PNAS PERSPECTIVE OPEN ACCESS

From science to impact: Conserving ecological connectivity in large conservation landscapes

Robin Naidoo[a,b,1], Cody Aylward[a], Wendy Elliott[c], Annika Keeley[d], Margaret Kinnaird[c], Michael Knight[e,f], Cristian-Remus Papp[g,h], Kanchan Thapa[i], and Rafael Antelo[j]

Edited by Silu Wang, University at Buffalo, Buffalo, NY; received July 23, 2024; accepted March 14, 2025 by Editorial Board Member Douglas J. Futuyma

Implementing ecological connectivity conservation in large landscapes requires cutting-edge science combined with consideration of ecological, socioeconomic, and cultural factors that collectively shape the outcomes of conservation efforts. We outline a theory of change (ToC) for connectivity conservation to improve the ecological condition of landscapes and biodiversity and the ecosystem services upon which humans depend. We review connectivity conservation efforts on four continents in large landscapes that span gradients of latitude, fragmentation, biodiversity value, socioeconomic characteristics, and the richness of data used to assess connectivity and target action. We share the substantial but variable progress made in each landscape and outline specific challenges to achieving conservation goals. Opportunities and challenges in public and private sectors can further leverage the potential of large-scale connectivity conservation to reduce isolation and improve gene flow in functional landscapes worldwide.

landscape connectivity | animal movement | gene flow

As the world's remaining natural areas become increasingly diminished in the Anthropocene (1, 2), ensuring that biodiversity strongholds remain connected is an important conservation priority (3, 4). Connected landscapes allow animals to access the daily, seasonal, and lifetime resources they require to survive and reproduce (5). Connected landscapes are particularly important for wide-ranging species (e.g., large terrestrial vertebrates), especially those with migratory or nomadic life histories that move hundreds or thousands of kilometers during their lifetime. For these species, a single protected area (PA) or other conservation unit may be insufficient to ensure population persistence (6). Because the median size of the world's terrestrial PAs is less than 1 km^2 (7), even smaller species may need areas with mixed land uses, including unprotected spaces such as public lands, private landholdings, and industrial concessions (8). In these mixed-use landscapes, gene flow and the persistence of species will only occur if connectivity among natural landscapes is conserved.

Methods to assess landscape connectivity are maturing and can be variously classified, including structural vs functional (9, 10) and single vs multiple species (11). Structural connectivity refers to the physical arrangement of landscape elements (e.g., size, habitat type) and assumes that animal movement is correlated with observed landscape structure. In contrast, functional connectivity explicitly considers movement, often by mapping "resistance surfaces" from a sample of satellite-collared animals and subsequent connectivity modeling, but more recently from direct observation of connectivity from collaborative, large-sample satellite-tagging studies (12, 13). Additional approaches include simulating animal movements and deriving connectivity metrics from simulated movement trajectories (14, 15). Furthermore, next-generation sequencing and the increasing availability of big-data genomic resources and analytical pipelines are deepening our understanding of connectivity by examining how landscape structure affects gene flow within species (16, 17). These approaches have typically had a single-species focus, with multispecies or community-level assessments recognized as a necessary advance (11).

Despite substantial scientific progress, connectivity plans must achieve actual conservation gains. Unfortunately, the "implementation gap" long noted in general conservation planning (18) also occurs in connectivity conservation. While the importance of connectivity among PAs is recognized in conservation planning (19), managing unprotected lands requires different approaches compared to conventional PA conservation. As such, an interesting juxtaposition has emerged. On the one hand, sophisticated technology, algorithms, and big data are increasingly used to assess connectivity (13, 16). On the other hand, more qualitative "inclusive conservation" approaches are being adopted that prioritize cocreation and/or devolution of conservation interventions to Indigenous Peoples and local communities (IPs and LCs), as well as engaging public and private sectors in multistakeholder platforms (20, 21). A key

Author affiliations: [a]World Wildlife Fund (WWF)-US, Washington, DC 20037; [b]Department of Forest Resources Management, University of British Columbia, Vancouver, BC V6T 1Z4, Canada; [c]World Wide Fund for Nature (WWF)-International, PO Box 62440-00200, Nairobi, Kenya; [d]Center for Large Landscape Conservation, Bozeman, MT 59771; [e]World Wildlife Fund (WWF)-Namibia, PO Box 9681, Eros 10009, Windhoek, Namibia; [f]Center for African Conservation Ecology, Department of Zoology, Nelson Mandela University, Port Elizabeth 6031, South Africa; [g]Department of Taxonomy and Ecology, Faculty of Biology and Geology, Babeş-Bolyai University, Cluj-Napoca 400084, Romania; [h]World Wide Fund for Nature (WWF)-Romania, Bucharest 030925, Romania; [i]World Wide Fund for Nature (WWF)-Nepal, Kathmandu 44600, Nepal; and [j]World Wildlife Fund (WWF)-Bolivia, Santa Cruz, Bolivia

Author contributions: R.N., W.E., M. Kinnaird, M. Knight, C.-R.P., K.T., and R.A. designed research; R.N., W.E., A.K., M. Kinnaird, M. Knight, C.-R.P., K.T., and R.A. performed research; R.N., C.A., and A.K. analyzed data; and R.N., C.A., W.E., A.K., M. Kinnaird, M. Knight, C.-R.P., K.T., and R.A. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission. S.W. is a guest editor invited by the Editorial Board.

Copyright © 2025 the Author(s). Published by PNAS. This open access article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

PNAS policy is to publish maps as provided by the authors.

[1]To whom correspondence may be addressed. Email: robin.naidoo@wwfus.org.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2410937122/-/DCSupplemental.

Published July 28, 2025.

Downloaded from https://www.pnas.org by 108.64.85.146 on September 29, 2025 from IP address 108.64.85.146.

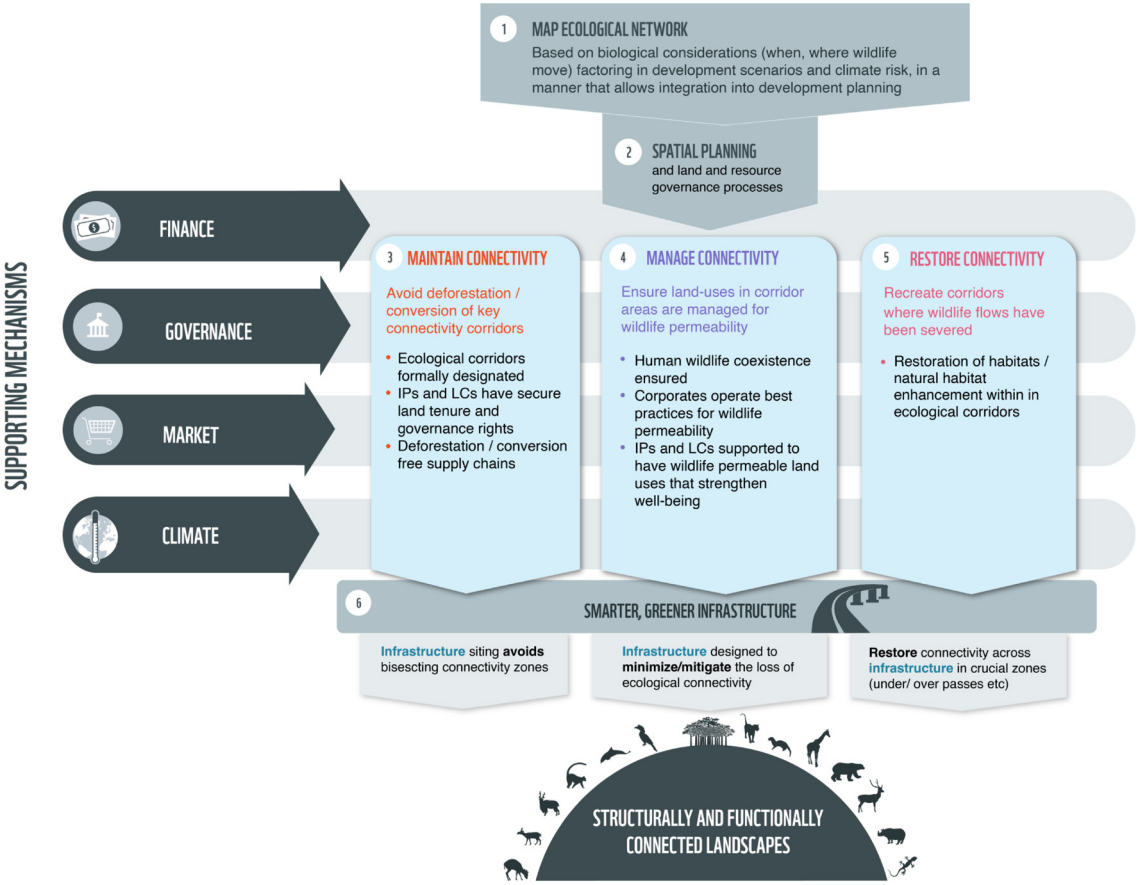


Fig. 1. Theory of change (ToC), large landscape connectivity conservation.

challenge is to integrate these contrasting approaches to deliver connectivity conservation results.

