



# Indigenous territories and protected areas are crucial for ecosystem connectivity in the Amazon basin

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Ecosystem connectivity—the uninterrupted flow of natural processes within and among ecosystems—is critical for maintaining healthy ecosystem functions. However, in the Amazon drainage basin, multiple anthropogenic activities are rapidly disrupting connectivity. To assess the severity of this problem, we analyzed the spatial distributions of six major anthropogenic activities: dam construction, deforestation, fire, mining, oil and gas exploitation, and roads. We examined their impacts across four key landscapes: Amazonian Andes, lowland nonflooded forests, wetlands, and rivers. Using a resistance-based connectivity model, we quantified connectivity across terrestrial, wetland, and river ecosystems and found a marked decline in connectivity across the basin. A central focus of our study was the role of Indigenous Territories and Protected Areas (ITPAs), which collectively cover over 50% of the basin. Our findings show that ITPAs sustain significantly high levels of ecosystem connectivity. Only 14 to 16% of ITPA land is impacted by anthropogenic activities, compared to 38% in unprotected areas. Terrestrial ecosystems in the southern and eastern Amazon are heavily impacted by deforestation, mining, and fires, with significantly higher connectivity inside ITPAs than in unprotected areas ( $P < 0.01$ ). Wetlands and riverine ecosystems also face severe fragmentation, particularly from dams and illegal mining—but maintain stronger connectivity within ITPAs (wetlands:  $P < 0.01$ ; rivers:  $P < 0.001$ ), with the few remaining free-flowing Andean rivers increasingly isolated from the lowland Amazon. Strengthening governance and sustainable initiatives in ITPAs, in partnership with local inhabitants, represents an expedient, efficient, and cost-effective strategy for conserving ecosystem connectivity in the Amazon basin.

Amazonian Andes | ecosystem function | ecosystem connectivity | traditional communities | wetlands

The Amazon River drainage basin (1, 2) (hereafter, the Amazon basin) is home to the most diverse continental biota, hosting about 10% of all described plant and animal species (3). From high-elevation *paramo* and *puna* ecozones, through mid-elevation cloud forests and torrential hillstream canyons, to lowland rainforests with meandering rivers, seasonally flooded wetlands, and open savannas, the Amazon basin constitutes a heterogeneous mosaic of landscapes (4). Connectivity—here defined as the degree to which natural processes can occur unimpeded within and among ecosystems (5, 6)—is a core feature of Amazonian ecosystem functions. Ecosystem connectivity regulates the energy and nutrient flows underlying soil and water chemistry (7, 8), as well as the evolutionary and ecological processes of species' dispersal, gene flow, and adaptation, which generate and maintain biodiversity (6).

The interconnectivity between the Tropical Andes and Lowland Amazonia affects essential hydrological and biological processes governing ecosystem dynamics from local to global scales (9–11). Lowland forests export water vapor that contributes to rainfall in the Andes mountains through so-called aerial rivers (12), while the Andes export sediment and nutrient-rich surface waters back to the lowlands (13), facilitating lateral and vertical exchange of water, nutrients, and organisms (9, 10, 14). Many Amazonian rivers originate in the Andes, contributing about half of the Amazon's total aquatic discharge, and transporting about a billion tons of sediments, organic matter, and nutrients annually to the Atlantic Ocean (10, 15). The ever-changing courses of Amazonian waterways across geographic space and geological time have complex effects on connectivity patterns across populations in multiple taxa, alternately connecting and severing portions of riverine and riparian ecosystems while forming and eroding dispersal barriers for nonflooded (*terra-firme*) ecosystems (3, 16).

The Tropical Andes and Lowland Amazonia also share a complex and intertwined evolutionary history spanning millions of years (3, 17, 18) through multiple natural and

## Significance

Maintaining ecosystem connectivity in the Amazon drainage basin (from the Andes to the lowland rainforests) is crucial for sustaining biodiversity and ecosystem function. Our study reveals that Indigenous Territories and Protected Areas (ITPAs) have significantly higher connectivity and lower human impact than nonprotected areas. The long-term conservation and connectivity of the Amazon basin depends on the strengthening of governance and sustainable initiatives in ITPAs, in close collaboration with local communities.

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seminatural (i.e., partially domesticated) riparian and forested corridors. Prominent among these connections are wetlands, which act as important nurseries for most lowland fishes (19–21), serve as food sources (22), and facilitate the trans-Amazonian dispersal of many terrestrial and aquatic specialized plants (23) and animals (24). Ecosystem connections between the Andean and lowland portions of the Amazon basin also provide the climatic gradients now recognized as one of the key elements for species resilience facing climate change (25, 26). However, combined anthropogenic impacts threaten ecosystem integrity (26–28) and connectivity across the Amazon basin. Recent major anthropogenic impacts—large-scale human activities that have fundamentally altered ecosystems in the last 50 y (16, 27, 29)—are increasingly fragmenting ecosystem connectivity across the Amazon. These impacts act synergistically and, for the first time in human history, are leading to a scenario of functional collapse of Amazonian water and nutrient cycling, climatic regulation, and biodiversity maintenance (26, 29–32). Therefore, it is important to identify the key terrestrial and aquatic areas for maintaining ecosystem function and services that rely on connectivity.

We compiled available spatial data from remote-sensing observations (*SI Appendix*, Fig. S1 and Table S1) (33) to map ecosystem connectivity across the Amazon basin and to quantify the impacts of six major anthropogenic activities known disrupt ecological connections: dams (2023), deforestation (2001 to 2020), fires (2016 to 2021), mining (2023), oil and gas exploitation (2023), and roads (2020). While previous studies have documented the detrimental effects of these activities on ecosystem degradation (28) and the role of Indigenous Territories (ITs) and Protected Areas (PAs) in mitigating such impacts (34, 35), their effects on ecosystem connectivity remain poorly understood. For instance, deforestation rates in ITs were between 85% (in 1985) and 92% (in 2000) lower than in adjacent non-Indigenous areas (36, 37). Similarly, PAs have shown a buffering effect (38), yet the extent to which they maintain ecosystem connectivity amid escalating anthropogenic pressures remains unclear.

