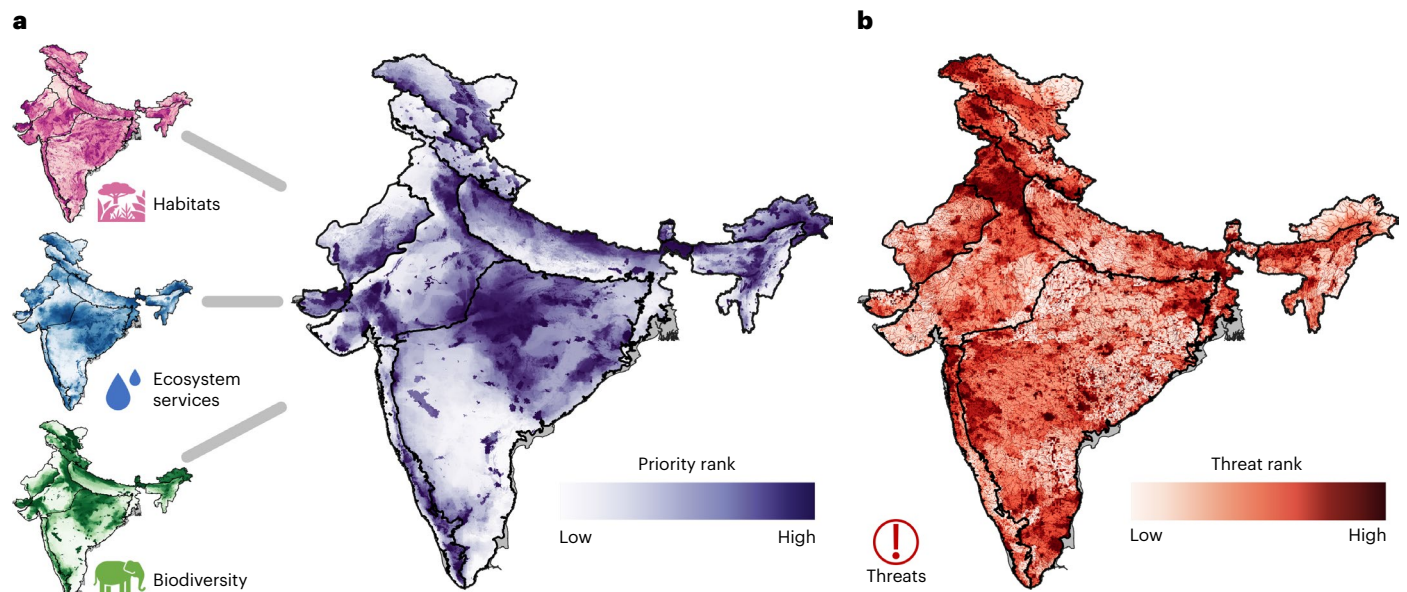
Fig. 2 | Theme-wise results from prioritization analyses. a, Priority maps based on Habitats (top left), Ecosystem Services (centre left), Biodiversity (bottom left) and the composite analysis of the three themes (right). **b**, Theme-specific results from the prioritization analysis of Threats.

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 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
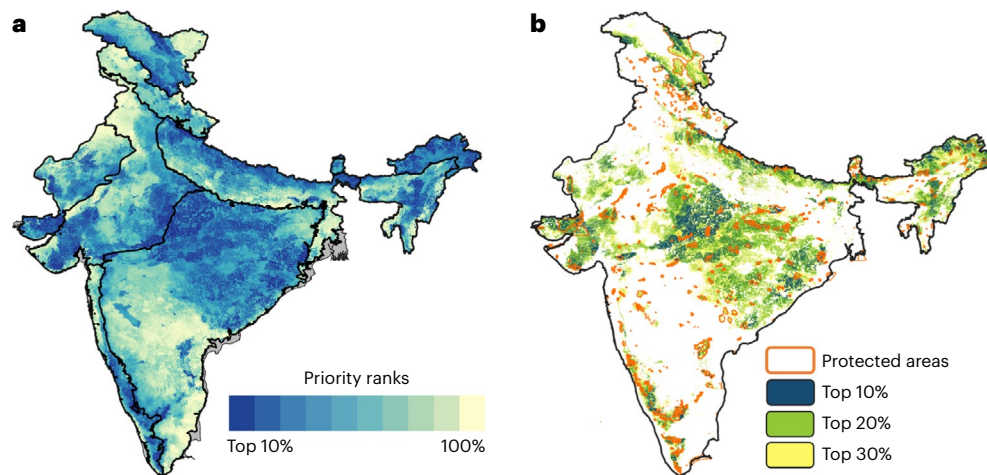
Fig. 3 | **Composite spatial priority maps and overlap with extant Protected Area network. a**, Conservation priority ranks for India, computed zone-wise and combined. **b**, Top 30% priority areas in each zone demarcated as a set of three 10% blocks. Designated PAs are overlaid to show the extent of overlap and spatial congruence with high priority locations.