We describe how to bridge this gap and implement connectivity planning in large conservation landscapes. As an interdisciplinary team of research scientists and conservation practitioners, we have worked with numerous partners to build on best practices in connectivity science and community-based implementation and have developed a theory of change (ToC) that will achieve conservation impacts. We review progress in four globally significant conservation landscapes (22) that represent a diversity of ecosystems, socioeconomic contexts, and focal species. We find that while there has been progress over the last two decades, gains have been variable and functional connectivity has declined in three of the landscapes. We conclude by discussing how public and private sectors can complement local interventions to secure connectivity in large landscapes.

ToC for Large-Landscape Connectivity

Our ToC (i.e., a description of interventions that facilitates change and achieves outcomes) to guide ecological connectivity conservation summarizes lessons from multiple, long-term initiatives, including those discussed here (Fig. 1). Inspired by these landscape conservation experiences, it begins with mapping an area's "ecological network" [i.e., a system of core habitats connected by corridors; (23)]. The next step involves engaging in government-led spatial planning processes that define how infrastructure, agriculture, and other anthropogenic land uses occur in landscapes, as described for the Kavango-Zambezi and Terai Arc landscapes. By ensuring ecological corridors and the core sites they connect are considered in these plans, development can be shaped to maintain the ecological resilience of the landscape, rather than driving further habitat loss and fragmentation (24). The next elements of the ToC are maintaining, managing, and restoring connectivity.

Maintaining connectivity ideally involves formal designation of ecological corridors in national legislation. Bhutan, for example, has designated ecological corridors in which only conservation-compatible land uses are allowed (25). In other countries, ecological corridors may be designated as various types of protected or conserved areas where appropriate (26). Further approaches include ensuring supply chains are free of deforestation or other habitat conversion, corporate sector commitments that prohibit destruction of important connectivity areas, and where appropriate, supporting legal challenges to development plans that erode connectivity. From a local stakeholder perspective, supporting the land tenure rights of IPs and LCs can help to reduce threats to connectivity (27).

Managing connectivity involves ensuring ecological corridors enable wildlife movement and facilitate gene flow. Most ecological corridors contain a gradient of habitats ranging from natural to heavily modified, including agriculture, extractive industries, infrastructure, and human settlements. While large, mobile mammals can sometimes traverse inhospitable land cover types (28), encouraging primary-production sectors to manage farms, ranches, and extractive concessions for ecological connectivity and gene flow is imperative. This can

Downloaded from https://www.pnas.org by 108.64.85.146 on September 29, 2025 from IP address 108.64.85.146.

involve better placement of fencing; for example, fencing only younger palms that are vulnerable to wildlife damage, rather than entire oil palm concessions, retains substantial areas for wildlife movement in Sabah, Malaysia (29). Intact riparian zones within monocultures can function as movement corridors (30) and help reduce human–wildlife conflict (31). Involvement of IPs and LCs in corridor management is critical to incentivize locally led land uses that increase connectivity (see Pantanal-Chaco case study below), promote equitable benefit sharing, and strengthen human well-being (32). Successful management of connectivity should eventually increase gene flow among populations; monitoring can harness approaches to establish baseline population genetic structure (33) and distinguish between historical and recent (i.e., anthropogenic) population isolation (34).

Restoring connectivity is required when connectivity has been severed. Restoring forests or other natural elements within a corridor connecting two isolated protected areas can enhance ecosystem restoration, as it benefits the specific place being restored (i.e., the corridor) as well as the broader area being reconnected. Restoration can be led by multiple entities, including communities and corporations. As described below, restoration of the Khata corridor in Nepal's Terai Arc landscape was conducted by communities and is now managed by community-led cooperatives (35). In Borneo, the Sabah Softwoods Berhad Corporation reforested a 14-km-long corridor within an oil palm concession that connects two forest reserves, enhancing connectivity for several species including endangered Bornean elephants (*Elephas maximus borneensis;* 29). Restoring connectivity can involve reducing degradation within corridors, for example, through development of management plans that reduce overgrazing (36). To restore gene flow, landscape features impacting genetic connectivity can be identified using landscape genetics approaches (37) or by inferring "effective migration surfaces" from spatially explicit genomic data (38).

Following the Carpathian ecoregion experience below, we broadened our ToC to ensure that new infrastructure avoids ecological corridors where possible, while mitigating existing infrastructure impacts (e.g., by restricting vehicle speeds) and restoring connectivity with under- or over-passes (39, 40). Effective connectivity conservation also requires supporting mechanisms in the financial, governance, and market spheres, including those linked to climate change adaptation and mitigation (41). Connected landscapes are a key climate adaptation approach as they allow wildlife to adaptively move to climatically suitable areas (42, 43). Monitoring and evaluation of landscape connectivity over time should form the basis of adaptive management of the ToC. The temporal dimension is important to consider for gene flow, as other than highly inbred populations (44) the benefits of restored connectivity may not manifest in genetic data for several generations (45). Finally, effective and equitable management of protected and conserved areas is fundamental for conservation success (46); thus, efforts to improve management are important complements to the ToC.

Case Studies

The first three case studies commenced before the TOC was drafted and hence strongly informed its development. The last case study began after the TOC was finalized and thus closely followed its structure.

Kavango-Zambezi Transfrontier Conservation Area (KAZA). KAZA spans ~520,000 km^2 across parts of five southern Africa countries: Angola, Botswana, Namibia, Zambia, and Zimbabwe. It is a mosaic of national parks, wildlife management areas, communal lands, and private landholdings and includes several RAMSAR and World Heritage Sites (Fig. 2). About 3 million people live in KAZA, most practicing subsistence agriculture (47). KAZA was established in 2011 to create a world-class tourism destination through sustainable development, with a goal of improving human well-being while ensuring transboundary flows of tourism and the wildlife that supports it; as such, ecological connectivity is at the heart of KAZA's objectives. The region's sandy terrain and seasonal, semiarid climate (average annual rainfall of ~600 mm falling within November–March) means that wildlife is strongly dependent on surface water, with permanent rivers and their floodplains providing critical dry season habitat. In the limited wet season, pans fill with rainfall and allow wildlife to disperse away from rivers (48). These wet season movements include some of the world's great remaining long-distance migrations of plains zebra *Equus quagga* (49, 50), savannah elephants *Loxodonta africana* (51), and African buffalo *Syncerus caffer* (52). Connectivity in KAZA is therefore highly dynamic, varying seasonally as a function of prevailing environmental conditions.

The sheer size of KAZA—bigger than 80% of the world's countries—presents challenges to delineating core wildlife areas and corridors that may connect them. Early evaluations involved expert assessments of important areas for wildlife movement and migrations (55) and the synthesis of independent wildlife survey data to estimate national-level wildlife populations across the transfrontier landscape (56). More recently, KAZA's governance structure (including a secretariat and formal recognition of conservation objectives by participating countries) has enabled several coordinated, transfrontier studies on elephants, a key focal species. A recent transboundary aerial survey of elephants was the largest multicountry aerial survey for wildlife ever undertaken in Africa (57). Furthermore, a recent landscape connectivity assessment synthesized data from the greatest number of African elephant GPS collars ever assembled by collaborating research groups (53). Similar efforts are underway to assess transfrontier carnivore connectivity and to improve livestock management, the latter of which negatively impacts landscape connectivity in KAZA, particularly because of veterinary fencing (58). Genetic connectivity and population structure have also been assessed for species such as elephants (59) and African buffalo (60).

Satellite tracking data has been key in identifying critical connectivity areas across KAZA. At transfrontier scales, "macrocorridors" connecting core PAs and other disparate parts of KAZA have been mapped and include places where transfrontier movements are either concentrated by anthropogenic development (e.g., fences, settlements, roads) or dispersed across areas with low human populations and few barriers to movement (53). At finer scales, information from local communities has complemented GPS tracking data to identify "microcorridors" that elephants and other species use to navigate through human-occupied areas (54). Strategies to

Downloaded from https://www.pnas.org by 108.64.85.146 on September 29, 2025 from IP address 108.64.85.146.