To evaluate connectivity at the Amazon basin scale, we applied an approach based on resistance surfaces in raster format. In this framework, resistance values represent the degree of deviation from a pristine state, with higher values indicating stronger barriers to connectivity of ecological processes. In other words, a fully connected landscape has a resistance value of zero (no human impact). As human impact on the ecosystem increases, resistance values also rise, leading to reduced connectivity. Our goal is to identify key areas crucial for maintaining connectivity across the Amazon basin and pinpoint regions that are most disconnected. By comparing ecosystem connectivity inside and outside ITPAs, we assess the extent to which these areas effectively preserve connectivity compared to nonprotected regions. Integrating connectivity assessments into conservation planning can help address the complex, interconnected challenges facing the Amazon, ensuring the long-term resilience of its ecosystems and the well-being of the communities that rely on them.

## Results

We found considerable anthropogenic effects on four target landscapes: 23% of the extent of lowland forests, 24% of rivers, 25% of wetlands, and 28% of the Amazonian Andes are affected by at least one category of impact (Fig. 1). The percentages are lower in IT (14%) and PA (16%) than outside those areas (38%) across all landscapes. ITPAs have higher ecosystem connectivity than nonprotected areas for all three major ecosystems assessed: non-flooded terrestrial, wetland, and riverine ecosystem areas (Fig. 2).

Unprotected areas significantly exhibit the highest number of disruption across nonflooded terrestrial (Fig. 2*D*), wetland (Fig. 2*E*), and riverine (Fig. 2*F*) ecosystem areas, with fewer changes observed in ITPAs categories.

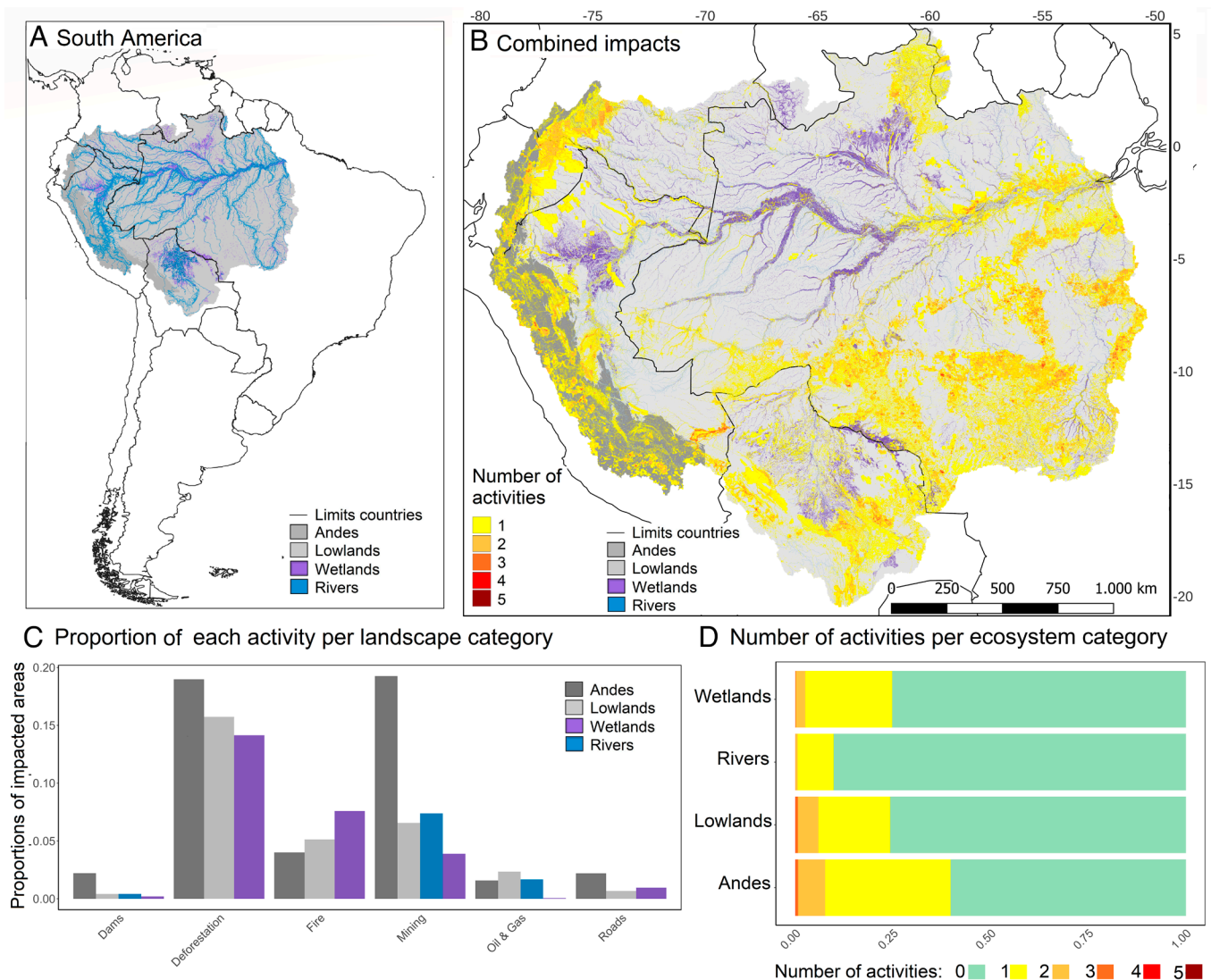
**Impacts on Terrestrial Ecosystems.** Nonflooded terrestrial environments located south of the Amazon River, on the Brazilian Shield, and in the eastern Amazon basin, are highly impacted by the activities analyzed (Fig. 1). Deforestation, followed by mining and fires, are the most prevalent impacts, with greater impacts outside ITPAs (*SI Appendix*, Fig. S2). Connectivity in terrestrial ecosystems is higher within ITPAs than in nonprotected areas [Negative Binomial generalized linear mixed model (GLMM), AIC = 4,274.1, log-likelihood = -2,129.1;  $P < 0.01$ ; Fig. 2*D*]. Connectivity between the Amazonian Andes and lowlands is generally low (Figs. 2*A* and 3*A*), mainly because of deforestation, mining, and oil and gas exploitation in the foothills of Colombia, Ecuador, and Peru (*SI Appendix*, Fig. S1).

