Title: Functional Connectivity of the World's Protected Areas

One-Sentence Summary: Functional connectivity model reveals opportunities for global conservation and a national tool for monitoring connectivity.

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Abstract: Global policies call for connecting protected areas (PAs) to conserve the flow of animals and genes across changing landscapes, yet whether global PA networks currently support animal movement, and where connectivity conservation is most critical, remains largely unknown. Here, we map the functional connectivity of the world's terrestrial PAs and quantify national PA-connectivity through the lens of moving mammals. We find that mitigating the human footprint may improve connectivity more than adding new PAs, although both strategies together maximize benefits. The most globally important areas of concentrated mammal movement remain unprotected, with 71% of these overlapping with global biodiversity priority areas, and 6% occurring on land with moderate-to-high human modification. Conservation and restoration of critical connectivity areas could safeguard PA-connectivity while supporting other global conservation priorities.

Main Text: Our current global system of protected areas (PAs) has been insufficient at slowing biodiversity loss (*1*, *2*). PAs are constrained in size, ecological representation and governance (*3*), and 90% or more exist within a matrix of human-dominated, increasingly fragmented land (*4*) that is changing rapidly (*5*, *6*), endangering animal movement (*7*, *8*) and survival (*9*). As a result, PAs and the animal populations they contain can become isolated, interrupting the flow of vital ecological and evolutionary processes that maintain populations, ecosystems and adaptive capacity (*9–11*). For these reasons, the Aichi Target 11 of the Convention on Biological Diversity's 2020 Strategic Plan for Biodiversity stipulated ensuring connectivity among PAs (*12*) while expanding the global network to 17% of terrestrial areas. While these targets remained unmet by the end of 2020, discussions informing the post-2020 global biodiversity framework continue to champion the importance of connectivity, both as a stand-alone target and a component of other relevant targets (*13*, *14*). To date, only a few evaluations of the connectedness of the world's PAs exist (*4*, *15*, *16*) and none explicitly map the functional connectivity of PAs.

Here, we modelled the functional connectivity of terrestrial PAs for medium to large mammals worldwide (excluding Antarctica) to quantify the connectedness of each PA and map the world's most critical areas for connectivity conservation. To begin, we generated a global resistance-to-movement surface using a model relating the average response of mammal movement (624 individuals of 48 mammalian species) to the human footprint index (HFI; an index that combines the effects of infrastructure, land use and human access across the planet) (*7*, *17*). We then applied circuit theory, which relates animal movement across a heterogenous landscape to the flow of electrical current across a circuit of resistors (*18*, *19*), to estimate functional connectivity in two distinct ways (fig. S1). First, we quantified 'effective resistance' -

a metric previously shown to predict gene flow (*19*, *20*) - for each PA to obtain a global index of PA isolation (Fig. 1). Effective resistance is a measure of the total resistance of all pathways between nodes in a circuit, and reflects the degree to which each node (in our case, each PA) is isolated from all others. Second, we mapped the flow of electrical current, reflecting mammal movement probability, across all possible land-based travel routes between all PAs larger than ~35 km^2 (Fig. 2 and fig. S6). By using a model of observed mammal movements to create our resistance surface, validating our results against independent GPS data from 407 individuals representing 11 species of mammals (fig. S9; tables S3 and S4), and confirming consistent connectivity patterns across dietary guilds, body sizes larger than 2.4 kg and a model including small PAs (< 35 km^2) (figs. S10-S12), our analysis permits a thorough assessment of the global functional connectivity of PAs for terrestrial mammals with high movement capacity.

As expected, the least isolated PAs occur within the world's two most intact biomes – boreal forest and tundra (Fig. 1 and fig. S3). Nonetheless, we found important contrasts between PA isolation and previously developed global connectivity indicators designed to assess different components of connectivity (fig. S5). For example, countries assigned a connectivity value of zero by the ConnIntact indicator (*4*) (a structural connectivity metric not related to animal movement) received a variety of functional connectivity scores using our PA isolation index (Fig. 3). Additionally, although PA isolation was moderately correlated with the existing global connectivity indicators (Pearson's r ranged from 0.32 – 0.56; Fig. 3), they identified a different set of countries as being the most connected (table S2). For example, PA isolation identified Canada, which has the second-largest area of wilderness after Russia, as the 3rd most connected country, while the other three indicators identified Canada as only the 15th, 53rd or 109th most connected country. Our results suggest that the PA isolation index provides a new view of connectivity, from the lens of mammals moving through natural and anthropogenic lands, that complements how connectivity is evaluated by other existing global indicators.