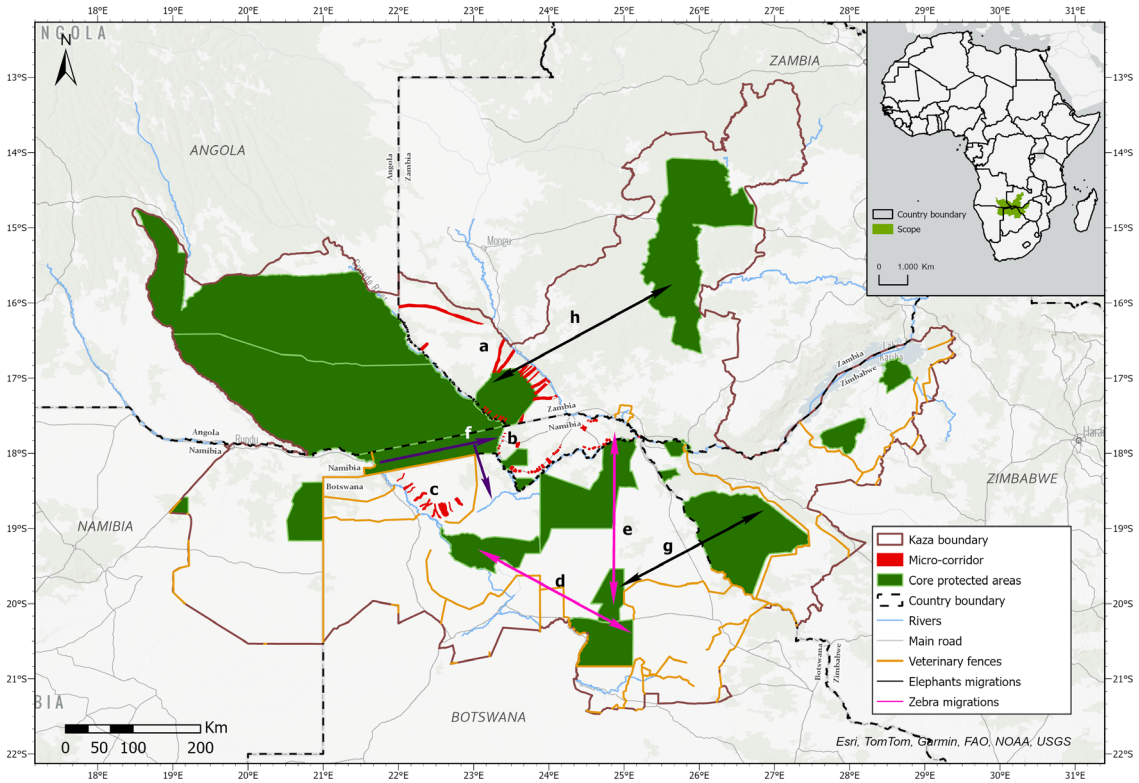


Fig. 2. Kavango-Zambezi transfrontier conservation area, with core protected areas (green), savannah elephant microcorridors in Zambia (a: ref. 53), Namibia (b: ref. 53), and Botswana (c: ref. 54), and larger movements/migrations of plains zebra (d: ref. 49; e: ref. 50), African buffalo (f: ref. 52), and savannah elephant (g: ref. 51; h: ref. 53).

incentivize and secure connectivity include reducing human-wildlife conflict (61, 62), increasing benefits to local communities from wildlife conservation (63), and wildlife-friendly land-use planning and policy engagement with governments (64). Implementation of these actions requires collaboration among scientists, practitioners, local and national government officials, and civil society.

The most recent applied research efforts on connectivity have focused on how changing landscape conditions may impact future connectivity. Research is addressing how communities are experiencing climate change impacts and human-wildlife conflict (65), the conservation impacts of human population growth and associated increases in infrastructure, settlements, and cultivation (66), and the connectivity of KAZA's main rivers (67). Africa is poised to experience the most rapid population growth of any continent (68). The associated expansion of infrastructure (69) coupled with increasing aridity from climate change (70) requires continued monitoring and predictions of future changes in wildlife connectivity for successful long-term conservation in KAZA.

Terai Arc Landscape (TAL). The TAL spans ~50,000 km^2, connecting large mammal habitat across 15 protected areas in Nepal and India (71, 72). Diverse habitats including grasslands, forests, and wetlands support endangered species such as tiger (*Panthera tigris*), greater one-horned rhinoceros (*Rhinoceros unicornis*), and Asian elephant (*Elephas maximus*). With 8.1 million people in Nepal alone, human-wildlife conflict in TAL is common and strategies for coexistence within the multiple ethnic groups are critical (31). Large-scale habitat degradation from infrastructure development and climate change, including drought and forest fires, is a significant threat to landscape connectivity (73).

In the 1990s, conservation biologists in TAL conceptualized a landscape with habitat corridors between PAs to support connectivity for large mammals (71). This metapopulation design viewed PAs as nodes in a linked network and utilized existing wildlife data, land cover analysis, and field surveys to identify key connectivity areas (Fig. 3). The multipronged approach highlighted the need for diverse conservation efforts (e.g., protection, management, and restoration, as described in the ToC) to support wildlife and the livelihoods of local communities (74) and has resulted in strategies to conserve forest connectivity and facilitate wildlife dispersal across the landscape (72, 75).

For example, PA coverage in Nepal increased from 16 to 23.3% over the last two decades (76); the new PAs (e.g., Banke National Park and extensions of Parsa and Suklaphanta National Parks) provide substantial additional habitat for species recovery (77, 78). Major habitat restoration efforts include managing grasslands and wetlands, fencing habitat edges, tree planting in degraded areas, and control of invasive species; these efforts have helped shape our ToC. Community-based conservation involving IPs and LCs in planning, sustainable forest management, and livelihood development has fostered support for conservation, especially in corridors and buffer zones (75, 79). Antipoaching efforts, including the disruption of illegal wildlife trade routes and enhanced species protection (80, 81) have also facilitated wildlife movements.

These conservation interventions in the TAL have bolstered structural connectivity (82) and potentially functional

Downloaded from https://www.pnas.org by 108.64.85.146 on September 29, 2025 from IP address 108.64.85.146.

connectivity for some species (63). Periodic land cover assessments show net forest gain in corridors that may facilitate tiger use (72, 83, 84). The Khata corridor—joining Bardia National Park in Nepal with Katerniaghat Wildlife Sanctuary in India—has frequent tiger movements documented by annual camera trap (85) and occupancy surveys (84, 86), although gene flow apparently remains limited among PAs in the larger landscape and isolated subpopulations may exist (85). Urban development, poaching, and insufficient prey may be preventing adequate numbers of tigers from arriving and breeding in new areas, although recent structural connectivity increases may simply take additional time to be reflected in tiger genomes. Long-term monitoring programs, local community engagement in wildlife monitoring within their lands (74, 84), and collaborative efforts among scientists, practitioners, policymakers, and IPs and LCs have been vital for developing comprehensive impact assessment frameworks that reflect outcomes of connectivity conservation in TAL (74, 84).

Rising temperatures, altered precipitation patterns, and extreme weather events are worsening habitat loss, fragmentation, and human-wildlife conflict. Increased drought has sparked large forest fires in TAL (87), while human-wildlife conflict has intensified with climate change and poses a significant societal challenge (87). Combining community-based conservation with climate adaptation measures is helping manage climate risk, with initiatives for forest and wetland restoration providing promising nature-based solutions to address regional challenges (88). Engaging with IPs and LCs has enhanced our understanding of their cultures, needs, and aspirations, aiding conservation goals (89, 90). Through local participation, the recognition of traditional knowledge, equitable benefit sharing, and capacity building, these stakeholders are now actively contributing to connectivity conservation in TAL (91). Finally, seizing current opportunities for the designation of other effective area-based conservation measures (26) may complement corridors and help counter threats to connectivity in the TAL.

Pantanal - Chaco (PACHA). The PACHA landscape (initially conceived in 2021) comprises 1,586,090 km^2 shared by Argentina (26.1% of the area), Bolivia (17.2%), Brazil (34.2%), and Paraguay (22.5%). The Pantanal is the world's largest continuous floodplain (92) while the Chaco constitutes the world's largest continuous dry forest (93). PACHA includes part of the Cerrado biome, a vast savanna where waters of the Pantanal originate, and part of the Yunga biome, encompassing diverse tropical forests along the Andes' eastern slope. PACHA contains extraordinary levels of biodiversity internationally recognized by RAMSAR (15 sites) and UNESCO (Chaco Biosphere Reserve). The landscape's heterogeneity is also reflected in its 3 million people, including the Ayoreo, the last Indigenous group in voluntary isolation outside the Amazon. In the Bolivian section of PACHA, the Guarani Indigenous group governs most of the territory, while private landowners dominate the rest of the landscape. Conservation strategies in PACHA are tailored to each group.

Current threats to PACHA include deforestation and land conversion, driven primarily by soy and beef production (94). These threats are affecting water recharge patterns and changing water dynamics, including flood pulses of the Pantanal (95), destroying species habitats and reducing ecological connectivity, especially in the Chaco biome, one of the largest deforestation fronts in the world (96).