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 CO_2 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 feasible[37]. 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 (for example, the expansion of oil palm plantations[40]) or (3) difficult to quantify in terms of their long-term consequences (for example, loss of connectivity[41]). 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 India[42]. 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 random[45]. 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 sites[46].

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 policy[47]. 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 services[48]. 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 synergy[49]. 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 scale[50], transpiration from a large patch of forest can increase rainfall in other regions and benefit agriculture and communities elsewhere[51]. 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 Report[52]. 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 de-prioritizing 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 species[53]. 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 services[54]. 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 Mission[55] 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.
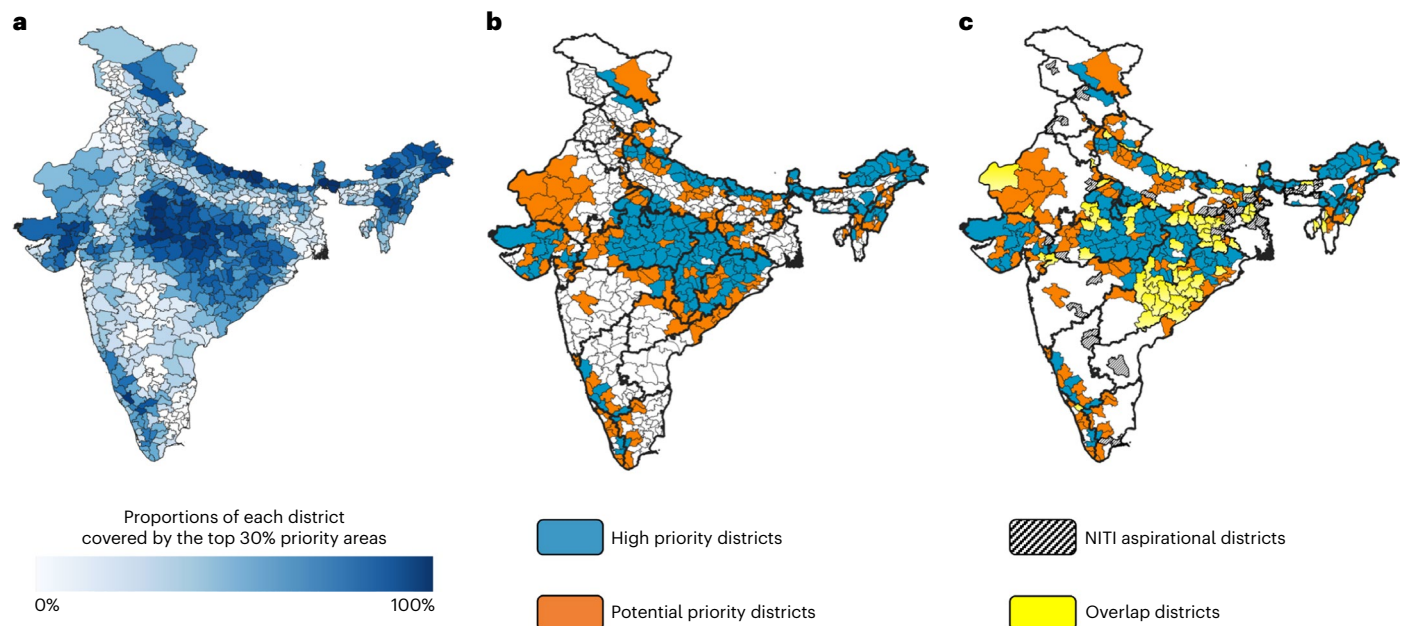
Fig. 4 | Priority areas and India's administrative units. a, Proportions of each district covered by areas identified as the top 30% priority locations. **b**, Districts in the top quantile (25%) identified as 'high priority' districts (169) and the next 25% quantile identified as 169 'potential priority' 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.

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 resources[56], 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]. 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 Panwar[60] 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 results[65]. 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 Seth[67]. For instance, the land-cover types labelled 'Grassland', 'Human-made grassland', '*Lasiurus–Panicum* grassland', '*Cenchrus–Dactyloctenium* grassland', '*Aristidia–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 agriculture[70] (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.

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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

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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.
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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.

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