Because restoration (*21*) and PA expansion (*22*) are important complementary strategies for biodiversity conservation, we evaluated potential benefits to PA isolation from decreasing a country's human footprint (e.g., via restoring degraded habitats (*23*)) and increasing a country's PA coverage, using a linear mixed effects model with continent as a random intercept. We found that reducing a country's aggregate human footprint would have twice the effect on reducing national PA isolation compared to increasing a country's PA estate (fig. S4). Although the cost and ease of implementation of these strategies is expected to vary substantially among different land-use and sociopolitical contexts, we found that on average a 50% reduction in the human footprint would decrease national PA isolation by 28% (95% CI: 21-42%), whereas a 50% increase in PA coverage would decrease national PA isolation by only 12% (95% CI: 6-19%). Utilizing both strategies in combination, however, has the greatest benefit, decreasing PA isolation by 43% (95% CI = 30-76%). These results suggest that habitat restoration and favorable land management practices that improve the permeability of anthropogenic landscapes to animal movement (*21*, *23*, *24*), could add to formal protection efforts to improve connectivity. Such combined strategies can also provide significant benefits to humans (*23–25*), thus advancing the post-2020 global biodiversity framework vision of "living in harmony with nature" (*14*).

Areas where the flow of animal movement is concentrated are places with the potential to disproportionately reduce connectivity if further restricted or destroyed (*19*); therefore, we identified these concentrated flows (hereafter referred to as critical connectivity areas) using the upper 90th percentile values of our mapped mammal movement probabilities (Fig. 2). We found that two-thirds of critical connectivity areas are currently unprotected and 6% occur on unprotected moderate-to-highly-modified land (Fig. 4A; based on an underlying HFI threshold, HFI $\geq$ 4, used by others (4, 6, 28)). Further, roughly 23% of critical connectivity areas are both unprotected and occur on land suitable for future agricultural expansion (*27*) (Fig. 4B). Critical connectivity areas occurring on modified lands, or soon-to-be-modified lands, represent high priorities for conservation: small but vital pinch points that if conserved or managed to limit further modification (e.g., through conservation easements, payments for ecosystem services, community-based conservation or working lands conservation (*24*)) could achieve major gains in safeguarding connectivity through anthropogenic landscapes.

We found that 50 of the 846 global ecoregions recently identified with the greatest potential to protect biodiversity (*22*) also contribute disproportionately to connectivity; unprotected portions of these priority ecoregions have on average twice the predicted probability of mammal movement and contain more than half of the world's unprotected critical connectivity areas (fig. S7). We also examined the proportion of critical connectivity areas that overlap with the Global Safety Net – a proposed global conservation scheme that identifies new priority areas for expanded protection (*22*). We found that roughly 71% of unprotected critical connectivity areas, including a majority of those suitable for future agricultural expansion (*27*), overlap with these Global Safety Net priority areas (Fig. 4B and fig. S8). Further, > 60% of the critical connectivity areas overlap with unprotected portions of other global conservation prioritization schemes (Fig. S8). Areas of overlap with global conservation priorities represent key places where potential conservation synergies could maintain globally-significant areas for connectivity, while also preserving other important biodiversity elements.

Our study illustrates the critical value of natural and permeable anthropogenic lands to the flow of mammal movement between PAs. However, we do not explicitly examine unprotected natural lands as potential sources and destinations of movement. Therefore, our global connectivity map will be most useful for understanding the intensity of connectivity patterns among formal PA networks, relative to other connectivity areas around the world, and should be paired with locally-derived connectivity studies to effectively evaluate where to prioritize local connectivity conservation. Including unprotected natural land (e.g., other effective area-based conservation measures) as additional nodes in future studies would help to characterize the connectedness of PAs to the broader network of natural areas. Future studies should also examine climate change effects on connectivity, as animal movement and connectivity needs are likely to be affected either directly or indirectly by changing climates. We also acknowledge that because our connectivity model is informed only by mammal movements, it may not capture connectivity for other taxa or for other species of mammals not deterred by human impacts.