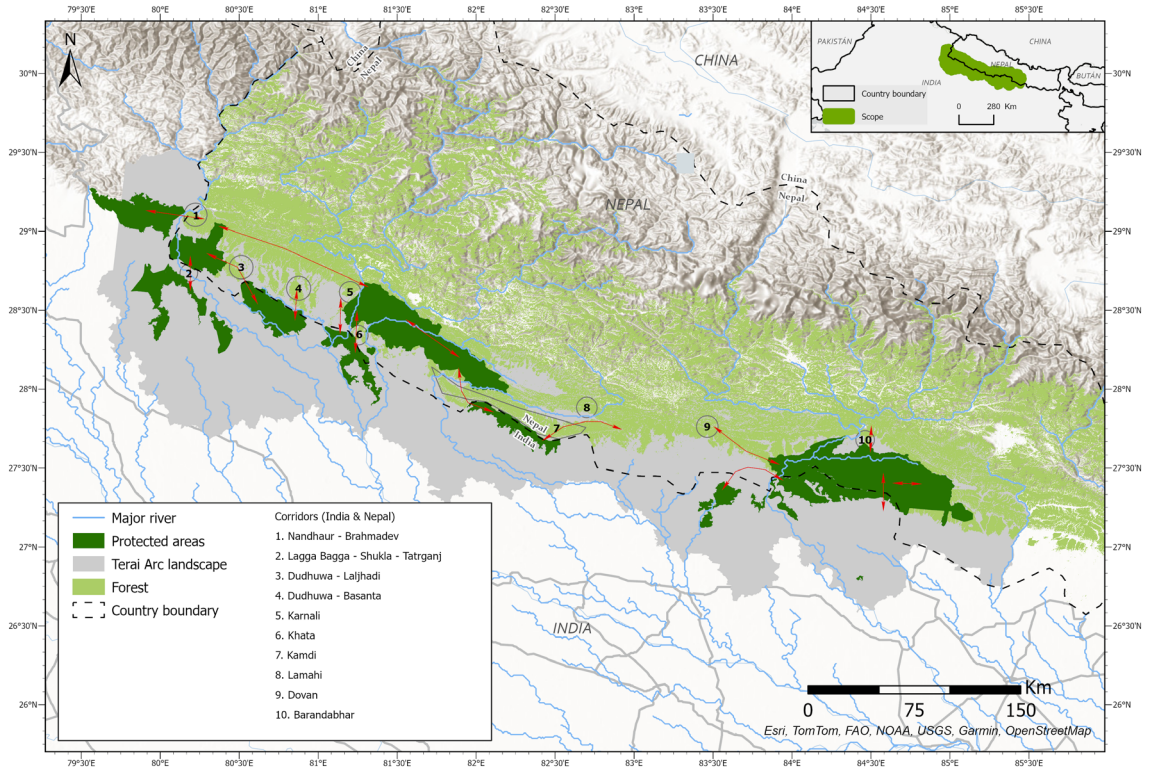


Fig. 3. Transboundary protected areas between Nepal and India, connected by forest corridors in the Terai Arc Landscape (TAL). Red arrows show observed/hypothesized movements of large mammals among protected areas (71, 72).

Downloaded from https://www.pnas.org by 108.64.85.146 on September 29, 2025 from IP address 108.64.85.146.

To assess ecological connectivity in PACHA, we selected jaguars (*Panthera onca*) as a focal species. Jaguars are the Americas' largest felid and an umbrella species that while widely distributed throughout Central and South America, faces many threats (97). Genetic studies have revealed no subspecies of jaguar, emphasizing the importance of maintaining interconnected habitats for long-term viability (98). In the 1990s, a network of core breeding areas known as jaguar conservation units, linked by corridors that would ensure gene flow between populations from Argentina to Mexico, was identified (99). More recently, nongovernmental and state actors outlined the necessary actions to achieve range-wide jaguar conservation, including land protection and corridor implementation (100). PACHA is at the southern part of the jaguar's range, and all four countries sharing the landscape have national conservation action plans that contain connectivity strategies. This region thus offers promising opportunities to conserve jaguar connectivity at the southern end of its distribution, contributing to its range-wide persistence.

To conserve jaguar connectivity in PACHA and following the ToC, practitioners and scientists modeled, mapped, and prioritized ecological corridors among protected areas and Indigenous territories, resulting in an ecological network of connected protected areas (101); (Fig. 4) A variety of actors (WWF, Fundación Vida Silvestre Argentina, local partners) are implementing the following interventions to maintain or increase jaguar connectivity across PACHA: a) validating jaguar corridor use with camera traps; b) promoting sustainable forest management and improving economic incentives for conservation among Indigenous women living in corridors in Bolivia and Paraguay to process nontimber forest products (e.g., honey, handicrafts, plant extracts for the pharmaceutical industry); c) collaborating with cattle ranchers to promote integrated fire management in the Brazilian Pantanal, where fires have dramatically increased since 2020; d) strengthening coexistence by supporting cattle ranchers in the Brazilian Pantanal and Bolivian and Argentinian Chaco to implement human–jaguar conflict mitigation; e) encouraging public policy implementation in the Argentinian Chaco so communities living in corridors where deforestation is prohibited can access the economic incentives provided under forest law; and f) strengthening corridor governance in Bolivia, by building indigenous capacity to detect early warning signals of fires, deforestation, and human encroachment via remote sensing.

Jaguar population data from ongoing camera trap studies and connectivity metrics (e.g., ref. 4) will be used to measure the impact of interventions and to validate connectivity models. While legal and illegal deforestation in the Chaco is expected to persist, focusing conservation measures on priority corridors, including the formal declaration of critical corridors as PAs, should help maintain long-term connectivity for jaguars and associated species in PACHA.

Carpathian Ecoregion Conservation Area. The Carpathian ecoregion covers almost 210,000 km^2 across Central and Eastern Europe in seven countries: Czech Republic, Slovakia, Poland, Hungary, Ukraine, Romania, and Serbia (102). The Carpathians are home to over 60,000 native species and 500 vertebrate taxa, including threatened species such as brown bear (*Ursus arctos*, ~7,200 individuals), gray wolf (*Canis lupus*, ~3,000 individuals), and Eurasian lynx (*Lynx lynx*, ~2,300 individuals) (103). These population sizes represent approximately half the European bear population and one-third of the wolf and Eurasian lynx populations (104). The Carpathians also accommodate over 17 million people in both remote villages and major cities (102).

Following the collapse of the Soviet Union after 1989, Central and Eastern Europe, including the Carpathian countries, witnessed rapid changes in land use and cover, propelled by significant shifts in agriculture, socioeconomic conditions, and rural-to-urban migration (105). This transition contributed to farmland abandonment and erosion of cultural traditions, which, while posing a threat to the area's cultural biodiversity (106), facilitated range expansion and population increases of area-sensitive species such as large carnivores. Conversely, the expansion of transport infrastructure and residential development increased fragmentation of the Carpathian landscape, especially in the region's western countries which exhibit higher levels of development than their eastern counterparts (104).

Acknowledging the exceptional biodiversity of and increasing threats to the Carpathians, the Carpathian Convention was adopted in 2003 by the seven countries that share the mountain range. This agreement supports collaborative conservation and sustainable development within the region. Several ecological connectivity projects have been cocreated by key stakeholders under the Convention's framework. These projects involve collaboration among research institutions, universities, NGOs, PA managers, and government bodies overseeing environmental affairs, spatial planning, and transportation. Through such collaborative efforts, a methodology for identifying ecological corridors in the Carpathian ecoregion was developed (107) and underpinned the establishment of a Carpathian ecological network for large carnivores. After quantifying habitat suitability and barrier impacts for key species (*SI Appendix*, Fig. S1), subsequent landscape connectivity modeling (e.g., random walks, least cost paths; ref. 12) facilitated delineation of core areas, stepping stones, linkage zones, and corridors (Fig. 5). Validation of corridors leveraged national and international expert opinion and species occurrence data from camera traps, GPS telemetry, and snow tracking (108). This ecological network for large carnivores pinpoints corridor restoration requirements, identifies overlaps with development projects (especially transport infrastructure), and helps mitigate adverse impacts of such projects.

The main connectivity objectives at the Carpathian Convention level are prevention of further habitat fragmentation and maintenance of connectivity (109). This will occur via refinement of core areas, stepping stones, and ecological corridors; restoration and management of corridors; mainstreaming biodiversity into transport development; improving spatial planning to better reflect ecological networks; and knowledge exchange/cooperation with other mountain regions and neighboring areas. Although major steps have been made toward conserving ecological connectivity, no methodology has been endorsed by Carpathian countries for formal designation of ecological corridors, as the ToC recommends. A key reason is the absence of political will for such

Downloaded from https://www.pnas.org by 108.64.85.146 on September 29, 2025 from IP address 108.64.85.146.