**Impacts on Wetlands.** Connectivity within ITPAs is higher than in non-ITPA regions (Negative Binomial GLMM, AIC = 6,501.4, log-likelihood = -3,242.7,  $P < 0.01$ ; Fig. 2*E*). In addition to the direct impacts of water control and diversion structures, several major Amazonian wetlands have become disconnected from other regions of the Amazon due to dams, deforestation, and fires (Figs. 1*C* and 2*B*). Areas of higher connectivity (Fig. 2*B*, blue polygons) are widespread in the central Amazon basin, including floodplains along major rivers such as the Juruá and Negro. In contrast, areas with lower connectivity (Fig. 2*B*, red to yellow polygons) are more common in the southeastern Amazon, where anthropogenic disturbances such as deforestation and fire are more extensive. Although large wetland systems exist in western Amazonia (e.g., in Peru and Bolivia), their high internal variability may result in the presence of smaller patch sizes, reflecting natural ecological patterns rather than fragmentation. Therefore, the observed variation in connectivity should be interpreted with caution and in context—not all small or low-connectivity polygons indicate degradation.

**Impacts on Rivers.** Although connectivity in riverine ecosystems is higher within ITPAs than in nonprotected areas (Negative Binomial GLMM, AIC = 5,415.2, log-likelihood = -2,699.6,  $P < 0.001$ ; Fig. 2*E*), virtually all Andean rivers are severely impacted by dams and illegal in-stream mining that compromise connectivity between the headwaters and lowland sections of rivers (Fig. 3*B* and *C*). Of the major rivers that flow directly from the Andes, only five are free or almost free of dams: the Putumayo, Napo, Japurá, Madre de Dios, and Beni rivers (Fig. 3*B*). Yet, two of them—the Madre de Dios and Beni, which are tributaries of the Madeira—are disconnected from the lower Madeira and Amazon rivers by two large (>10 MW) dams on the Madeira River (Fig. 3*B*). Despite the presence of multiple dams near their headwaters, the Marañón and Ucayali rivers are still well-connected between the central Andes and the Amazon River (Fig. 3*B*). All major rivers flowing from the Andes to the lowland Amazon are severely impacted by illegal mining (Fig. 3*C*).

## Discussion

The Amazon basin, one of the most biologically diverse and ecologically critical regions on the planet (3, 4), is increasingly under threat from a suite of anthropogenic pressures that include deforestation, mining, dams construction, fires, oil and gas exploitation, and roads. Our study reveals that approximately



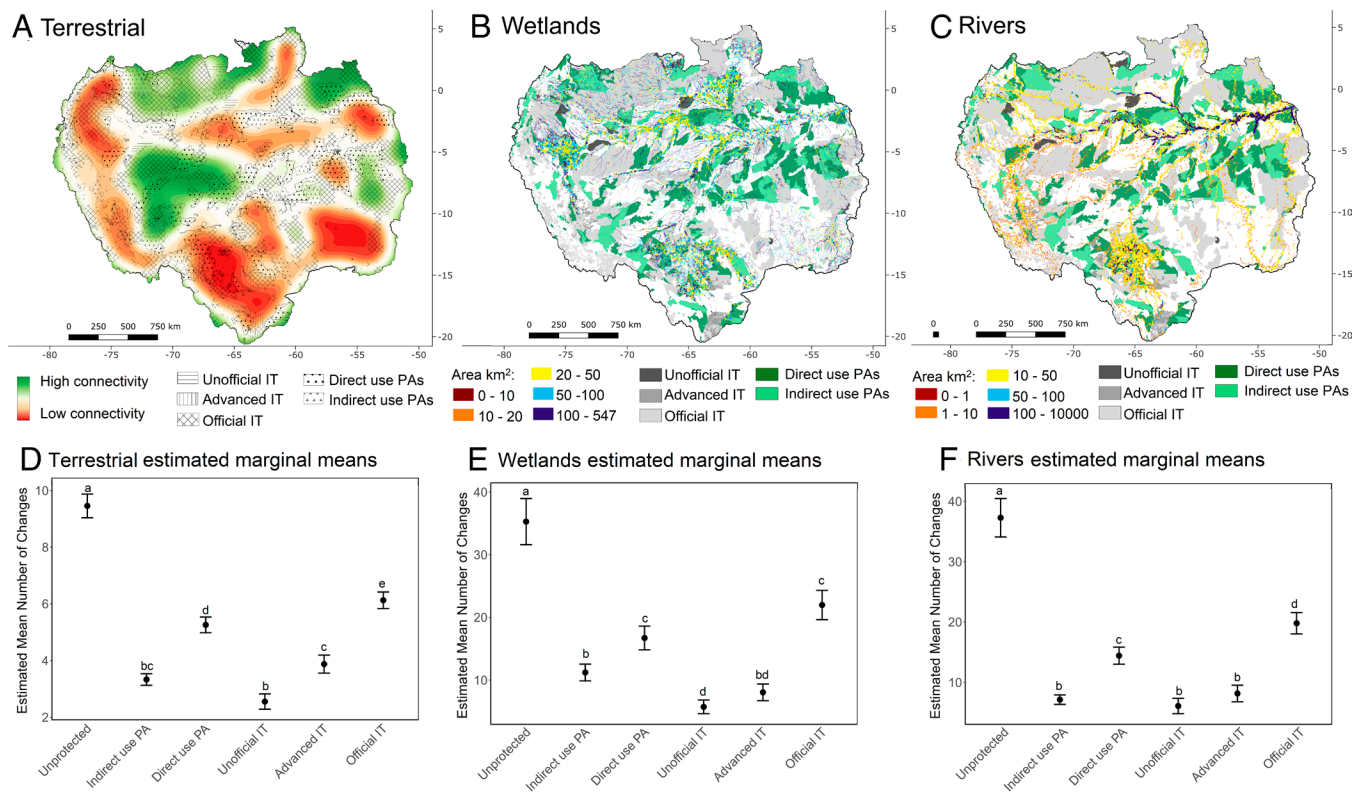
**Fig. 1.** Anthropogenic impacts in the Amazonian Andes (dark gray), wetlands (purple), rivers (blue), and lowland terrestrial ecosystems, including rainforests and savannahs (light gray). (A) The limits of the Amazon drainage basin. (B) Combined impact of human activities. Colors denote the numbers of anthropogenic activities impacting an area: yellow (one activity), orange (two activities), light red (three activities), red (four activities), dark red (five activities). (C) Proportion of area impacted by each of six anthropogenic activities in the Amazonian Andes (dark gray), lowland forests (light gray), wetlands (purple), and rivers (blue); (D) Proportion of combined impact across the Andes, wetlands, rivers, and lowlands: green (zero activities), yellow (one activity), orange (two activities), light red (three activities), red (four activities), dark red (five activities).

