

Beyond boundaries: Global natural lands connectivity

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TITLE

Beyond boundaries: Global natural lands connectivity

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ABSTRACT

Protecting and maintaining ecosystem connectivity is crucial for stemming the biodiversity crisis, but current tools and indicators assessing connectivity primarily focus on connectivity among protected areas, not across ecosystems. Here, we develop a map of global connectivity across all natural lands that accounts for the cumulative impacts of human modification. We then parse this continuous connectivity into categories directly relevant for conservation actions (i.e.,

spatial planning, restoration, and protection). We find that most global natural lands (66%) retain high levels of connectivity, particularly in tundra, boreal, and conifer forest biomes, which often fall outside of protected areas. Conversely, 29% of global terrestrial areas have low levels of connectivity due to high human modification, which is prevalent in Asia, Europe, and North America, and in temperate and tropical forested biomes. Our results underscore that focusing only on connectivity of protected areas misses ecologically important areas that currently lack protection and may fail to identify important conservation and restoration areas for connectivity that could benefit biodiversity. To inform global conservation goals, such as those enumerated in the Kunming-Montreal Global Biodiversity Framework (GBF), we summarize continental-, country- and biome-level patterns and illustrate how this whole-landscape connectivity data can be used to inform applications for GBF Goal A Targets 1 (on spatial planning), 2 (on restoration) and 3 (on protection).

KEYWORDS

Connectivity, circuit theory, Omniscape, human modification, conservation planning, biodiversity targets

HIGHLIGHTS

- We map global terrestrial natural lands connectivity, accounting for global human modification of lands
- Nearly one-third of land shows low connectivity driven by intensive human activity
- Current protected-area-based connectivity assessment approaches miss key connectivity areas across unprotected lands
- Categorization of outputs distinguishes diffuse, channelized, and impeded landscapes to guide conservation, restoration, and planning
- Results support implementation of the Kunming–Montreal Global Biodiversity Framework by identifying priority areas for protection and restoration

1. INTRODUCTION

The biodiversity crisis is fueled by rapid losses in the extent and integrity of ecosystems due to human-driven land modification and climate change^{1–6}. Ecological connectivity, defined as the

“unimpeded movement of species and flow of natural processes”⁷, is critical to ecosystem and species conservation and has been established as a key conservation component in the Convention on Biological Diversity (CBD)’s Kunming-Montreal Global Biodiversity Framework (GBF)^{8–10}. Yet despite the importance of management, protection, and restoration of “all lands”, data and guidance to fully support the implementation of these targets within the GBF are lacking or incomplete^{8,11}. Most of the work on developing indicators for monitoring connectivity has focused on protected areas (PA), which importantly has raised awareness of the importance of ecological connectivity¹². However, addressing the coupled biodiversity and climate crises will require a “whole landscape” approach to connectivity, where all lands, regardless of their protection status and ecological condition, are adequately considered and valued appropriately¹³.

Under the GBF, 195 countries aim to meet four long-term biodiversity conservation goals by 2050. The first, Goal A, targets that “the integrity, connectivity, and resilience of all ecosystems are maintained, enhanced, or restored” by 2050. Under Goal A, signatories aim to achieve multiple targets by 2030. Targets 1, 2, and 3 relate to spatial planning, restoration, and protection of ecosystems, and GBF guidance provides multiple indicators for measuring progress towards meeting each target. Target 3 contains particular emphasis on connectivity, stating that PAs and other effective conservation measures (OECMs) should be connected through corridors and “integrated into wider landscapes, seascapes and the ocean”. A PA is “a geographically defined area, which is designated or regulated and managed to achieve specific conservation objectives”⁸. The current set of proposed indicators only provide methods for evaluating linkages between PAs and OECMs⁸, yet cost-effective actions will require integrated approaches that

carefully address all three targets. Despite the focus on PAs in Target 3, there are many unprotected areas that must be considered that are potentially relevant for connectivity.

While PAs are a necessary conservation tool, the current global PA network is geographically and ecologically biased toward areas that are inherently difficult to access in steeper, higher, or more remote terrain and are sparsely populated^{14–17}. Focusing connectivity indicators solely on corridors between PAs will result in biased assessments of areas deemed important for connectivity. For example in an analysis to identify globally important areas of mammal movement between PAs, Brennan et al.¹⁸ filtered PAs by size due to processing constraints, and some areas known to harbor high biodiversity (United States Appalachian region, Madagascar, India, and Southeast Asia¹⁹) were identified as low connectivity values due to reliance on PA to PA connectivity metrics. Here, we present an additional connectivity metric representing the global connectivity of natural lands. We identify areas of connectivity importance outside of the current PA system to inform where future additions to the PA and OECM network could contribute to conservation goals.

Omnidirectional connectivity in the absence of specific source and destination locations, independent of the amount or distribution of PAs, is needed to sustain biodiversity and achieve the ecological representativeness proposed in the GBF targets^{8,15,20–22}. With this work, we produce the first global implementation of Omniscape, an omnidirectional implementation of circuit-theoretic modeling²³. Here, every pixel, can act as a source for potential species movement^{24,25}. Applied across any land cover map, independent of political or administrative boundaries, results may be more ecologically accurate in some cases, as it represents gradients in ecological condition without implying that species recognize anthropogenic boundaries. The result is a continuous dataset representing continuous structural connectivity²⁶ across a study

area^{24,25,27}. To help guide further work and allow users to identify areas that can help increase connectivity within the context of the Global Biodiversity Framework, we aimed to create a general map of natural lands connectivity, assuming that these areas could be traversed by many generalist species (see *Methods* for further information of model parameterization). We used this approach to go beyond connectivity corridor planning, and to facilitate the use of connectivity science in broader conservation goals, such as restoration and climate mitigation goals^{11, 28}

High movement areas resulting from Omniscape models are often interpreted as corridors and treated as conservation priorities, but additional translation is needed to turn continuous outputs into meaningful information for prioritization of conservation efforts. In the past, translation of connectivity data to policy applications has been challenging. One approach is to categorize model outputs, but categorization has not been a standard post-processing step, though breaking continuous outputs into categories could help users understand and interpret the patterns of movement potential. For example, Cameron et al. (²⁹) categorized connectivity data across California based on management and land tenure status to prioritize sites for conservation. More recently, Anderson et al. (³⁰) mapped climate connectivity for the continental United States and categorized flow based on the distribution and variation of the model outputs and combined those products with other data to delineate an expansion of the US PA network.

We build on this body of work to produce a map of global natural lands connectivity where each terrestrial pixel is treated as a source and destination. These data represent the capacity of natural vegetation to allow species movements as determined by levels of human modification at 1 km resolution and with respect to the estimated median dispersal distance of many bird and mammal species (*Methods*). We developed six categories of connectivity that can be used to evaluate the extent to which the connectivity of natural lands is channelized, diffuse,

or impeded (Table 1). Our approach allowed us to produce maps that illustrate how the spatial pattern and intensity of human impacts impede or channel movement and indicate natural areas where connectivity is most likely to be unconstrained. This work is broadly applicable to inform global conservation goals, such as those enumerated in the GBF. To demonstrate its utility, we provide summaries to inform global, national, and sub-national decision making and show how this whole-landscape connectivity approach can be used to support global biodiversity goals.

Table 1 | Definitions of terms for inputs, outputs, and categories from the global Omniscape connectivity modeling process, with corresponding color coding used to display connectivity categories in subsequent figures.

Model Component	Term	Definition
Inputs	Source	The presumed capacity of a site to function as a source for species or gene movement (in this study, all natural lands; ³¹).
	Resistance	Landscape impedance to movement potential, derived in this study from a measure of human modification ³² .
Outputs	Flow, F (current)	The representation of species movement source areas across a resistance surface.
	Potential flow, F_p	The representation of hypothetical movement from sources without resistance. Flow potential allows us to ask: given the amount and configuration of source pixels, how much flow would be expected in the absence of barriers ²⁴ ?
	Normalized flow, F_n	The ratio of flow to potential flow. Normalized flow enables more accurate identification of the mechanisms underpinning different flow magnitudes such as where barriers are redirecting flow ²⁴ .
	Channelized movement area	High flow in relatively narrow pathways near distinct barriers of high resistance. Resistance levels in these areas can vary from low to high; channelization indicates increasing importance of these paths as other options have been lost.
Output categories		Areas where flow patterns are similar to what would be expected with a homogeneous surface of low resistance. This includes: Intensified areas: moderately high flow areas, adjacent to higher resistance areas from which flow has been redirected.
	Diffuse movement area	Robust areas: moderate flow across low resistance; many redundant options for movement, indicating natural areas with the least disruption of flow. Dampened areas: lower flow areas within a low resistance neighborhood. The weaker current flow relative to robust diffuse can indicate more resistance, or lower source strengths.
	Impeded movement area	Flow is restricted and directed away from these locations due to high resistance. This includes: Weak areas: low flow across minimally permeable lands with moderately high to high resistance; Obstructed areas: highly restricted flow, reflecting redirection to other areas by high resistance.