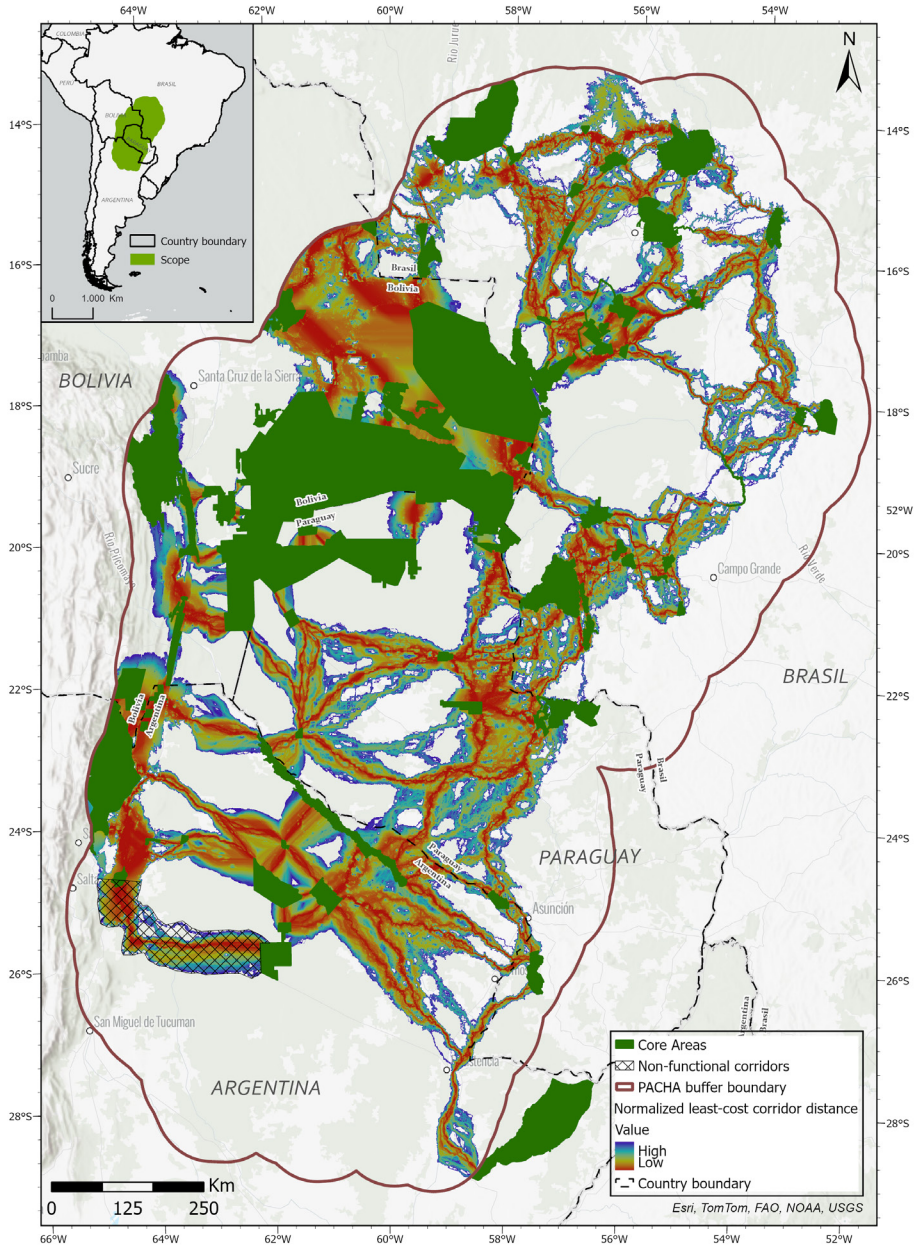


Fig. 4. Jaguar corridors between core protected areas in the Pantanal-Chaco (PACHA) landscape (101). Warmer colors represent lower-cost routes. One corridor is considered nonfunctional due to lack of recent jaguar observations.

designation, necessitating alternative conservation measures such as land swaps or locally relevant protected areas.

In addition to lack of formal acknowledgment of corridors, addressing the overarching challenge of climate change, already apparent in habitat shifts and distribution changes in large carnivores, is a key priority. Carnivores are extending their ranges in pursuit of additional feeding opportunities, leading to increased human–wildlife conflict. This is especially acute in Romania, home to the largest brown bear population in Europe, where between 2000 and 2015, there were 131 bear attacks, including 11 fatalities (110). To confront these challenges, digital twin models (111) are being created to forecast impacts of climate change on distribution and space use of large carnivores, along with future locations of human–wildlife conflicts. The results will contribute to informed decision-making and new measures to address changes in Carpathian landscape connectivity and human-wildlife conflict.

Quantifying Changes in Landscape Connectivity

Approaches to quantifying landscape connectivity have received substantial recent attention, with metrics representing structural (112) and functional—based on movement (4) or genetics (113)—connectivity proposed as appropriate indicators. To quantitatively compare functional connectivity over time in each case study landscape, we calculated protected area isolation (PAI; ref. 4) from 2000 to 2018, using a 1-km^2 global time series of human footprint (114) to ensure consistent measurement across sites (see *SI Appendix*). PAI is measured as the median pairwise "effective resistance" [i.e., the resistance between two points in a network; (115)] among all pairs of PAs in a landscape and reflects the estimated functional connectivity for a range of mammal species (1). Higher PAI values reflect greater

Downloaded from https://www.pnas.org by 108.64.85.146 on September 29, 2025 from IP address 108.64.85.146.

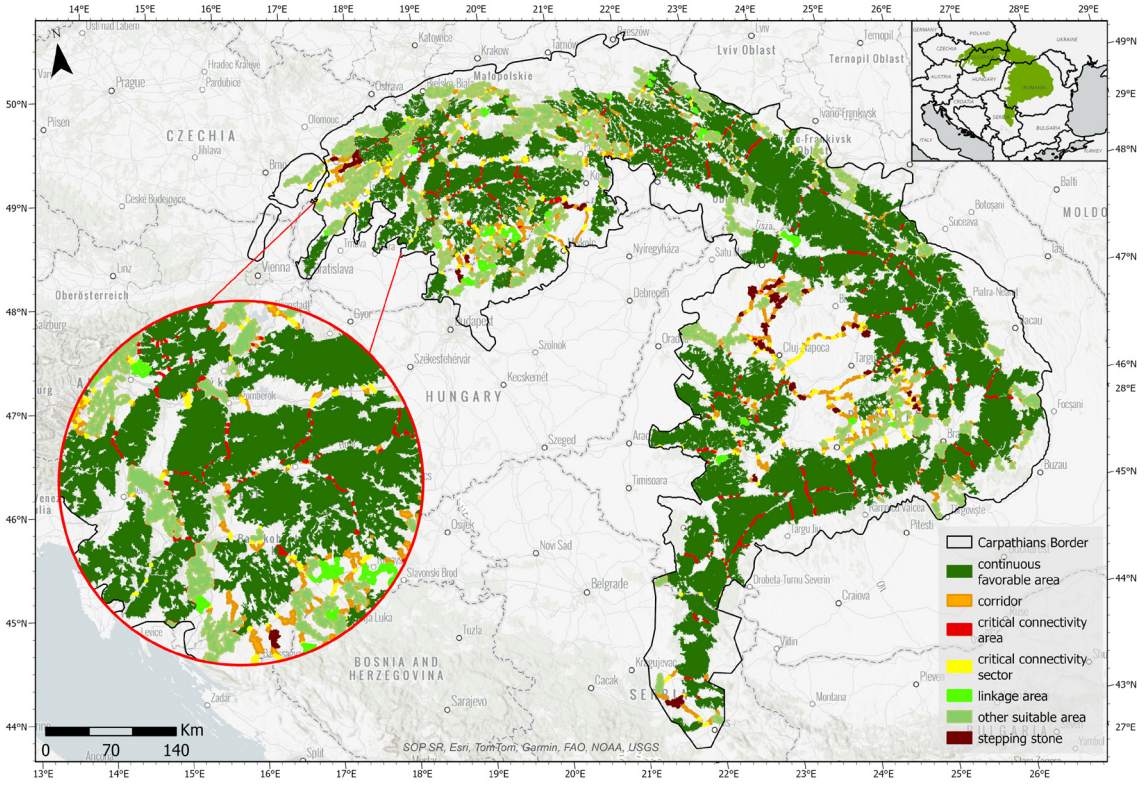


Fig. 5. The ecological network for large carnivores in the Carpathian Ecoregion conservation area (108).

isolation of PAs and therefore represent lower functional connectivity of a landscape.

We find that three of the four landscapes have experienced varying degrees of functional connectivity erosion over the last 19 y (*SI Appendix*, Fig. S2), due to increasing anthropogenic development as reflected in the human footprint. Nonetheless, increases in PAI values from 2000 to 2018 were relatively modest for PACHA (2.2%), KAZA (3.7%), and the Terai Arc (4.8%). In contrast, functional connectivity in the Carpathians displayed a modest increase (i.e., PAI declined) of 2.4%, despite substantial year-to-year variation in PAI values (*SI Appendix*, Fig. S2*D*). However, the Carpathians also had the highest absolute values of PAI, with connectivity in 2018 approximately three times lower than in PACHA, which was the most connected landscape (median PAI values: Carpathians = 13.3; Terai Arc = 10.1; KAZA = 6.0; PACHA = 4.3). Given that 152 of 159 protected areas across all four landscapes existed prior to 2000, differences in PAI scores and trends are primarily a function of changes in the human footprint.

For the Carpathians, much of the landscape has long been used by humans. However after the fall of communism in 1989 and accession of most countries in the region to the European Union, environmental legislation improved, protected areas increased, and the Carpathian Convention facilitated nature conservation. Similarly, the Terai Arc was densely populated and highly fragmented before the first efforts to improve landscape connectivity. While such efforts have successfully protected specific corridors, the high increase in PAI over recent time reflects continuing, landscape-wide habitat (mostly forest) degradation. The more connected landscapes, PACHA and KAZA, have historically had relatively low human populations who maintain agropastoral livelihoods. Nonetheless, habitat loss and fragmentation due to urbanization, linear development (e.g., roads, railways), and agropastoral activities are increasing the landscapes' human footprint. Both landscapes are also beginning to experience significant climate impacts that will further threaten connectivity, especially via droughts in KAZA and catastrophic fires in PACHA.