one-quarter of lowland forests, rivers, wetlands, and Amazonian Andes are affected by at least one impact category (Fig. 1). This degradation has led to significant declines in ecosystem connectivity, with potentially severe consequences for biodiversity, ecological function, and climate regulation. Notably, our findings indicate that connectivity within ITPAs remains higher compared to nonprotected areas, underscoring their critical role in maintaining ecological functions and the value of strategically increasing the network of ITPAs within the Amazon basin.

**Connectivity in Amazonian Ecosystems.** It is alarming that about 25% of the most diverse and extensive ecosystems on Earth have been affected by anthropogenic impacts (27) (Fig. 1), resulting in habitat destruction and a loss of ecosystem connectivity across the Amazon basin. Of particular concern is the rapid decline of connectivity between the Amazonian Andes and lowland terrestrial areas—which is happening due to deforestation, mining, and oil and gas exploitation in the foothills of Colombia, Ecuador, and Peru (Fig. 3A and *SI Appendix*, Fig. S1). We suggest that special

attention be given to transboundary areas that are relatively well-connected but which face increasing anthropogenic pressure due to weak state enforcement, judicial challenges, lack of collaborative efforts, threats related to drug trafficking and illegal logging, mining, and fishing (39). Effective cross-border cooperation and strengthened governance are essential to maintain connectivity in these regions (40, 41).

The impacts of human activities on connectivity vary across ecosystems and regions but are often interrelated. Fires have degraded seasonally flooded wetlands (42), particularly during drought years, while dams fragment riverine networks, disrupting the longitudinal flow of organisms, sediments, and nutrients (43). In many cases, these disturbances interact, creating compounding or cascading effects. For example, the construction of large hydro-power projects—such as Belo Monte Hydroelectric Power Plant on the Xingu River—has triggered widespread deforestation due to road expansion, settlement growth, and associated infrastructure development (44, 45). Similarly, dams alter flood regimes, increase fire susceptibility in wetland areas, and cause biodiversity



**Fig. 2.** Ecosystem connectivity in the Amazon basin. (A) Amazonian nonflooded areas (including tropical rainforests, white-sand ecosystems, and savannas) with kernel density connectivity map (see text); ITs and PAs are shown as polygons with different patterns. (B) Amazonian wetlands (permanently and seasonally flooded areas) showing regions of the connected areas at threshold = 0, where large connected areas are shown in blue, small connected areas are shown in red, and intermediate areas in yellow; ITs and PAs are shown as polygons with different colors. (C) Amazonian large rivers (Stream Orders 6 to 10) showing functionally connected areas, where large connected areas are shown in blue, small connected areas are in red, and intermediate areas in yellow; ITs and PAs are shown as polygons with different colors. Estimated marginal means for (D) nonflooded terrestrial, (E) wetland, and (F) riverine ecosystem areas, showing the number of changes in connectivity across different protection categories: unprotected, indirect use PAs, direct use PAs, unofficial ITs, advanced ITs, and official ITs, with significant differences showed by small caps letters.

loss (46–49). Understanding how these pressures overlap and reinforce one another is essential for developing integrated conservation responses tailored to the unique vulnerabilities of each ecosystem.