2. RESULTS

To promote connectivity data in decision making and conservation planning, we categorized complex, continuous connectivity data into policy-relevant outputs; we then produced a global map describing connectivity patterns across all lands (Fig. 1, Fig. S1). The categories derive from classifying Omniscape model outputs (the flow (F), flow potential (F_p), normalized flow (F_n) datasets; Table 1) and the resistance data (levels of land modification³²) to create six categories of connectivity that describe the unique combinations of these layers and the flow patterns and magnitudes given the human modification resistance layer (*Methods*; Table 1, Table S1).

We then condensed the six categories to ‘channelized’, ‘diffuse’ (i.e., ‘intensified’, ‘robust’, and ‘dampened’), and ‘impeded’ (i.e., ‘weak’ and ‘obstructed’) categories for brevity, although figures and tables present all six main and subcategories. Land within the diffuse category represents the goal for connectivity—zones characterized by multiple potential dispersal pathways and more limited anthropogenic impact on species movement patterns. Areas with impeded connectivity occur where there is likely a high level of land modification and where potential movement is much lower than expected (Fig. 2). Channelized connectivity areas have the highest flow (i.e. “corridors”). However, contrary to intuitive thought, these areas should not be the focus of connectivity conservation, especially where diffuse connectivity zones occur. These are areas where surrounding land modification has forced flow through an area that is surrounded by high human development, resulting in much higher flow than expected in the absence of modification (which would lead to diffuse connectivity).

We find that 66% of natural lands globally have diffuse connectivity, 29% have low connectivity (i.e. movement likely ‘impeded’), and 5% have channelized connectivity. When

comparing the percent diffuse per country to other global connectivity indicators (PAI¹⁸, PARC^{33,34}, ProNet³⁴, and ProtConn³⁵) recommended as GBF indicators and with 2024 updates¹⁶, we found low correlations across each indicator. Percent diffuse is most correlated with PARC at $r = 0.68$. Other correlations with percent diffuse range from -0.42 to -0.11 (Table 2).

Table 2 | Pearson correlation coefficients across log-transformed connectivity indices. Percent of diffuse connectivity category per country (>10,000 km²) vs. Protected Area Index¹⁸ (PAI), Protected Area Representativeness and Connectedness³³ (PARC), Protected Areas Network³⁴ (ProNet), and Protected Connected³⁵ (ProtConn) connectivity indicators as updated in UNEP-WCMC and IUCN (¹⁶).

	% Diffuse	PAI	PARC	ProNet	ProtConn
% Diffuse		--0.0003	0.63	-0.25	-0.11
PAI	--0.0003		-0.14	0.09	0.03
PARC	0.63	-0.14		-0.19	0.20
ProNet	-0.25	0.09	-0.19		0.53
ProtConn	-0.11	0.03	0.20	0.53	

2.1

Connectivity patterns in biomes and continents

Due to pronounced fragmentation, temperate broadleaf and mixed forests have the highest proportion of impeded movement potential, followed by mediterranean forest, woodlands, and scrub (Fig. 3; Table S2). Tundra, boreal, and tropical moist forest biomes have the highest proportion of diffuse areas where potential movement is unimpeded. Across biomes, Mediterranean forests, woodlands, and scrub have the highest proportion of channelized areas (6%) and the lowest amount of diffuse areas (58%; Fig. 3; Table S2), reflecting high levels of land modification. Deserts and xeric shrublands have the least amount of channelized movement areas (93% diffuse), likely because these areas also have lower land modification. Tundra and boreal forests/taiga both have 97% diffuse movement areas, followed by montane grasslands and shrublands. Tundra and boreal areas also have the least amount of impeded areas.

In general, across continents Africa has the highest proportion of diffuse movement areas and the lowest proportion of channelized movement areas (91% and 1%, respectively); whereas Asia has the lowest proportion of diffuse movement areas and highest level of channelized movement areas (74% and 4%, respectively). Asia has the highest and Oceania has the lowest proportion of impeded areas (23% and 7%, respectively; Fig. 4; Table S3). In addition, the biome-level patterns of low connectivity (indicated by proportion impeded) varied by continent, with Europe and North America exhibiting high levels of impeded areas in temperate grasslands relative to other continents.

2.2

Connectivity patterns in countries

Unsurprisingly, smaller countries with a large proportion of land modification have the greatest percentage of impeded areas (Fig. 4, Table S4). The Netherlands, Belgium, Moldova, and Denmark all have the highest proportion of impeded movement area ($\geq 85\%$) and the lowest proportion of diffuse movement areas ($\leq 14\%$). In contrast, relatively large countries with low levels of land modification and expansive natural land cover have the highest proportion of diffuse movement areas. This includes many nations across Africa and some South American countries, such as Peru, Bolivia, and Colombia (Fig. 4; Table S4).

2.3

Global Biodiversity Framework application

The categorized connectivity data can be combined with other datasets (e.g., species occurrences, habitats, ecosystem services.³⁷), to facilitate the consideration of connectivity in global and national-level biodiversity commitments. We illustrate conceptually how our connectivity data and categories can be used to inform GBF Goal A Targets 1 (regarding spatial planning), 2 (restoration), and 3 (protection), though there are uses and applications beyond these targets). We do not attempt to identify specific sites for conservation interventions, as this process should be done in collaboration with local communities, consider competing land uses and multiple actions, and incorporate localized data, context, land tenure, and inclusion of equity considerations in line with rights-based approaches to conservation.

Target 1 (spatial planning): Our data can inform biodiversity-inclusive spatial conservation planning, which recognizes the importance of considering ecological connectivity in the design of conservation networks within landscapes or seascapes³⁷.

Alternative spatial scenarios can be evaluated based on their ability to improve connectivity, for example by increasing protection of channelized areas that represent the

last remaining pathways of connectivity and to increase movement options through targeted restoration as described in Target 2 (see below). These represent areas important for maintaining or enhancing connectivity across entire landscapes – not just between or among PAs – and can facilitate the consideration of whole landscapes in global and regional spatial connectivity planning.

Target 2 (restoration): Identifying where connectivity has been lost, as found in weak, obstructed, or channelized areas — in concert with other information such land tenure, competing land uses, biophysical suitability, and feasibility for ecological recovery — can guide site selection and efficient allocation of resources for restoration. Restoring areas close to channelized flow areas can help preserve and enhance connectivity and restoring areas in weak or obstructed flow may help improve connectivity, depending on the cause of loss (Fig. 5).

Target 3 (protection): These data can also be used to identify priority sites for future conservation actions, including siting of new PAs and OECMs. In overlaying the categorized connectivity data with global PA locations, we found that many countries with a high percentage of diffuse connectivity areas within their territory have low levels of protection; but more concerningly, there are many countries with low levels of protection and high levels of impeded movement areas (Fig. 4; Fig. 6). These data allow users to better understand the landscape context of a PA. For example, if a country's PAs primarily fall within diffuse areas, biodiversity may benefit from conservation measures focused in channelized areas. If PAs are surrounded by impeded areas, future conservation efforts may focus on channelized areas between PAs (Fig. 5).

For example, Australia has reached approximately 20% protection¹⁶ with the majority of PAs occurring in the desert and xeric shrublands biome and in other diffuse areas (i.e. are connected). To advance reaching both Targets 2 and 3, concentrating future conservation in more modified areas may be advantageous from the point of view of improving connectivity and providing potential additional benefit to both people and wildlife, rather than in areas that are already well-protected and connected. Future siting of PAs, OECMs, or conservation and management actions could be targeted at remaining channelized areas within modified areas to maintain existing connections. If restoration is feasible, these efforts could be focused near currently protected channelized areas to enhance these connections and increase their resilience.