Despite these trends, across all landscapes connectivity losses could have been substantially higher without several activities articulated in the ToC: creation of strong and diverse partnerships; community-led governance and involvement; collection of robust wildlife and land cover data; and formal recognition of corridors and other important areas for connectivity by various levels of government. Each landscape has actioned variable elements of the ToC (summarized in *SI Appendix*, Table S1), and we hypothesize that connectivity loss will decline or be reversed with further action on elements in the ToC.

Supporting Mechanisms for Ecological Connectivity

In addition to "Climate," the ToC outlines other key supporting mechanisms needed to secure ecological connectivity: "Finance," "Governance," and "Market." Recent years have seen significant strengthening of these latter supporting mechanisms.

Regarding "Governance" (i.e., public sector policy), a fundamental shift came from commitments to connectivity in the Convention on Biological Diversity's (CBD) Kunming-Montreal Global Biodiversity Framework (GBF), adopted by 196 governments in 2022. In the GBF, governments committed to "maintain, enhance, or restore…connectivity…of all ecosystems" by 2050 (Goal A), and by 2030 to restore at least 30 per cent degraded ecosystems in order to "enhance…connectivity" (Target 2); to effectively conserve through protected and conserved areas at least 30 per cent of the planet ensuring these

Downloaded from https://www.pnas.org by 108.64.85.146 on September 29, 2025 from IP address 108.64.85.146.

areas are "well connected" (Target 3); and to "significantly increase the…connectivity of…green and blue spaces in urban and densely populated areas" (Target 11). In addition, governments have committed via Target 1 to ensure "biodiversity inclusive spatial planning" and reduce the loss of areas of "high ecological integrity" to near zero.

While the GBF provides a monitoring framework (116) to assess whether biodiversity targets are being met, connectivity is a gap in its "headline" indicators (i.e., a limited set of high-level indicators that CBD parties must report against). PAI is currently listed as a secondary, "complementary" indicator in the monitoring framework, and as we show above, could provide a useful approach to measure delivery against GBF connectivity targets. Other developments in global policy include the UN General Assembly resolution on connectivity (https://digitallibrary.un.org/record/3907486?ln=en&v = pdf) and the prominence of connectivity within the Convention on Migratory Species. The science–policy interface on connectivity will be enhanced with the upcoming International Platform on Biodiversity and Ecosystem Services (IPBES) spatial planning and connectivity assessment.

Regarding the "Finance" and "Market" supporting mechanisms, biodiversity loss is now recognized as a key risk to business (117), which has led to increased frameworks and policies to mitigate risk, including those aimed at enhancing connectivity. For example, one multinational now requires that all sourcing farms "maintain or create wildlife corridors as feasible given their farm size" (118). The recently established Task Force for Nature Related Financial Disclosures (https://tnfd.global) commits 300+ participating companies to disclose activities located in "areas important for ecological connectivity—including important ecological corridors, areas, and routes that are important for seasonal migratory patterns and areas that provide adaptive space for species to spread across a landscape in the face of changing environmental conditions" (119).

The increasing sophistication with which connectivity conservation is being conducted in landscapes, combined with strengthened supporting mechanisms in governance, finance, and markets, offers potential to achieve connectivity outcomes. However, these advances come at a time when our planet is dealing with ever-increasing drivers of connectivity loss. Our ToC and case studies highlight the complexities of achieving connectivity conservation at local, national, and global levels. As such we face a race against time to combine local efforts with global levers to secure the resilient and connected landscapes upon which humanity and the rest of the living world depend.

Data, Materials, and Software Availability. All study data are included in the article and/or *SI Appendix*.

ACKNOWLEDGMENTS. We thank Gonzalo Dieguez and Ana Eljall for generous mapmaking assistance.

1. M. A. Tucker *et al.*, Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science* **1979**, 466–469 (2018).
2. J. Geldmann, A. Manica, N. D. Burgess, L. Coad, A. Balmford, A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. *Proc. Natl. Acad. Sci.* **116**, 23209–23215 (2019).
3. J. F. Brodie *et al.*, Connecting science, policy, and implementation for landscape-scale habitat connectivity. *Conserv. Biol.* **30**, 950–961 (2016).
4. A. Brennan *et al.*, Functional connectivity of the world's protected areas. *Science* **1979**, 1101–1104 (2022).
5. P. Taylor, L. Fahrig, K. With, "Landscape connectivity: A return to the basics" in *Connectivity Conservation*, K. Crooks, M. Sanjayan, Eds. (Cambridge University Press, 2006).
6. R. D. Williams, C. Rondinini, D. Tilman, Global protected areas seem insufficient to safeguard half of the world's mammals from human-induced extinction. *Proc. Natl. Acad. Sci.* **119**, e2200118119 (2022).
7. IUCN and UNEP-WCMC, *The World Database on Protected Areas (WDPA)* (UNEP-WCMC, Cambridge, UK, 2013).
8. C. M. Aylward *et al.*, Patch size and connectivity predict remnant habitat occupancy by an endangered wetland specialist, the salt marsh harvest mouse. *Landsc. Ecol.* **38**, 2053–2067 (2023).
9. L. Fahrig *et al.*, in *Landscape connectivity*, R. A. Francis, J. D. A. Millington, G. L. W. Perry, E. S. Minor, Eds. (Routledge, 2020).
10. M. Boulet, S. Couturier, S. D. Côté, R. D. Otto, L. Bernatchez, Integrative use of spatial, genetic, and demographic analyses for investigating genetic connectivity between migratory, montane, and sedentary caribou herds. *Mol. Ecol.* **16**, 4223–4240 (2007).
11. S. L. R. Wood *et al.*, Missing interactions: The current state of multispecies connectivity analysis. *Front. Ecol. Evol.* **10**, 830822 (2022).
12. R. J. Fletcher, N. S. Burrell, B. E. Reichert, D. Vasudev, J. D. Austin, Divergent perspectives on landscape connectivity reveal consistent effects from genes to communities. *Curr. Landscape Ecol. Rep.* **1**, 67–79 (2016).
13. A. M. M. Sequeira *et al.*, The importance of sample size in marine megafauna tagging studies. *Ecol. Appl.* **29**, e01947 (2019).
14. S. U. Kumar, Ż Kaszta, S. A. Cushman, Pathwalker: A new individual-based movement model for conservation science and connectivity modelling. *ISPRS Int. J. Geoinf.* **11**, 329 (2022).
15. J. Whittington, M. Hebblewhite, R. W. Baron, A. T. Ford, J. Paczkowski, Towns and trails drive carnivore movement behaviour, resource selection, and connectivity. *Mov. Ecol.* **10**, 17 (2022).
16. P. A. Hohenlohe, W. C. Funk, O. P. Rajora, Population genomics for wildlife conservation and management. *Mol. Ecol.* **30**, 62–82 (2021).
17. L. D. Bertola *et al.*, Giraffe lineages are shaped by major ancient admixture events. *Curr. Biol.* **34**, 1576–1586.e5 (2024).
18. A. T. Knight *et al.*, Knowing but not doing: Selecting priority conservation areas and the research-implementation gap. *Conserv. Biol.* **22**, 610–617 (2008).
19. C. R. Margules, R. L. Pressey, Systematic conservation planning. *Nature* **405**, 243–253 (2000).
20. C. M. Raymond *et al.*, Inclusive conservation and the post-2020 global biodiversity framework: Tensions and prospects. *One Earth* **5**, 252–264 (2022).
21. B. Louman *et al.*, Access to landscape finance for small-scale producers and local communities: A literature review. *Land (Basel)* **11** (2022).
22. D. M. Olson, E. Dinerstein, The global 200: A representation approach to conserving the earth's most biologically valuable ecoregions. *Conserv. Biol.* **12**, 502–515 (1998).
23. J. Hilty *et al.*, Guidelines for conserving connectivity through ecological networks and corridors. Best Practice Protected Area Guidelines Series No. 30 (IUCN, 2020).
24. M. Gurrutxaga, J. Marull, E. Domene, J. Urrea, Assessing the integration of landscape connectivity into comprehensive spatial planning in Spain. *Landsc. Res.* **40**, 817–833 (2015).
25. P. Thinley, Technical comments on the design and designation of biological corridors in Bhutan: Global to national perspectives. *J. Renew. Natural Resour., Bhutan* **6**, 91–106 (2010).
26. C. N. Cook, Progress developing the concept of other effective area-based conservation measures. *Conserv. Biol.* **38**, e14106 (2024).
27. M. Camino *et al.*, Indigenous lands with secure land-tenure can reduce forest-loss in deforestation hotspots. *Glob. Environ. Chang.* **81**, 102678 (2023).
28. A. T. H. Keeley, P. Beier, B. W. Keeley, M. E. Fagan, Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. *Landsc. Urban Plan.* **161**, 90–102 (2017).
29. C. Cheah, P. Imm, K. Pei Hue, R. Nathan, Can the oil palm industry and elephant conservation be reconciled? A case study in Kalabakan, Sabah. Gajah, *J. Asian Elephant Spec. Group* **53**, 30–38 (2021).
30. V. Boron *et al.*, Jaguar densities across human-dominated landscapes in Colombia: The contribution of unprotected areas to long term conservation. *PLoS One* **11**, e0153973 (2016).
31. P. J. Nyhus, Human–wildlife conflict and coexistence. *Annu. Rev. Environ. Resour.* **41**, 143–171 (2016).
32. F. Berkes, Community-based conservation in a globalized world. *PNAS* **104**, 15188–15193 (2007).
33. J. K. Pritchard, M. Stephens, P. Donnelly, Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959 (2000).
34. S. Roques *et al.*, Effects of habitat deterioration on the population genetics and conservation of the jaguar. *Conserv. Genet.* **17**, 125–139 (2016).
35. V. Pérez-Cirera, S. Cornelius, J. Zapata, *Powering Nature: Creating the Conditions to Enable Nature-based Solutions* (WWF, 2021).
36. W. O. Odadi, J. Fargione, D. I. Rubenstein, Vegetation, wildlife, and livestock responses to planned grazing management in an African pastoral landscape. *Land. Degrad. Dev.* **28**, 2030–2038 (2017).
37. S. Manel, M. K. Schwartz, G. Luikart, P. Taberlet, Landscape genetics: Combining landscape ecology and population genetics. *Trends Ecol. Evol.* **18**, 189–197 (2003).
38. D. Petkova, J. Novembre, M. Stephens, Visualizing spatial population structure with estimated effective migration surfaces. *Nat. Genet.* **48**, 94–100 (2016).
39. D. Denneboom, A. Bar-Massada, A. Shwartz, Factors affecting usage of crossing structures by wildlife–A systematic review and meta-analysis. *Sci. Total Environ.* **777**, 146061 (2021).
40. D. J. Glista, T. L. DeVault, J. A. DeWoody, A review of mitigation measures for reducing wildlife mortality on roadways. *Landsc. Urban Plan.* **91**, 1–7 (2009).
41. Q. C. Chukwudum, Climate finance across sub-Saharan Africa: Decision trees and network flows. *S. Afr. J. Sci.* **120**, 15837 (2024).
42. P. Beier, Conceptualizing and designing corridors for climate change. *Ecol. Restor.* **30**, 312–319 (2012).
43. J. L. McGuire, J. J. Lawler, B. H. McRae, T. A. Nuñez, D. M. Theobald Achieving climate connectivity in a fragmented landscape. *Proc. Natl. Acad. Sci.* **113**, 7195–7200 (2016).
44. C. B. Quinn, P. B. Alden, B. N. Sacks, Noninvasive sampling reveals short-term genetic rescue in an insular red fox population. *J. Hered.* **110**, 559–576 (2019).
45. P. Samarasin, B. J. Shuter, S. I. Wright, F. H. Rodd, The problem of estimating recent genetic connectivity in a changing world. *Conser. Biol.* **31**, 126–135 (2017).