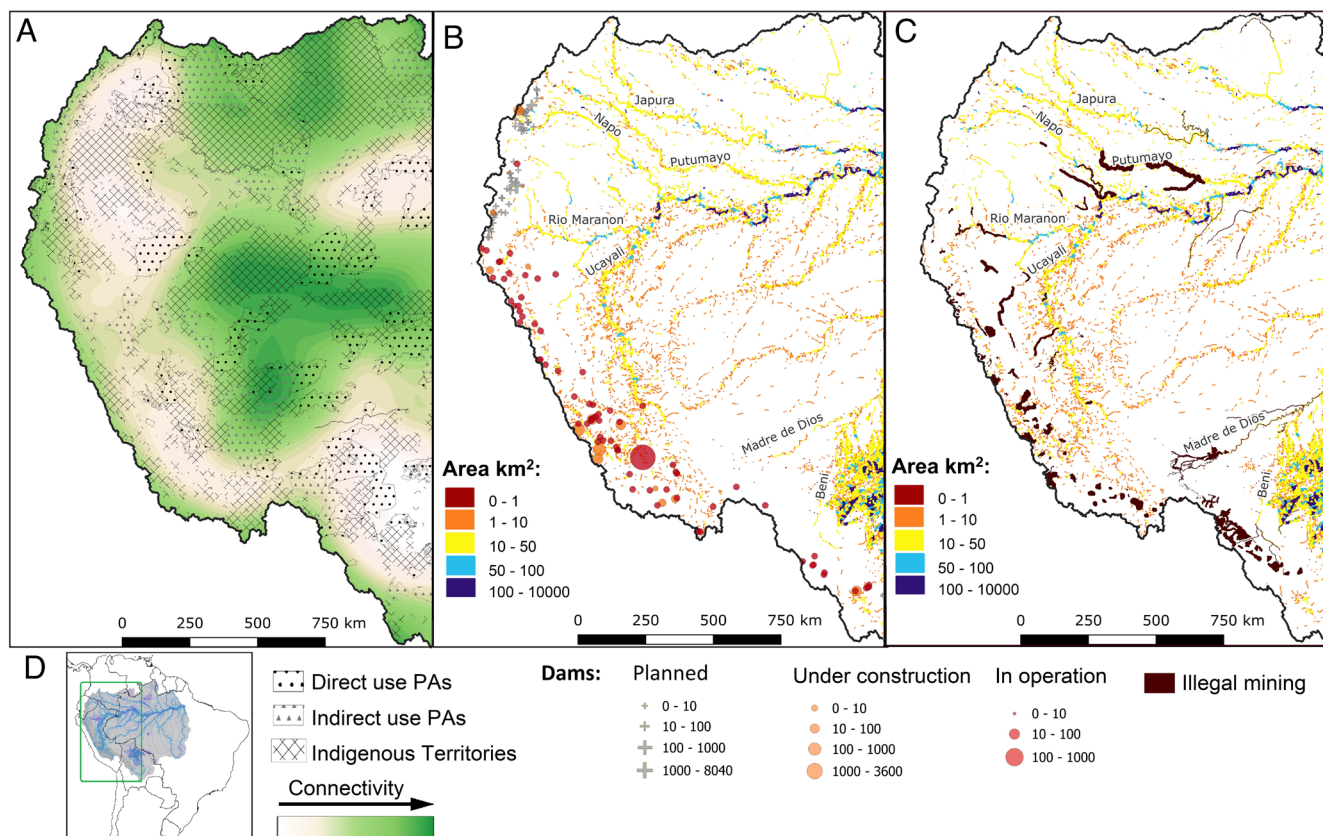
Seasonally flooded wetlands along Amazonian rivers are crucial for biodiversity, carbon storage, water purification, water cycling, and local livelihoods (50–52). Seasonal flooding of these wetlands is regulated by the complex dynamics of annual flood pulses (53) and unique chemical and physical water characteristics (54), that shape their ecological roles and recovery potential after disturbances. Wetland connectivity is crucial, both for biodiversity conservation and sustaining bioeconomic activities that support local livelihoods. Examples of the latter include the management of the giant *Arapaima gigas* fish (55) and the collection of Non-Timber Forest Products (56). Connectivity loss poses severe threats to the conservation of aquatic and terrestrial biodiversity and the ecological processes that underpin wetland health.

We observe similar patterns in aquatic riverine systems. Riverine connectivity at the interface of the Amazonian Andes and lowlands is being disrupted by the rapid proliferation of dams, water diversion structures, and in-stream mining activities (43, 57, 58). Although rivers show a lower proportion of areas directly affected by human disturbances in our analysis (*SI Appendix, Fig. S1A*), this likely underestimates the true impact of dams. Unlike localized land-based activities, dams exert far-reaching effects that extend upstream and downstream, disrupting hydrological and ecological processes across the entire riverscape (43, 59). Currently, at least 163 dams are operating in the Amazon, with 74 more under construction and 212 in

the planning stages (33, 59). Of the 96 long (>500 km) rivers in the Amazon basin, 73 were free of dams in 2019, but only 51 will remain free if existing dam projects are completed (59). For instance, the Madre de Dios and Beni rivers are disconnected from the lower Madeira and Amazon rivers by two large dams that interrupt the flow of sediments, nutrients, and aquatic organisms through the Madeira subbasin (43). Despite the presence of multiple dams near their headwaters, the Marañón and Ucayali rivers remain largely connected along their courses, serving as vital riverine corridors between the central Andes and the Amazon River (Fig. 3C). Similarly, while the Coca-Codo Sinclair dam affects much of the Napo basin (Coca River), its southern portion remains free of dams—though, like the others, it is heavily impacted by illegal mining activities (Fig. 3C).

Given the extensive water-control infrastructure projects fragmenting and disconnecting Amazonian rivers, maintaining and restoring aquatic connectivity is a significant challenge for the near future. It is crucial to avoid building new dams in the Amazon, and essential to implement methods to improve sediment transport, river connectivity, flow regulation, biodiversity maintenance, and reduce the greenhouse gas emissions of existing dams (60). We emphasize the importance of maintaining the free-flowing rivers that connect the Andes to the lowland Amazon—the Putumayo, Napo, Japurá, Madre de Dios, and Beni Rivers. Furthermore, more agile law enforcement and integrated transboundary governance are needed to halt the negative ecological impacts of in-stream mining (61).