3. DISCUSSION

Nearly all countries have agreed to ambitious goals and targets in the GBF that build on decades of science and advocacy. Restoration, protection, and ecosystem connectivity are foundational to Goal A within the GBF. Yet to date the technical tools and evidence for how best to consider and integrate connectivity across whole landscapes have been lacking. We help fill this gap by conducting a global natural areas connectivity analysis which considers broad-scale connectivity across entire landscape gradients and providing a method for categorizing the complex outputs in a way that is policy relevant. Beyond our analysis, these methods can be applied across finer scales to meet landscape-level needs at higher resolutions and using country/region-specific data.

We find that when whole landscapes are considered, the majority of Earth's remaining natural terrestrial areas lie within connected zones (66% of terrestrial lands have diffuse movement potential). Conservation efforts should focus on protecting these well-connected and channelized areas, since many countries with high amounts of diffuse movement areas have low levels of protection (Fig. 6). In addition, restoring impeded and channelized areas (areas that

have lost connectivity due to human-driven land modifications) should also be a conservation target. With a growing human population and ongoing development expansion, diffuse movement areas could become channelized or impeded without continued or improved conservation actions. This information should be used in concert with conversion risk mapping (e.g.,³⁸) and as well as other connectivity measures. When whole landscapes are not included in connectivity analyses, unprotected but biologically important areas could be left out of conservation planning, leading to reduced species and ecosystem persistence over time⁹.

The categorization method we developed strengthens the ability to communicate the importance of connectivity for conservation planning in two ways. First, it recognizes at least two ways that connectivity can be compromised: it can be impeded, in which movement is reduced or lost compared to unmodified landscapes. Second, it can be channelized, in which movement in a channel is increased even as it is reduced in other areas of the landscape. Channelized systems have lost redundancy in movement options that provide resilience to a system and increase the risk of complete loss of connectivity in the face of future land use and climate changes. The second advantage of this categorization derives from explicitly evaluating the site-specific resistance values, which enables us to model the impact of site-specific interventions on whole landscape connectivity.

3.1

Comparison to other connectivity measures

The low correlation of diffuse movement areas per country with other connectivity metrics suggests that our data provides complementary information (Table 2). Indeed, our results differ from prior connectivity analyses in several important ways. First, analyses that model connectivity between PAs miss connections elsewhere. If not used in concert with non-PA based

connectivity measures, these results will bias connectivity conservation towards areas of PA occurrence, the global pattern of which is geographically and ecologically biased in remote areas potentially jeopardizing important but unprotected areas for both nature and people^{15,16}. By using natural land cover as our source data and modeling connectivity across all lands irrespective of conservation status, our data depict the ecological connectivity regardless of PA occurrence. For example, the Appalachian region of the eastern United States has a low density of large, globally registered PAs but has swathes of channelized areas which are remaining connections running along mountain ridges in a north-south orientation (Fig. 2). These areas are potentially important for maintaining connectivity for wildlife as climate changes. Yet, these ecologically important areas are not identified in other connectivity assessments^{18,35}. In addition, our approach and results remain robust to sociopolitical instability resulting in PA downgrading, degazettement, or degradation or when PAs are unreported³⁹.

Biased protection is also reflected in the distribution of connectivity categories within biomes. For instance, temperate broadleaf and mixed forests and grasslands, mediterranean forests, woodlands, and scrub, and tropical and subtropical dry broadleaf forests all have high proportions of impeded lands and low proportions of land protection³⁶. Our results underscore the need for enhanced conservation measures in these biomes. A lack of PA prevalence in these biomes may direct conservation elsewhere when relying on PA-based connectivity analyses. Lack of protection and PA-centric consideration of connectivity in grasslands, for example, can be seen in the midwestern United States, southern Brazil, and India. These areas have moderate levels of human land pressures but remain important for maintaining connectivity across broad landscapes.

At a continental scale, there are areas identified as highly connected when solely examining distance between PAs (e.g., ProtConn³⁵), even though these areas have low proportions of diffuse and high proportions of impeded areas. If we use the percent of diffuse area as a measure of landscape connectivity, Africa ranks the highest globally, followed by Oceania (Fig. 5; Table S3). Using distance-based metrics focused on PAs, without consideration of surrounding landscape permeability, Europe is the most connected continent, with the Americas ranking second. This difference stems from geographically clustered PAs in the EU and Americas, within landscapes of moderate-to-high levels of human modification, resulting in impeded lands between PAs. PAs may be geographically near one another, but movement between PAs may not be likely given the surrounding landscape. Many countries with low connectivity as indicated by ProtConn³⁵ were dominated by the diffuse category in our analysis, indicating redundancy in movement pathways throughout most of these countries' land areas (Mexico, Panamá, Colombia, Ecuador, Madagascar, Papua New Guinea, Nepal; Fig. 1, Table S4). Many of these countries have large amounts of diffuse connectivity through natural lands that remain unprotected. Our results are similar to the findings of Ward et al. (⁴⁰), where Europe had the lowest PA connectivity, when measured by intact lands as defined by levels of human pressure.

Our work enables evaluation of the effectiveness of the existing PA networks in ensuring connectivity. Countries with high amounts of diffuse areas where protection is under the 30% target should identify whether there are unprotected channelized areas (bottom right, Fig. 6). Countries with low amounts of diffuse areas, moderate protection, and high amounts of channelized areas should ensure diffuse areas are protected to maintain connectivity redundancy (center of the graph, Fig. 6). Countries with low amounts of diffuse areas, low proportions of

protection, and low amounts of channelized areas likely have high land modification and conservation efforts may be better suited for non-area-based conservation or restoration measures, such as in the EU (Fig. 6). The categorized connectivity data allows jurisdictions to identify key locations for restoration to bolster existing connectivity.

In contrast to previous efforts, our work represents structural connectivity across natural land cover considering the gradient of anthropogenic land modification, regardless of species or taxa. Where prior connectivity analyses have taken a functional connectivity approach, their results depict areas important for the particular focal species or taxa and their findings must be used in concert with other species and ecosystem condition information to inform global biodiversity goals. For example, Brennan et al. (¹⁸) show low connectivity across much of Southeast Asia, likely reflecting the lack of large PAs^{41,42}, rather than this area's inherent connectivity value. When modeling connectivity across all natural land cover, we found impeded, diffuse, and potentially important channelized areas across South and Southeast Asia, including the Indian subcontinent (Fig. 2). India is dominated by impeded areas and the remaining channelized areas could be conserved or managed to maintain the existing connectivity (Table S2).

3.2

Caveats and notes for global natural lands connectivity

The differences in our results compared with others reinforce the complexity and contextuality of measuring ecological connectivity. Multiple measures should be used to assess and track global connectivity to capture the multiple aspects of connectivity; both between PAs and OECMs and to the wider landscape. We modeled connectedness of terrestrial natural vegetation globally, not connectivity for any one species or type of geography. We assumed that human pressures, as

determined by human modification data reflect land cover alterations impacting movement, represent meaningful resistance from anthropogenic barriers for many species^{43,44}. While we did not attempt to define specific mechanisms of resistance, negative impacts of human modification on animal movement are shown to include decreased habitat quality, increased mortality or predation risk, and associated behavioral responses (avoidance)⁴⁵⁻⁴⁷. We recognize that for some species, especially human-tolerant or commensal species, this assumption may not apply, but these species are also often not of conservation concern. Rather, this modeling effort is intentionally designed to apply to species that are negatively impacted by human pressures on a landscape that can cause destruction, degradation, and impairment of ecological processes (as outlined by the IUCN biodiversity threats classification⁴⁸ and adopted by global human modification mapping³²).

To identify more small-scale connectivity patterns, relevant for short distance dispersers, such as herpetofauna and most plants^{49,50}, our methods can be downscaled using local data since the global results were sensitive to some parameterization decisions. Our global team (see *Methods*) specifically identified grassland areas with low human modification as sensitive to slight increases in human modification due to pasture/grazing. We subsequently removed the pasture/grazing layer from our analysis, which assumes limited impacts of grazing lands on movement potential. While there are caveats to our model, global products such as ours have broadscale utility (e.g.,⁵¹), and this work will provide critical context to identify important patterns of variation in connectivity constraints and where to guide more in-depth assessments. By no means is this work meant to replace local or landscape-tailored modeling and planning where fine-scale data are available to answer more targeted questions.