Downloaded from https://www.pnas.org by 108.64.85.146 on September 29, 2025 from IP address 108.64.85.146.

46. S. L. Maxwell *et al.*, Area-based conservation in the twenty-first century. *Nature* **586**, 217–227 (2020).
47. J. Salerno *et al.*, Wildlife impacts and vulnerable livelihoods in a transfrontier conservation landscape. *Conserv. Biol.* **34**, 891–902 (2020).
48. R. Naidoo *et al.*, Mapping and assessing the impact of small-scale ephemeral water sources on wildlife in an African seasonal savannah. *Ecol. Appl.* **30**, e02203 (2020).
49. H. L. A. Bartlam-Brooks, M. C. Bonyongo, S. Harris, Will reconnecting ecosystems allow long-distance mammal migrations to resume? A case study of a zebra Equus burchelli migration in Botswana *Oryx* **45**, 210–216 (2011).
50. R. Naidoo *et al.*, A newly discovered wildlife migration in Namibia and Botswana is the longest in Africa. *Oryx* **50**, 138–146 (2016).
51. A. Tshipa *et al.*, Partial migration links local surface-water management to large-scale elephant conservation in the world's largest transfrontier conservation area. *Biol. Conserv.* **215**, 46–50 (2017).
52. R. Naidoo, P. Du Preez, G. Stuart-Hill, P. Beytell, R. Taylor, Long-range migrations and dispersals of African buffalo (Syncerus caffer) in the Kavango-Zambezi Transfrontier Conservation area. *Afr. J. Ecol.* **52**, 581–584 (2014).
53. R. Naidoo *et al.*, Landscape connectivity for African elephants in the world's largest transfrontier conservation area: A collaborative, multi-scalar assessment. *J. Appl. Ecol.* **61**, 2483–2496 (2024).
54. A. Songhurst, G. McCulloch, T. Coulson, Finding pathways to human-elephant coexistence: A risky business. *Oryx* **50**, 713–720 (2016).
55. KAZA Tfca Secretariat, *Kavango-Zambezi Transfrontier Conservation Area: Master Integrated Development Plan, 2014–2019* (KAZA TFCA Secretariat, 2014).
56. M. J. Chase *et al.*, Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ* **4**, e2354 (2016).
57. E. M. S. Bussiere, D. Potgieter, *KAZA Elephant Survey 2022, Volume I: Results and Technical Report* (KAZA TFCA Secretariat, 2022).
58. R. Naidoo *et al.*, Challenges to elephant connectivity from border fences in the world's largest transfrontier conservation area. *Front. Conserv. Sci.* **3**, 788133 (2022).
59. A. de Flamingh *et al.*, Integrating habitat suitability modeling with gene flow improves delineation of landscape connections among African savanna elephants. *Biodivers. Conserv.* **33**, 3231–3252 (2024).
60. C. W. Epps, S. K. Wasser, J. L. Keim, B. M. Mutayoba, J. S. Brashares, Quantifying past and present connectivity illuminates a rapidly changing landscape for the African elephant. *Mol. Ecol.* **22**, 1574–1588 (2013).
61. M. La Grange, C. Matema, B. Nyamukure, R. Hoare, The virtual fence dynamic: A breakthrough for low-cost and sustainable mitigation of human-elephant conflict in subsistence agriculture? *Front. Conserv. Sci.* **3**, 863180 (2022).
62. R. A. Pozo, T. Coulson, G. McCulloch, A. L. Stronza, A. C. Songhurst, Determining baselines for human–elephant conflict: A matter of time. *PLoS One* **12**, e0178840 (2017).
63. B. Child, G. Barnes, The conceptual evolution and practice of community-based natural resource management in southern Africa: Past, present and future. *Environ. Conserv.* **37**, 283–295 (2010).
64. A. Songhurst, J. Stevens, M. Manfredo, G. McCulloch "Planning across landscapes" in *IUCN SSC Guidelines on Human-Wildlife Conflict and Coexistence*, IUCN, Ed. (IUCN, 2023).
65. N. K. Advani, "on-the-ground solutions to help people and wildlife in a changing climate" in *Island Ecosystems: Challenges to Sustainability*, S. J. Walsh, C. F. Mena, J. R. Stewart, J. P. Muñoz Pérez, Eds. (Springer International Publishing, 2023), pp. 79–87.
66. S. A. Cushman, N. B. Elliot, D. W. Macdonald, A. J. Loveridge, A multi-scale assessment of population connectivity in African lions (Panthera leo) in response to landscape change. *Landsc. Ecol.* **31**, 1337–1353 (2016).
67. M. Thieme *et al.*, Measures to safeguard and restore river connectivity. *Environ. Rev.* **00**, 1–21 (2023).
68. P. D. United Nations Department of Economic and Social Affairs, *World Population Prospects 2022: Summary of Results* (United Nations, 2022).
69. P. A. Lindsey *et al.*, Shepherding sub-Saharan Africa's wildlife through peak anthropogenic pressure toward a green anthropocene. *Annu. Rev. Environ. Resour.* **47**, 91–121 (2022).
70. E. Williams, C. Funk, P. Peterson, C. Tuholske, High resolution climate change observations and projections for the evaluation of heat-related extremes. *Sci. Data* **11**, 261 (2024).
71. E. Wikramanayake *et al.*, Designing a conservation landscape for tigers in human-dominated environments. *Conserv. Biol.* **18**, 839–844 (2004).
72. K. Thapa *et al.*, Tigers in the Terai: Strong evidence for meta-population dynamics contributing to tiger recovery and conservation in the Terai Arc Landscape. *PLoS One* **12**, e0177548 (2017).
73. N. Carter, A. Killion, T. Easter, J. Brandt, A. Ford, Road development in Asia: Assessing the range-wide risks to tigers. *Sci. Adv.* **6**, eaaz9619 (2020).
74. E. Wikramanayake *et al.* "The Terai Arc Landscape: a tiger conservation success story in a human-dominated landscape" in *Tigers of the World: The Science, Politics and Conservation of Panthera Tigris*, R. Tilson, P. J. Nyhus, Eds. (Academic Press, ed. 2, 2010), pp. 163–174.
75. A. R. Bhandari, S. R. Bhatta, "Forest restoration: Conservation outcomes and lessons from Terai Arc Landscape, Nepal" in *Routledge Handbook of Rewilding*, S. Hawkins, I. Convery, S. Carver, R. Beyers, Eds. (Routledge, 2022), pp. 204–210.
76. S. Chowdhury *et al.*, Protected areas in South Asia: Status and prospects. *Sci. Total Environ.* **811**, 152316 (2022).
77. B. R. Lamichhane *et al.*, Rapid recovery of tigers *Panthera tigris* in Parsa Wildlife Reserve. Nepal. *Oryx* **52**, 16–24 (2018).
78. A. Harihar *et al.*, Recovery planning towards doubling wild tiger Panthera tigris numbers: Detailing 18 recovery sites from across the range. *PLoS One* **13**, e0207114 (2018).
79. D. Joshi, Community based conservation: Redefining boundaries. *J. For. Livelihood* **14**, 1–12 (2016).
80. P. K. Paudel, K. P. Acharya, H. S. Baral, J. T. Heinen, S. R. Jnawali, Trends, patterns, and networks of illicit wildlife trade in Nepal: A national synthesis. *Conserv. Sci. Pract.* **2**, e247 (2020).
81. K. P. Acharya, R. K. Thapa, K. J. Kuwar, B. P. Thapalia, P. K. Paudel, Policy and management actions that resulted in curbing rhinoceros poaching. *J. Appl. Ecol.* **57**, 1452–1458 (2020).