Beyond structural connectivity, it is necessary to account for the ecological processes that depend on the natural and predictable



**Fig. 3.** Connectivity of the Andes and western Amazonian lowlands. (A) Areas of high terrestrial connectivity, highlighting the IT (crossing lines points) and PA (points and triangles). (B) Areas in km<sup>2</sup> highlighting dams (sized by their potency in megawatts – MW) and major rivers that connect Amazon Andes to lowland yet free of dams. (C) Areas in km<sup>2</sup> highlighting connected rivers, illegal mining (dark red) and major rivers that connect Amazon Andes to lowland yet free of dams. Beni and Madre de Dios rivers are dam-free but have planned dams, and both drain to the Madeira River currently disrupted by two large dams. Marañon and Ucayali rivers are impacted by dams and illegal mining in their headwaters but represent two remaining rivers with connections between Central Andes and Amazon River. Large portion of the Napo basin (Coca River) is affected by the Coca-Codo Sinclair dam, but the southern portion of the basin is dam-free, yet with much illegal mining. We propose that these seven rivers be classified as protected *connectivity sanctuaries*, with a complete moratorium on construction of dams and water-diversion structures. (D) South America map, highlighting area shown in other panels.

flood pulse, flow of water, nutrients, and organisms in the Amazon basin. For instance, seasonal shifts in water level drive resource availability across terrestrial and wetland ecosystems resulting in ecosystem-scale movements of terrestrial vertebrates (62). Between rivers and wetlands, the lateral connectivity—including the seasonal migration of fish into floodplain wetlands, seed dispersal by river currents, and the movement of terrestrial fauna during flood pulses—is central to the functioning of the Amazon basin (20, 22, 23, 63). Also, longitudinal connectivity supports fish migrations between lowland and Andean regions, which are vital for reproduction, feeding, and nutrient cycling (64, 65). These functions are tightly linked to the timing and predictability of the flood pulse, and their disruption can have cascading consequences for biodiversity, fisheries, and the cultural survival of Indigenous and traditional communities (23, 66, 67). Recognizing and safeguarding these dynamic ecological linkages is essential for maintaining the functional integrity and resilience of the Amazon basin.

**The Critical Role of ITPAs in Maintaining Amazonian Ecosystem Connectivity.** Previous studies have shown that forest loss is substantially lower in ITs (36, 37) and that secondary growth in previously deforested areas is higher within ITs (34, 68). Land-use management practices within existing ITPAs, although heterogeneous, have successfully reduced deforestation and forest degradation for decades, preserving biodiversity, decreasing forest carbon emissions, and mitigating global climate change in various parts of the basin (35, 68–71). Our main finding is that this

reduction in habitat loss is sufficient to make the connectivity of terrestrial, wetland, and riverine environments in the Amazon markedly greater in ITPAs than in areas without protection. This underscores an often-overlooked contribution of ITPAs: Beyond reducing deforestation, they play a central role in maintaining ecological connectivity across the Amazon basin, which is critical for preserving biodiversity, ecosystem functionality, and long-term resilience. In this context, ITPAs emerge as one of the most powerful tools for mitigating the impacts of climate change in the region. As land-use pressures intensify and projections indicate a transition toward drier and more fragmented landscapes, the Amazon edges closer to a tipping point (72, 73). Many species, finely adapted to the basin's warm and humid conditions, are highly vulnerable to such shifts, with their decline threatening to destabilize ecological processes (74, 75). Expanding and reinforcing the ITPA network is therefore essential—not only to facilitate species movements in response to changing environments but also to preserve the Amazon's critical role in regulating regional and global climate.

The contribution of ITPAs, however, goes beyond formal protection status—it is deeply rooted in the daily practices, traditional knowledge, and political resistance of Indigenous peoples and local communities (IPLCs), who act as frontline defenders of these territories (76–78). Their stewardship is essential not only for safeguarding land from deforestation and degradation but also for maintaining cultural landscapes that promote ecological connectivity. Traditional land-use practices—such as rotational

agriculture, controlled burning, fishing agreements, and sacred natural sites—play a key role in sustaining functional ecosystems. In many cases, it is the collective action of IPLCs that prevents illegal incursions and resists extractive pressures, often at great personal risk (79). Recognizing their leadership and agency is critical to understanding why ITPAs remain effective in preserving connectivity across the Amazon (80–82).

Changes in the enforcement of environmental laws and policies regarding land conversion have strongly affected ecosystem quality and connectivity throughout much of lowland Amazonia (83–85). In Brazil, the *Action Plan for the Prevention and Control of Deforestation in the Legal Amazon* was implemented in 2004 and was highly successful in reducing deforestation (86, 87), until it was interrupted in 2019 (but again reestablished in 2023). Laws approved in Brazil during the years of 2019 to 2022 allowed more economic activities within ITs and reduced governance within PAs (88). While these policies are now being reversed, reestablishing governance and mitigating impacts is an ongoing challenge in most areas (58, 89, 90).

Given these circumstances, the importance of ITPAs is evident. Governmental action, political views, and economic pressures are prone to produce major and sudden policy changes that significantly affect deforestation rates. For example, in May 2023, Brazil's lower house of Congress approved regulations that limit the recognition of new IT, which can now only be established if Indigenous people can prove they occupied the land prior to 1988 (the year when the current Brazilian constitution was ratified). Although the Brazilian Supreme Court has decided that such regulation was unconstitutional, the later Senate approval was an important setback to many Indigenous communities that were displaced from their territories in the 1970s and 1980s (91). The Brazilian Supreme Court has now created a conciliation commission with underrepresentation of Indigenous people to discuss these regulations. However, the Indigenous groups assert that the objectives and rules of these proceedings have not been clearly and transparently outlined, as a result, lands that should be recognized as ITs will be vulnerable to new large-scale anthropogenic impacts (92).

Restoring local governance and eliminating illegal activities in existing ITPAs, and the demarcation and implementation of new ones, are pivotal for enhancing connectivity between the Amazonian Andes and lowlands, and for preserving the remaining well-connected areas of the world's largest tropical forest. Other Effective Area-Based Conservation Measures (OECMs) could be a useful tool for protecting traditional territories (93), such as fishing agreements (94) and Term of Authorization for Sustainable Use also foster collaborative efforts between local communities and governing bodies for more effective conservation. OECMs can attract incentives and investments to support local communities in achieving their conservation goals. Furthermore, the official homologation of IT and the establishment of PAs of direct use that foster socioenvironmental benefits and strengthen the role of local communities in conservation efforts remain critical for ensuring the long-term sustainability of the Amazon (95).