3.3

Technological improvements in connectivity modeling

Measuring and monitoring connectivity is not only theoretically challenging, but also technologically challenging. Fortunately, improvements in software and computing resources are rapidly enabling major advances to allow this modeling at high resolution. There are several modeling options for continuous circuit-theory connectivity modeling²⁷, but the implementation of Omniscape in the Julia language in particular allows relatively efficient global modeling that facilitates iterative parameter testing^{23,52–54}. We capitalized on increased cloud processing capabilities and the high-efficiency language Julia to run Omniscape globally⁵². The power to consider connectivity across a continuum of landscape conditions provides a powerful, flexible way to deliver decision-relevant products. We expect that faster runs, strengthened by deeper understanding of model behavior, will accelerate model co-creation with decision-makers and regional experts that can leverage, downscaled data and create models appropriate for specific connectivity questions. Increased processing speed allowed us to iteratively test model parameters and work closely with collaborators to refine the connectivity modeling inputs (e.g., human modification resistance surface), provide guidance on modeling parameterizations (i.e., how water was treated as movement barrier), and iteratively consult with experts on draft model outputs. Combined, these collaborative efforts and advancements refined our approach, improved the reliability of our outputs, thereby promoting higher relevance for conservation policy applications and goal setting processes.

3.4

Broader conservation applications

Beyond the GBF, there is global interest and growing momentum for restoration and protection of natural systems at scale for climate benefits, including natural climate solutions (NCS)^{55,56}.

Our map allows identification of sites for restoration and protection that maximize benefits to connectivity for biodiversity conservation in addition to carbon sequestration^{57–60}. When further paired with land tenure information and with community and local engagement, protection and restoration of natural systems can be powerful tools for durable conservation outcomes⁶¹. Users of our methods and map should apply best practices in engaging local communities and other critical local stakeholders for advancing GBF goals. Importantly, large-scale projects protecting connectivity on unprotected territories must meet the equity and justice concerns of local communities⁶². Global environmental agendas often lead to ambitious goals that can galvanize environmental advocates, but the impacts on local populations is not uniform. A next step may be to overlay human populations (e.g.,⁶³) and land tenure (e.g.,⁶⁴) with our global map to assess potential areas where careful planning and implementation will be critically important.

4. CONCLUSION

Ecosystems, species ranges, and human land uses are shifting, often in unpredictable ways, necessitating more holistic approaches to conservation that extend beyond PA boundaries^{65–67}. Protecting and maintaining ecological connectivity is critically important to address the biodiversity crisis. Indicators that can evaluate connectivity are needed to set targets and measure success towards global conservation goals such as those in the GBF⁸. There has been a lack of sufficient methods for whole landscape connectivity modeling, especially at the large scales that is required to meet national and global goals¹¹. Global connectivity indicators must consider unprotected as well as protected areas and efforts to stem biodiversity loss need to include the restoration and protection of natural lands outside of PAs⁴⁰. By presenting a continuous global natural lands connectivity map with a policy-relevant categorization, applicable across different landscapes and contexts, we can better inform policy and land-use planning. Such an approach

can avoid the pitfalls of relying exclusively on PA-centric connectivity indicators, which can result in biased information and direct conservation focus away from unprotected areas critical for whole landscape connectivity. As landscapes, ecosystems, and climate change, moving beyond the boundary to identify and preserve whole system connectivity is critical for conserving.

5. METHODS

There are many ways to model connectivity. We chose a circuit theory method that allowed us to emphasize how landscape patterns influence broad movement potential at multiple scales, from landscapes to continents. To estimate connectivity at the full global extent at 1 km resolution, we used Omniscape.jl, a moving window-based adaptation of the Julia language implementation of the circuit-theoretic modeling software Circuitscape^{23,53,68}. Circuit-theory models allow considering how movement may spread or be constrained in different parts of a landscape by using the mathematics of electrical circuit theory to describe cumulative patterns that represent traces of ‘random walkers’ as they encounter variable resistance using the analogy of electrical current flow⁶⁸. Resistance weights are assigned to pixels based on hypotheses of the degree to which the conditions in that pixel would support or inhibit movement. The assumption of random movement suggests that routes reflecting knowledge of the landscape (like annual migrations) are not well modeled with this approach⁶⁹. By treating movement as a random process, one may identify many possible movement routes. Likewise, one may identify constrained routes or areas where there are no movement routes. Omniscape is an expansion of Circuitscape, which considers connectivity between focal nodes or patches, by allowing modelers to evaluate connectivity in all directions (“omnidirectional” Circuitscape) to and from all pixels (for full details on the Omniscape approach, see ^{23,24}). Here, we deployed Omniscape

with separate resistance and source layers using a moving window radius of 125 km, globally at 1 km resolution.

5.1

Resistance data

We used an updated version of the global 300 m Human Modification (HM) dataset for 2022, refined specifically for modeling connectivity³², and coarsened it to 1 km using average-based resampling for the resistance layer. The HM includes the spatial extent and intensity of cumulative human pressures from settlement, agriculture, forestry, transportation, mining, energy production, electrical infrastructure, dams, pollution and human accessibility. For the connectivity resistance surface, we removed pasture/grazing and air pollution data, because we assumed they have low influence on species movement. For pixels intersecting major roads and highways, we assigned a value of 0.8 (for 300 m pixels) to decrease the muting of linear features when decreasing resolution (to 1 km).

In Omniscap, small differences in resistance at the low end of the range, especially in factors that occur in large swaths of a landscape (such as large blocks of agriculture) typically have a large influence on the results. Although HM has been used as resistance surfaces in connectivity modeling⁷⁰, few studies have explored using transformations on the resistance data to understand the model's sensitivity to the distribution of continuous values^{25,70}. Exponential functions may better describe the relationship of wildlife to landscapes during movement life history periods than non-exponential linear functions^{25,71,72}. Specifically, exponential transformations may better describe the relationship of raw HM to resistance with respect to broad-scale animal movement than the raw HM data itself⁷², since many species can move across higher modified areas while dispersing. This HM transformation reflects that negligibly to

moderately modified areas of the landscape may be readily used for movements, and only the most modified areas are unusable. These transformations are more ecologically sound when considering long-distance movements and allow for pattern exploration in the middle of the HM distribution^{71,72}. We used the function:

$$f = 100 - 99 \frac{1 - \exp(-c(1 - HM))}{1 - \exp(-c)}$$

where f is the transformed value of the HM and c is a rescaling parameter⁷¹. With larger c values, the transformation approaches an exponential function of the HM and smaller positive values approach a linear transformation. We tested $c = 0.25, 2, 4$, and 8 (Table S5) scaling parameters on the HM data during our sensitivity testing. After sensitivity testing (described below), we chose to report results using the $c=2$ transformation models.

5.2

Source data

A source layer in Omniscape is used to represent locations from which movement originates, such as a parcel of natural land or a protected area²⁴. A common source layer in connectivity modeling is the inverse of the resistance layer, especially in models where human modification is used as the resistance layer^{24,25}. Instead, we used natural land cover as our source to model a global ecological network. Natural land cover pixels better represent areas that will likely be moved from, and although correlated with HM, provides a clear way to represent ecological networks that connect major ecosystem types.