82. K. Thapa *et al.*, Carbonated tiger-high above-ground biomass carbon stock in protected areas and corridors and its observed negative relationship with tiger population density and occupancy in the Terai Arc Landscape, Nepal. *PLoS One* **18**, e0280824 (2023).
83. K. Thapa *et al.*, Linkages among forest, water, and wildlife: A case study from Kalapani community forest in Lamahi bottleneck area in Terai Arc Landscape. *Int. J. Commons* **12**, 1 (2018).
84. K. Thapa *et al.*, On the tiger trails: Leopard occupancy decline and leopard interaction with tigers in the forested habitat across the Terai Arc Landscape of Nepal. *Glob. Ecol. Conserv.* **25**, e01412 (2021).
85. K. Thapa *et al.*, Assessment of genetic diversity, population structure, and gene flow of tigers (*Panthera tigris tigris*) across Nepal's Terai arc landscape. *PLoS One* **13**, e0193495 (2018).
86. S. M. Barber-Meyer *et al.*, Influence of prey depletion and human disturbance on tiger occupancy in Nepal. *J. Zool.* **289**, 10–18 (2013).
87. K. P. Acharya, P. K. Paudel, P. R. Neupane, M. Köhl, Human-wildlife conflicts in Nepal: Patterns of human fatalities and injuries caused by large mammals. *PLoS One* **11**, e0161717 (2016).
88. D. Mehta, R. Pandey, A. Kumar Gupta, S. Juhola, Nature-based solutions in Hindu Kush Himalayas: Iucn global standard based synthesis. *Ecol. Indic.* **154**, 110875 (2023).
89. N. M. Dawson *et al.*, The role of indigenous peoples and local communities in effective and equitable conservation. *Ecol. Soc.* **26**, art19 (2021).
90. V. Reyes-García *et al.*, The contributions of indigenous peoples and local communities to ecological restoration. *Restor. Ecol.* **27**, 3–8 (2019).
91. B. Gurung *et al.*, Participatory threat assessment of two major wildlife corridors in the Terai Arc landscape. *Parks* **24**, 97–106 (2018).
92. K. M. Wantzen *et al.*, The end of an entire biome? World's largest wetland, the Pantanal, is menaced by the hidrovia project which is uncertain to sustainably support large-scale navigation. *Sci. Total Environ.* **908**, 167751 (2024).
93. H. R. Grau, N. I. Gasparri, T. M. Aide, Balancing food production and nature conservation in the neotropical dry forests of northern Argentina. *Glob. Chang. Biol.* **14**, 985–997 (2008).
94. M. J. Mosciaro *et al.*, Future scenarios of land use change in the Gran Chaco: How far is zero-deforestation?. *Reg. Environ. Change* **22**, 115 (2022).
95. M. C. S. Marques, D. A. Rodriguez, Impacts of the landscape changes in the low streamflows of Pantanal headwaters–Brazil. *Hydrol. Process.* **36**, e14617 (2022).
96. M. Baumann *et al.*, Frontier metrics for a process-based understanding of deforestation dynamics. *Environ. Res. Lett.* **17**, 095010 (2022).
97. B. W. Miller, A. R. Rabinowitz, *Por qué conservar al jaguar?* R. Medellín, *et al.*, Eds. (Fondo de Cultura Económica, 2002).
98. E. Eizirik *et al.*, Phylogeography, population history and conservation genetics of jaguars (*Panthera onca*, Mammalia, Felidae). *Mol. Ecol.* **10**, 65–79 (2001).
99. A. Rabinowitz, K. A. Zeller, A range-wide model of landscape connectivity and conservation for the jaguar. *Panthera onca*. *Biol. Conserv.* **143**, 939–945 (2010).
100. Jaguar 2030 Coordination Committee, *Jaguar 2030: Conservation roadmap for the Americas* (UNDP, UNEP, UNODC, Panthera, WCS, WWF, 2022).
101. T. Creech *et al.*, Expert-based jaguar connectivity analysis for the Pantanal–Chaco region. 2023. *Prepared by the Center for Large Landscape Conservation (Bozeman, MT, USA) under contract to WWF-Bolivia* (2023), pp 24.
102. UNEP, *Carpathians Environment Outlook 2007* (United Nations Environment Program, 2007).
103. G. Chapron *et al.*, Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* **1979**, 1517–1519 (2014).
104. C.-R. Papp, I. Dostál, V. Hlaváč, G. M. Berchi, D. Romportl, Rapid linear transport infrastructure development in the Carpathians: A major threat to the integrity of ecological connectivity for large carnivores. *Nat. Conserv.* **47**, 35–63 (2022).
105. D. Turnock, *The Human Geography of East Central Europe* (Routledge, 2003).
106. P. Angelstam, "Maintaining cultural and natural biodiversity in Europe's economic centre and periphery" in *The Conservation of Cultural Landscapes*, M. Agnoletti, Ed. (CABI, 2006).
107. Z. Okániková *et al.*, *Methodology for Identification of Ecological Corridors in the Carpathian Countries by Using Large Carnivores as Umbrella Species. Danube Transnational Programme Connect GREEN Project "Restoring and managing ecological corridors in mountains as the green infrastructure in the Danube basin"* (State Nature Conservancy of the Slovak Republic, 2021).
108. K. Vlková, V. Zýka, C. R. Papp, D. Romportl, An ecological network for large carnivores as a key tool for protecting landscape connectivity in the Carpathians. *J. Maps* **20**, 2290858 (2024).
109. C. R. Papp, H. Egerer, K. Kuraś, G. Nagy, *International Action Plan on Conservation of Large Carnivores and Ensuring Ecological Connectivity in the Carpathians* (UNEP Vienna Programme Office–Secretariat of the Carpathian Convention, WWF Romania, CEEWeb, Eurac Research, 2020).
110. G. Bombieri *et al.*, Brown bear attacks on humans: A worldwide perspective. *Sci. Rep.* **9**, 8573 (2019).
111. K. de Koning *et al.*, Digital twins: Dynamic model-data fusion for ecology. *Trends Ecol. Evol.* **38**, 916–926 (2023).
112. D. M. Theobald, A. T. H. Keeley, A. Laur, G. Tabor, A simple and practical measure of the connectivity of protected area networks: The pronet metric. *Conserv. Sci. Pract.* **4**, e12823 (2022).
113. S. Hoban *et al.*, Genetic diversity targets and indicators in the CBD post-2020 global biodiversity framework must be improved. *Biol. Conserv.* **248**, 108654 (2020).
114. H. Mu *et al.*, A global record of annual terrestrial human footprint dataset from 2000 to 2018. *Sci. Data* **9**, 176 (2022).
115. B. H. McRae, Isolation by resistance. *Evolution (N.Y.).* **60**, 1551–1561 (2006).
116. A. C. Hughes, R. E. Grumbine, The kunming-montreal global biodiversity framework: What it does and does not do, and how to improve it. *Front. Environ. Sci.* **11**, 1281536 (2023).
117. WEF, *The Global Risks Report 2024* (World Economic Forum, ed. 19, 2024).
118. Nestle, *Nestlé Responsible Sourcing Standard* (Nestec Ltd, 2018).
119. P. Linsley, R. Abdelbadie, R. Abdelbadie, The taskforce on nature-related financial disclosures must engage widely and justify its market-led approach. *Nat. Ecol. Evol.* **7**, 1343–1346 (2023).

Downloaded from https://www.pnas.org by 108.64.85.146 on September 29, 2025 from IP address 108.64.85.146.