The extent by which ITPAs maintain ecological connectivity varies across the Amazon basin, particularly in regions experiencing high levels of human disturbance (35), such as the Andes and the Deforestation Arc in the southern and eastern parts of the basin (Fig. 2). While our results reaffirm the critical role of ITPAs in preserving ecological connectivity, they also highlight the limitations of their effectiveness in highly degraded landscapes. It is also important to note that many Indigenous areas remain without official recognition, largely because of conflicts with economic

interests (96). This underscores the urgent need to formally acknowledge these areas and protect local Indigenous populations, their cultures, and territories.

To address these challenges, it will be imperative to strengthen governance mechanisms within ITPAs. This includes increasing monitoring and enforcement efforts in partnership with local communities (47), coupled with effective punitive measures against illegal invaders. Ensuring the protection of ITPAs requires a proactive approach to mitigating external pressures, which are often exacerbated by insufficient oversight, surveillance, and weak law enforcement (35, 97, 98). Additionally, the restoration of degraded lands surrounding ITPAs should be prioritized. Establishing buffer zones around ITPAs would not only enhance their protective capacity but also improve landscape-scale connectivity. Buffers could act as ecological shock absorbers, reducing the risk that external activities spill over into the boundaries of ITPAs. These zones can be designed to promote sustainable land use practices—such as community-based fishing agreements, agroforestry systems, and other inclusive models of natural resource management—that both support local livelihoods and reinforce conservation objectives.

This study demonstrates that ecosystem connectivity within ITPAs is higher than in nonprotected areas, but that significant threats are in place, highlighting the need to strengthen governance and restore local control to bolster ecosystem resilience. The severe disruption of riverine connectivity caused by dams and in-stream mining underscores the urgent necessity for policies that not only halt further large-scale infrastructure projects but also improve existing water management practices. Disparities in governance and policy enforcement within ITPAs point to the importance of consistent, coordinated efforts to curb illegal activities and promote sustainable land-use practices.

We show that the Amazon basin's connectivity is being rapidly compromised by synergistic anthropogenic pressures, especially in trans-Andean corridors. We document a significant loss of connectivity between the Andes and lowland Amazon, driven primarily by deforestation, illegal mining, and dam construction, particularly in Colombia, Ecuador, and Peru. This fragmentation jeopardizes fundamental ecological processes, including nutrient cycling, seasonal hydrology, fish migration, and species dispersal, all of which underpin the basin's biodiversity and ecosystem services. Importantly, we demonstrate that ITPAs harbor significantly higher connectivity than nonprotected areas across all major ecosystems. This highlights not only their role in reducing deforestation but also their overlooked role in maintaining functional connectivity at a basin-wide scale. Strengthening ITPA governance, formally recognizing unrecognized Indigenous lands, and halting the expansion of water-control infrastructure are key priorities for preserving the Amazon's ecological resilience. Protecting well-connected transboundary areas and designating key free-flowing rivers as connectivity sanctuaries are essential strategies for safeguarding the ecological integrity of the Amazon.

Collaborative actions among indigenous communities, governments, and local and international stakeholders are vital for the long-term conservation of this globally significant region. Future research should prioritize the development of adaptive management strategies that address the evolving environmental and sociopolitical challenges facing the Amazon, reinforcing ITPA governance and promoting sustainable activities. The strengthening and strategic expansion of the ITPA network will serve as a critical stronghold, buffering future political and environmental pressures and ensuring connectivity across the Amazon basin.

## Materials and Methods

We mapped ecosystem anthropogenic impacts in the Amazon drainage basin for four focal Amazonian landscapes: Amazonian Andes, lowlands, wetlands, and rivers. To delimit the study area, we used the wetlands map produced by the Large-Scale Biosphere-Atmosphere Experiment (1). We defined terrestrial lowlands as nonflooded areas <600 m of elevation, and Tropical Andes as ecosystems at ≥600 m elevation within the Amazon drainage basin (99). Terrestrial lowlands were bounded by nonflooded humid and dry forests and seasonally dry and burned savannas. Wetlands were defined as seasonally flooded forests, swamps, and estuaries (1). Large rivers [Strahler stream orders 6 to 10 (100)] were identified from HydroRivers (101). We plotted the ITPAs from RAISG (33) and classified them into the following categories: i) PAs of direct use, such as extractive reserves, which allow some economic activity and human occupation, ii) PAs of indirect use, such as national parks, which do not allow residencies, iii) "Official IT" which are IT with formal legal statuses (e.g., declared, demarcated, homologated), iv) "Unofficial IT" which are areas with indigenous presence but no formal land demarcation, and v) "Advanced IT" which are lands requested for protection but not yet officially recognized. When there was an overlap between PAs and Official ITs, we maintained the ITs terminology; when an Unofficial IT overlapped with a PA, we maintained the PA terminology.

To assess the integrity and functionality of Amazonian ecosystems, we evaluated ecosystem connectivity, which was defined as "the degree to which natural processes can occur unimpeded within and among ecosystems" (102). For connectivity analysis, we combine Andes and lowlands as we want to quantify the connectivity between them. As such, we ended up with three target ecosystems to assess connectivity: terrestrial areas, wetlands, and rivers. To evaluate connectivity, we generated a resistance raster—where lower resistance values indicate greater connectivity. The resistance raster was derived from the cumulative impact of anthropogenic activities (i.e., deforestation, fires, mining, oil and gas extraction, dams, and roads) combined with natural barriers such as large rivers in terrestrial landscapes. Each human activity was assigned an impact value based on empirical data from the Napo River basin, which included information on aquatic invertebrate community composition, habitat quality, and physicochemical parameters (103). These impact values were adjusted according to the focal ecosystem; for instance, dams were considered major barriers to river connectivity but had minimal impact on terrestrial connectivity (SI Appendix, Table S2).