We used the ESA World Cover 10 m v 200³¹ product as our source layer because we were interested in creating a natural lands connectivity model, with connectivity identified between areas of natural lands and it includes accuracy assessment and an uncertainty layer with an estimated 76% global accuracy, as created. We first labeled each class in the ESA World

Cover data as representing natural vegetation (e.g., tree cover, shrubland, grassland, bare/sparse, wetland, mangroves, moss/lichen) or non-natural (agriculture, urban) lands, then rescaled the data to 1 km² pixels. We used the proportion of natural lands within 1 km pixels as our source weight data. To do this, we first recoded the 10 m pixel World Cover data to 0's (pixels with non-natural land cover) and 1's (pixels with natural land cover). Then, we rescaled this data to 1 km, using the number of 0's (non-natural) and 1's (natural) to compute the proportion of each new 1 km pixel that was natural. The new pixel value was treated as the source weight of that 1 km pixel within the Omniscape model. Thus, pixels with a high proportion of natural areas had a high source value (i.e. a potentially high number of animals moving from that pixel to other pixels). Water

5.3

Water

The treatment of water in resistance data can have a significant impact on connectivity outputs⁷³. We developed a method for addressing water that aligned with the purpose of mapping terrestrial connectivity and our intent of informing conservation strategies that address the influence of human modifications on movement potential. In other studies, water has been treated in ways that range from “no data” (effectively complete barriers to movement) to low or moderate resistances, to approaches that scale the resistance of water to size of water body or flow rate, to maximum resistance (e.g.,^{24,25,30,74–76}). Through iterative testing for this work, we developed an approach intended to limit the effect of water on the model outputs⁷⁷, which does not involve identifying flow rate or water body size. To include water in a “neutral” way that does not prohibit or facilitate resulting flow (F), we first identified water pixels within 10 km of terrestrial pixels. Then, we identified a 40 km radius from each of these ‘near shore’ water pixels and

calculated the average resistance value of the terrestrial pixels within this 40 km radius. Next, we identified resistance values that were within 2% of the average resistance of the terrestrial pixels in the 40 km radius area. Finally, we assigned the near shore ocean and inland water pixels random resistance values, from the distribution of resistance values within 2% of the average resistance value in the 40 km radius. This approach ensured that the resistance values of water would not have higher or lower resistance than neighboring land. We assigned the maximum resistance value to water more than 10 km from land, assuming that few terrestrial species would be able to move in water >10 km from land. Finally, we masked water from the final output maps. Our map of water was based on the ESA CCI Global Water Bodies dataset (v4.0; ⁷⁸).

5.4

Model parameters

Omniscape allows for ‘blocking’ or grouping squares of pixels and using the center pixel as the source²³. This method decreases processing time and does not impact model results²⁵. In all cases, we used a block size 10% of the moving window radius to decrease model run time while maintaining model integrity²⁵. We tested radius sizes of 50 km, 125 km, and 425 km and we chose the radius size of 125 km to reflect potential dispersal distances of most birds and mammals, ranging from <1 km – 467 km, with medians ranging from <0.1 km to 87 km⁷⁹.

5.5

Model estimation

We computed all outputs on r6i.4xlarge EC2 virtual machine instances on Amazon Web Services (AWS), each containing 16 vCPUs and 128 GB of RAM. Models were estimated using Omniscape v0.5.8 running on Julia v1.9.2 with 6 threads. Model run time varied depending on

the window radius and ranged from several hours (for a 50 km radius) to approximately one week (for a 425 km radius).

5.6

Output categories

The Omniscape main outputs, F (potential flow or movement from source areas across a null or uniform resistance surface) and the F_n (flow in the presence of a resistance surface such as HM) provide complementary information to convey how the resistance and source data interact to influence the magnitude of flow across landscapes, and the degree to which movement is constrained by barriers²⁴. The F emphasizes the most likely places for movement to occur, highlighting key areas of concentration and broad movement zones between the most intact areas, in the absence of human modification, but with natural barriers. This allowed us to attribute changes in flow from F to F_n to human modification. The F_n , where the magnitude of flow is scaled to the regional magnitude of sources, identifies places where F has become concentrated relative to flow in the absence of resistance (F_p), even if the overall flow amount is moderate or low relative to other locations. This allows the model to highlight key movement zones and pinch points (areas where flow is restricted to narrow corridors) across the full range of resistance levels and geographic distributions of source areas.

The categorization was informed by four continuous components which were each categorized: the continuous flow pattern (impeded, diffuse, channelized) from the F_n , the F_p , F , and the HM resistance data. Based on prior work by Schloss et al. (⁷⁵) and Cameron et al. (²⁹), we categorized each of these four layers based on thresholds we identified which aligned with changes in the distribution of each data layer:

Normalized flow (F_n): Following comparisons of distributions with local data and our global data, we adopted the thresholds identified by Cameron et al. ⁽²⁹⁾, where $F_n > 1.7$ is channelized flow, $1.3 \leq F_n \leq 1.7$ is intensified flow, $0.7 < F_n \leq 1.3$ is diffuse flow, and $F_n < 0.7$ is impeded flow.

Flow potential (F_p): To determine the thresholds for the flow potential layer, we calculated the global distribution of flow potential and cumulative current and identified one threshold break for the flow potential data, opting to include the majority of data into one lower category ($\mu + 0.5$ SD) and defining values $> \mu + 0.5$ SD as ‘high’.

Flow (F): Because the flow layer is calculated and defined relative to the potential flow layer, we used the same values as the flow potential layer with the addition of a ‘very high’ category. We defined ‘very high’ cumulative flow as $> \mu_{Fp} + 1.5SD_{Fp}$.

Human modification layer: We based the thresholds for the HM on those identified in Kennedy et al. ⁽⁴³⁾. However, because we used the HM as it relates to how species may move across landscapes, we adjusted the thresholds to align with HM values as found within ESA World Cover land cover classes. Because tree cover and other natural classes were most abundant < 0.1 HM and because species can move across sub-optimal habitat, we combined the “very low” and “low” HM classes previously identified^{43,80}. Our HM classes were thus: < 0.1 “low”, $0.1 - 0.3$ “low-medium”, $0.3 - 0.7$ “medium-high”, and > 0.7 “high” modification.

We reclassified each of the above continuous layers according to the respective identified thresholds and combined all four layers to create one global categorized map with 96 potential unique categories. Sixty-three occurred globally. We then aggregated these categories through iterative review, minimizing within-class variance and maximizing between-class differences on

the basis of flow magnitude, spatial patterns identified by inspection against visual satellite imagery at multiple scales, and relative prevalence (i.e., global pixel counts). In so doing, we prioritized categorization by flow magnitude and pattern (i.e., ‘channelized’, ‘diffuse’, ‘impeded’), proceeded with initial refinement of subcategories (i.e., ‘intensified’, ‘robust’, ‘dampened’, ‘weak’, ‘obstructed’), then used differences between flow potential and cumulative flow to resolve the final groupings.

5.7

Sensitivity testing

We tested multiple model inputs and parameters to determine their effects on model outputs (Tables S5, S6, Fig S2). We ran models with different c values, model search radii, source layers, water treatment methods, slope, and treatment of grazing lands. We compared cumulative flow outputs using a Pearson correlation coefficient, calculated in R package terra v 1.7.71⁸¹ (Table S6). Models were all positively correlated and we chose parameters that maximized processing speed while representing general species dispersal capabilities.

5.8

Review process

Because we conducted a global analysis, we formed a review team of 14 conservation practitioners across six continents to fine-tune model inputs and ensure model validity. The team (including coauthors J.B.-G., C.R.D., J.F., M.N.-R., and M.F.R.) included conservation scientists with geospatial and/or connectivity modeling backgrounds with knowledge of African, Australian, Asian, North American, and South American landscapes. They were provided a data viewer with the input and output datasets, written materials about our methods, a video of our intent and methods, and a questionnaire guiding their review. After these review sessions, the

team reviewed the output datasets with respect to their knowledge of landscapes and other existing connectivity analyses. We then reviewed feedback received and made changes to the input data to address concerns raised by reviewers. Overall, across geographies, reviewers expressed concerns around the inclusion of pasture/grazing lands as a component of the resistance layer, which led us to use a modified version of the HM data^{32,43}.

5.9

Data summaries

To support country and regional decision making, we summarized movement potential by country, continent, biome, and protected areas boundaries. For summaries by biome, we used the biomes identified by Dinerstein et al. (³⁶⁸²). For protected areas, we used data from the World Database of Protected Areas⁸⁷. We followed Allan et al. (⁸²) by including China and India PAs using the 2017 WDPA data. We excluded marine protected areas, PAs that were “proposed” or in the “not applicable” protection categories. We created separate layers for each IUCN protection category: I-VI, “not reported”, or “not assigned” and converted these to 1 km² cell raster data, where any cell with $\geq 50\%$ overlap was included as protected. We combined these raster layers and removed any overlap, retaining the highest level of protection, where applicable.

To compare our data with other connectivity measures, we calculated Pearson correlation coefficients for countries $>10,000$ km² for the percentage diffuse within a country, protected area index¹⁸ (PAI), Protected Area Representativeness and Connectedness³³ (PARC), Protected Areas Network³⁴ (ProNet), and Protected Connected³⁵ (ProtConn) log-transformed connectivity indicators as updated in UNEP-WCMC and IUCN (¹⁵) using R v 4.4.3⁸³.

DATA AVAILABILITY

Both cumulative connectivity data and categorized connectivity data are available and may be downloaded from Harvard Dataverse at: <https://doi.org/10.7910/DVN/VOGJF1>.

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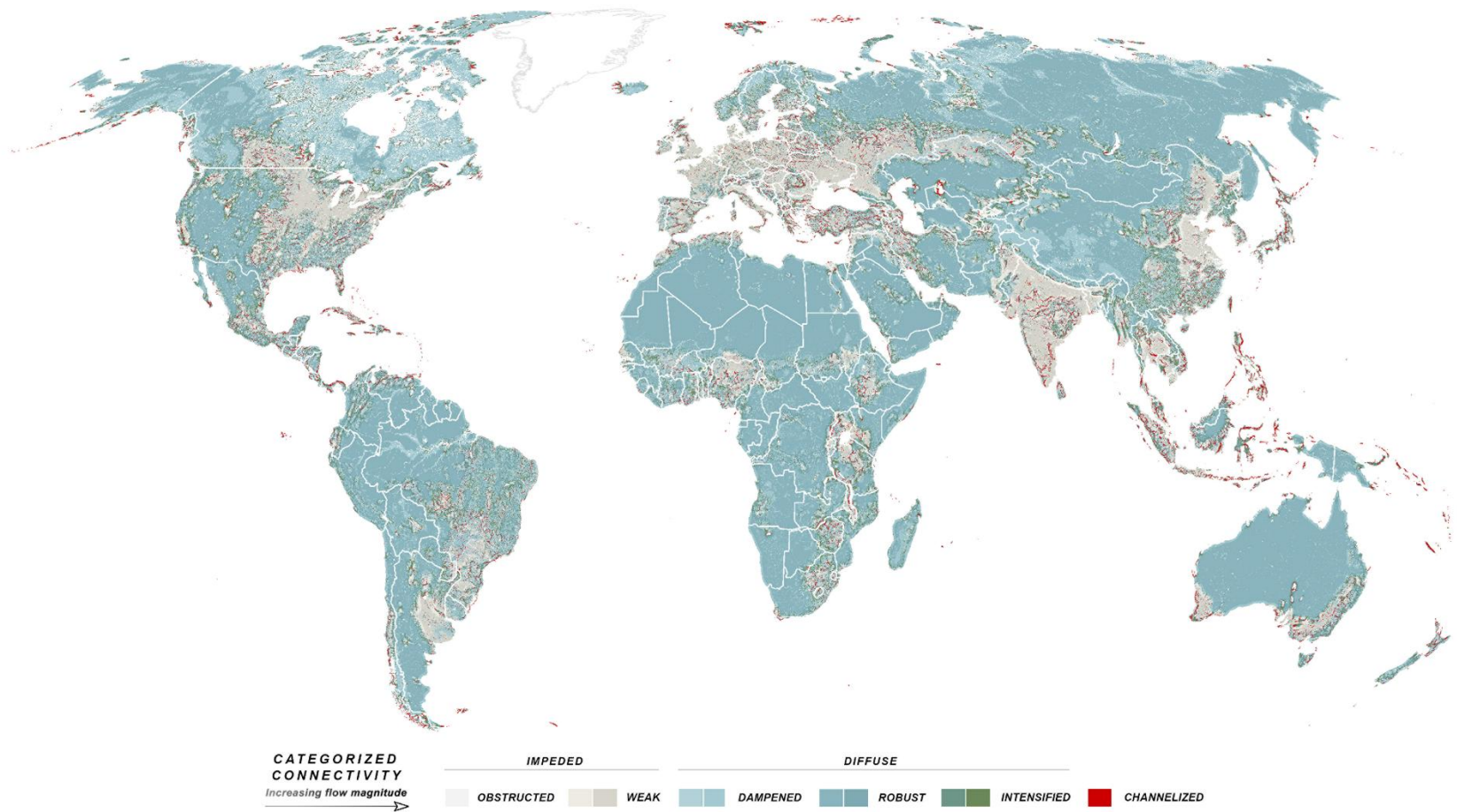
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AUTHOR CONTRIBUTIONS

Erin E. Poor – Conceptualization, methodology, project administration, writing, supervision, funding acquisition; Kimberly Hall – conceptualization, methodology, writing; Jesse Anderson – data curation, formal analysis, software, visualization; Melissa Clark – methodology, writing; Aaron Jones – conceptualization, visualization, writing, data curation, methodology; Christina M. Kennedy – conceptualization, methodology, writing; Carrie A. Schloss – methodology, writing; David M. Theobald – data curation, methodology, writing; Jaime Burbano-Girón – writing; Susan C. Cook-Patton – writing; C. Ronnie Drever – writing; Joseph Fargione – conceptualization, writing; James Fitzsimmons – writing; Mauricio Nunez-Regueiro – writing; Milena Fermina Rosenfield – writing; Yuta J. Masuda – funding acquisition, writing

893
894 **FIGURES**



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897 **Fig. 1 | Categorized global natural lands connectivity, given human-driven land modification.** Ideal connectivity can be
898 considered ‘robust diffuse’ and efforts to restore connectivity should focus on channelized or impeded areas, depending on local
899 context. The most common categories are rendered into low/high classes for increased ease of visualization.