Resistance values for each pixel were determined by summing the impact values of overlapping anthropogenic activities. For example, a pixel in a terrestrial ecosystem affected by both fire (impact value = 7) and roads (impact value = 6) received a cumulative resistance value of 13 (SI Appendix, Fig. S3). Higher resistance values indicate greater barriers to ecological connectivity. In addition to anthropogenic impacts, we also incorporated natural barriers into the resistance layers to account for inherent limitations to species movement that occur independently of human disturbance. Large rivers, for instance, naturally disrupt terrestrial connectivity limiting species dispersal (104). While human activities tend to increase resistance by fragmenting habitats and disrupting ecological continuity, natural features represent baseline constraints that define the underlying structure of landscape connectivity. Including both anthropogenic and natural sources of resistance allows for a more accurate assessment of how human activities further alter ecosystem functionality. Wetlands, characterized by frequent flooding, illustrate this dual-context approach: They were considered high-resistance areas in terrestrial environments but low-resistance areas in riverine settings (SI Appendix, Table S2).

The resistance raster obtained for each focal ecosystem was used to delineate polygons of functionally connected areas, where resistance values fell below a predefined threshold. Within each polygon, connectivity in an ecosystem is assumed to depend primarily on geographical distance, meaning that larger polygons represent areas with higher connectivity. Larger polygons arise when more pixels with low resistance values are spatially aggregated. We used the "grainscape" package v.0.4.4 (105) in R v.4.2.2 (106) to extract lattice-based connectivity units following Galpern et al. (105). First, we ran a lattice-based analysis to extract a minimum planar graph that represents the connectivity relationships for a lattice of focal points superimposed on the resistance raster. For terrestrial lowlands, we used focal points that were uniformly spaced at 56 km intervals. For rivers and wetlands, we extracted 20,000 random pixels from within the focal

environment. The grainscape package also enabled a scalar analysis to evaluate the relationship between connectivity (measured as the number of polygons) and resistance thresholds across the ecosystem. Resistance thresholds (x-axis) were varied to progressively relax the connectivity criteria, and the number of polygons (y-axis) was tracked as a response. Notably, sudden changes in the slope of the response curve may signify structural changes in the ecosystem patches. These changes could be ecologically meaningful, reflecting potential disruptions in ecosystem connectivity or shifts in landscape structure. For terrestrial and riverine ecosystems, the point of maximum curvature (as calculated using the second derivative method) of the response curve from the scalar analyses was selected as the reference threshold (225 for terrestrial and 35 for rivers; see SI Appendix "\_3SPANew2024\_GrainsOfConnectivity\_Grainscape.R"). In the case of wetlands, a conservative threshold of zero was used instead, because the curve jumped from zero to a horizontally stabilized line in a single step, making the second derivative method inapplicable. To map connectivity in the terrestrial environment, the centroids of the polygons were used to generate a kernel density map (Fig. 2A). High centroid density means a high resistance (low connectivity) and vice versa. For wetlands and rivers, we plot the polygons with a color gradient by their areas (Fig. 2B and C).

Since our primary focus was not on assessing connectivity at multiple scales, we applied a single scale (grain of connectivity) to the entire Amazon basin. To test the robustness of our findings, we conducted a sensitivity analysis to assess the effects of varying resistance raster coefficients on connectivity results. A total of 100 replicates for each environment were run with the original coefficients randomly varied by ± 10%, ± 20%, ± 30%, and ± 50% to determine their effects on the maximum curvature values (SI "\_4SPANew2024\_SENSITIVITY\_ANALYSIS.R"), and the connectivity analysis was repeated for each run. The results showed minimal differences in maximum curvature values and derived metrics across scenarios (SI Appendix, Fig. S4 and Table S3), indicating that while absolute values may influence fine-scale spatial patterns, the overall conclusions on landscape connectivity are consistent.

To assess the importance of ITPAs to maintain ecosystem connectivity, for each focal environment, we counted the number of connectivity polygons within unprotected areas, and within all five ITPAs categories. To account for differences in area, we used a regular grid composed of equally sized cells, each with an area equivalent to approximately 200 km<sup>2</sup>. Better protected categories were expected to have fewer different polygons inside them, which reflects higher connectivity within these areas. To test this assumption, a GLMM was fitted with the number of polygons as the response variable, the ITPA category as the explanatory variable, a negative binomial error distribution, and a logarithmic link function to account for the numerical nature of the response variable (counts). "Unprotected" was used as a reference category. The unique identifiers of each 200 km grid cell were included as random effects to account for spatial heterogeneity. The analysis was implemented using the "glmer.nb" function from the "lme4" v.1.2 package (107) in R. The estimated marginal means (also known as least-squares means) of the number of polygons were calculated and plotted. This statistical technique describes the average predicted response of a dependent variable across different levels of a factor, while controlling for other variables in the model. Post hoc comparisons among levels of the predictor variables were performed using the "contrast" and "regrid" functions of the "emmeans" v.1. package (108) and were represented with letters on the plot to indicate significant differences among the levels of ITPA categories. We calculated the pseudo-R-squared value with the trigamma function as recommended by Nakagawa et al. (109), employing the "r.squaredGLMM" function from the "MuMIn" v.1.18 package (110)(111). Additional R packages used for data curation were terra v.1.8.5 (112), tidyverse v.1.3.1 (113), ggplot2 v.3.5.1 (114) was used for data visualization. Maps were produced with QGIS software (115). All spatial data and R scripts used for this paper are available online at figshare.com (10.6084/m9.figshare.28089815).

**Data, Materials, and Software Availability.** Previously published data were used for this work (<https://www.raisg.org/pt-br/mapas/>) (33).

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