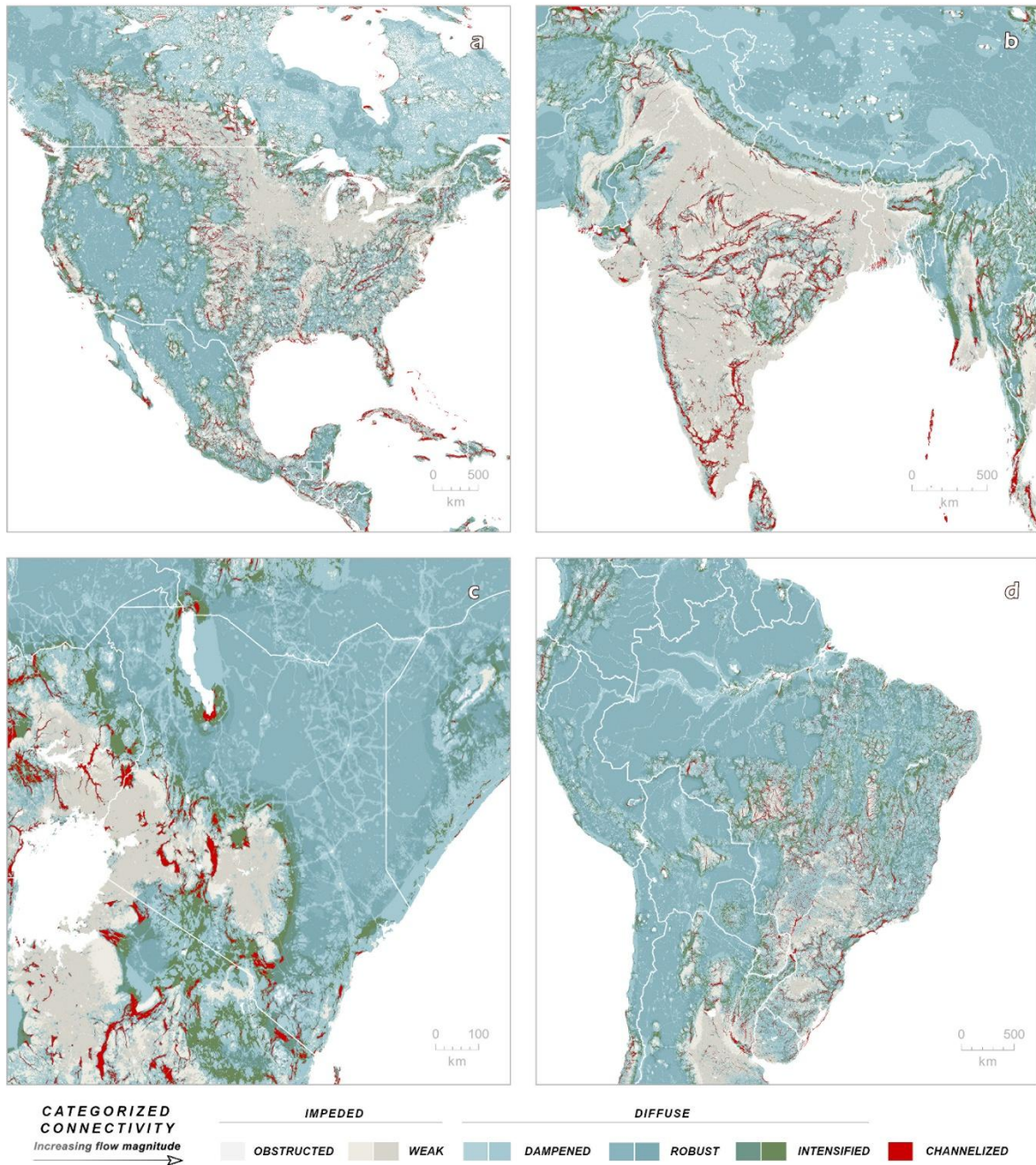


Fig. 2 | Categorized connectivity in four geographies. Global categorized connectivity data show areas where there are large amounts of moderate levels of land modification like the midwestern agricultural lands of the United States (a) and in populated areas such as in India (b). Movement potential is higher in areas constrained by land modifications, such as the North American southeast (a) and southeastern Kenya (c). Movement potential is at moderate levels where there are wide areas of natural lands with low levels of land modification, such as in the Amazon (d). The most common categories are rendered using high/low subclasses for increased ease of visualization.

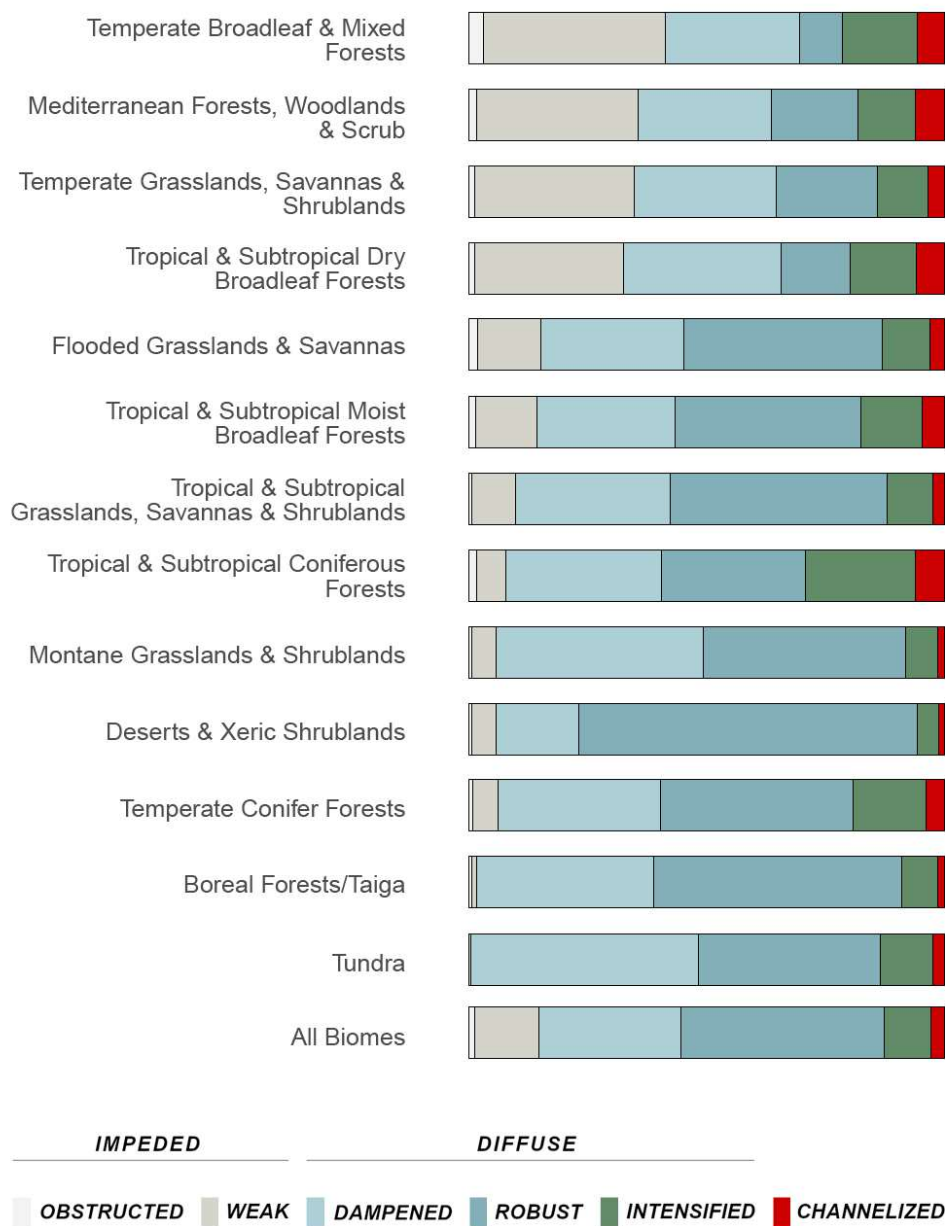


Fig. 3 | Connectivity categories across global biomes. Proportionate distribution of connectivity categories by biome³⁶, ordered by proportion of impeded movement areas. By area, temperate broadleaf & mixed forests and mediterranean forests, woodlands & scrub have low connectivity while boreal forests/taiga and tundra have the highest amounts of diffuse movement potential.

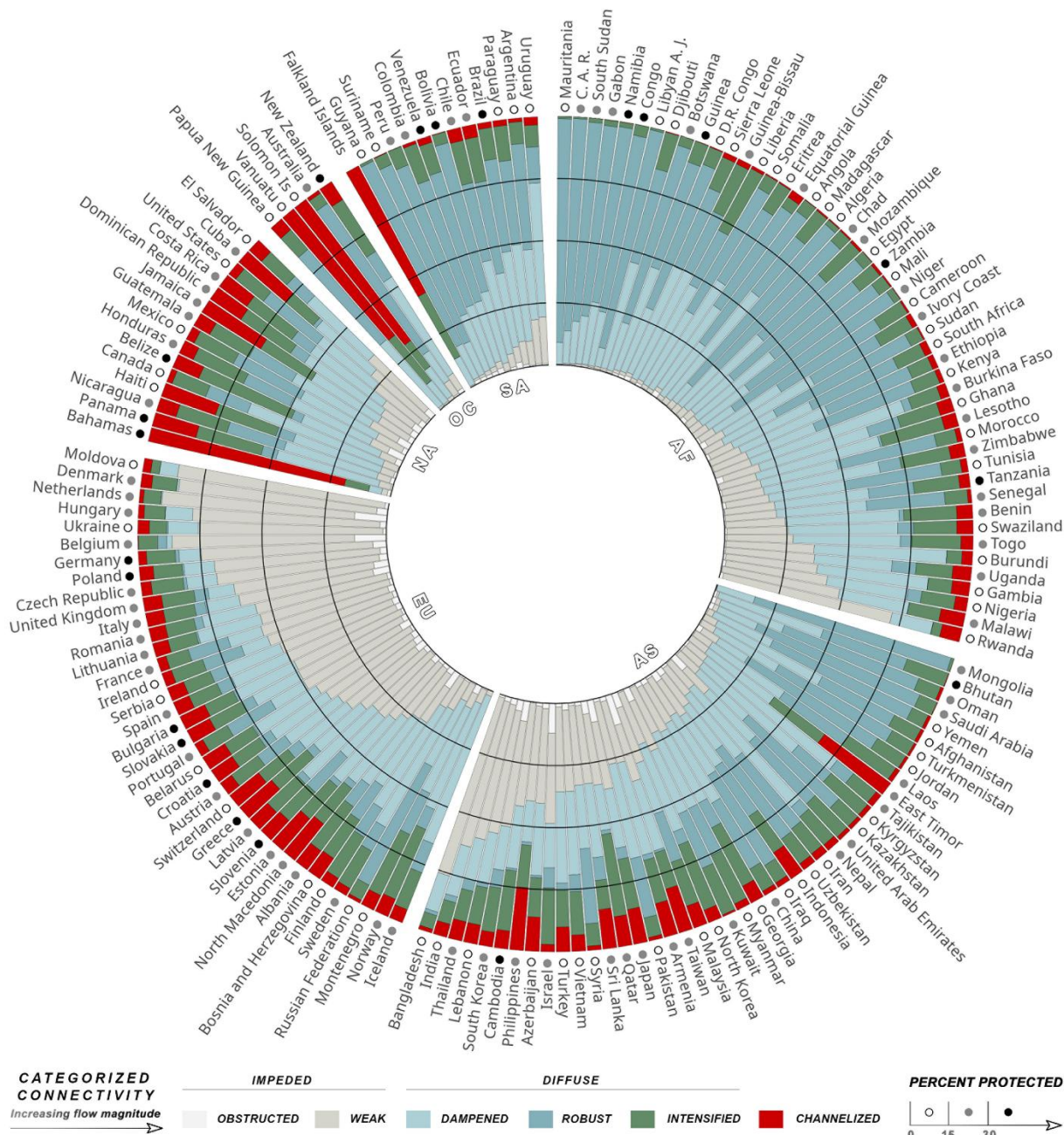


Fig. 4 | Connectivity categories across countries and level of protection. Diffuse movement areas dominate Africa while much of Europe has impeded movement potential. Within continents, countries are ordered from most to least impeded movement area, and black lines represent quantile breaks. Continents: AF – Africa; AS – Asia; EU – Europe; NA – North America; OC – Oceania; SA – South America.

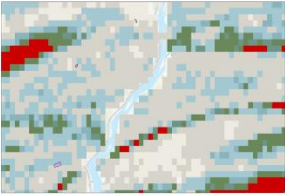
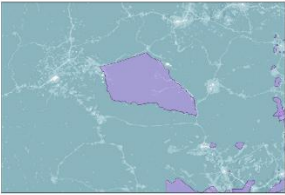
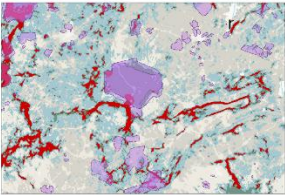
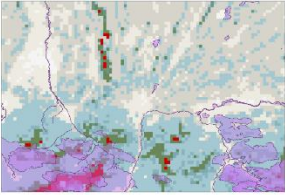
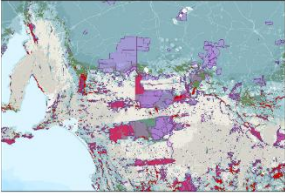
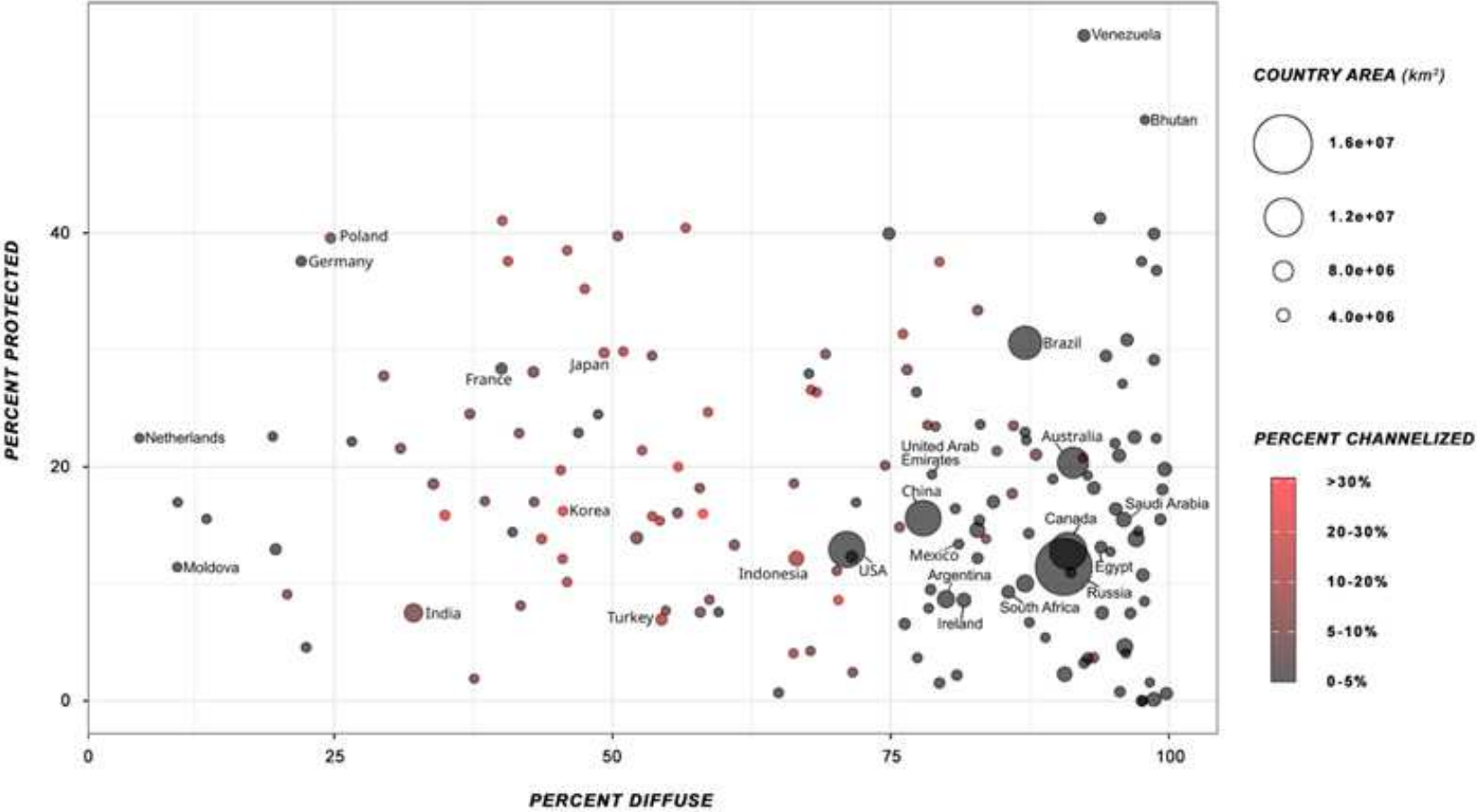
QUESTION	EXAMPLE LANDSCAPE	DESCRIPTION
TARGET 2: RESTORATION TO BENEFIT BIODIVERSITY AND IMPROVE CONNECTIVITY		
Where would restoration have potential to improve connectivity?		Weak flow "gaps" between channelized flow areas may indicate opportunities to enhance connectivity.
TARGET 3: EVALUATING THE CONNECTIVITY CONTEXT OF PROTECTED AREAS		
Which PAs are embedded in a "well-connected" landscape?	 	PA in a uniformly intact landscape context (robust flow). A PA with constraints to flow on one edge, but multiple potential movement pathways through varying resistances in other directions.
What is the pattern of connectivity between PAs?		An isolated PA, near several others with higher between-PA connectivity.
Are PAs capturing the range of important connectivity values?		The PAs here include several channelized flow areas, as well as dampened, robust, and intensified flow areas.
CATEGORIZED CONNECTIVITY Increasing flow magnitude IMPEDED OBSTRUCTED WEAK DIFFUSE DAMPENED ROBUST INTENSIFIED CHANNELIZED PROTECTED AREAS (PAs)		

Fig. 5 | Application of categorized connectivity data to the Global Biodiversity Framework. Contributions to Targets 2 and 3 of the Kunming-Montreal Global Biodiversity Framework can partially be informed using global categorized connectivity data as shown by these example landscapes. Diffuse areas represent high redundancies in movement pathways, channelized areas typify constrained movement potential, and impeded areas indicate low movement potential.

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929 **Fig. 6 | Level of diffuse and channelized movement areas and level of protection within countries.** Many large countries have
930 moderate levels of protection and higher levels of diffuse movement areas, where increased protection could be targeted (Brazil,
931 Australia, and China, for example). Small countries with high levels of channelization and moderate levels of protection may target
932 protection to preserve remaining corridors or restore areas.

Supplementary Files

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