Despite its exclusive use of mammal movement data, our model revealed substantial overlap of critical connectivity areas with global conservation priorities that aim to protect a variety of taxonomic groups. However, the vast majority of these critical connectivity areas are currently unprotected and face future habitat conversion (Fig. 4). Since formal protections in these areas could be contested over livelihoods or food supply needs, alternative working-lands conservation strategies (e.g., silvo-pastoral, agroforestry and other agroecological management practices) will also be needed to maintain connectivity. Such strategies, which also provide significant benefits to humans (e.g., pollination services and pest control) (*24*), could represent an important other effective area-based conservation measure (OECM), contributing to global conservation policy targets.

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Supplementary Materials:

Materials and Methods

Figs. S1 to S16

Table S1 to S4

References (30–65)

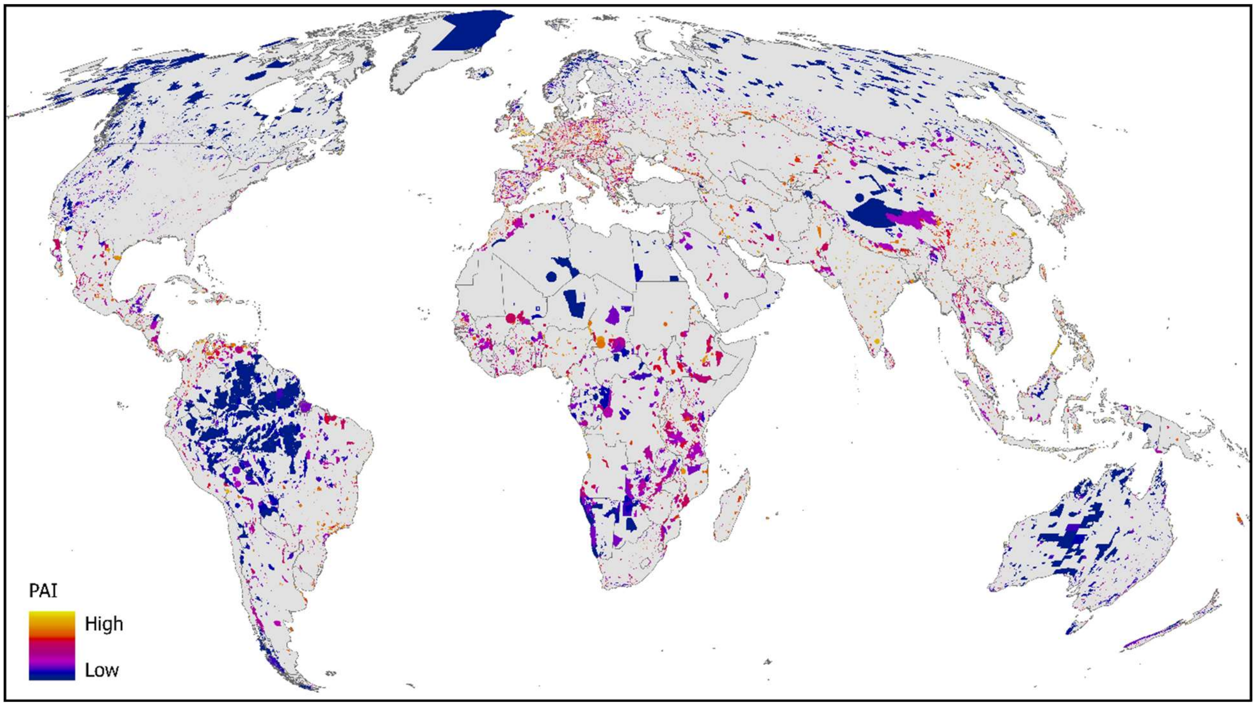

Fig. 1. Protected area isolation (PAI). Isolation of the world's terrestrial PAs, as measured by effective resistance to mammal movement.

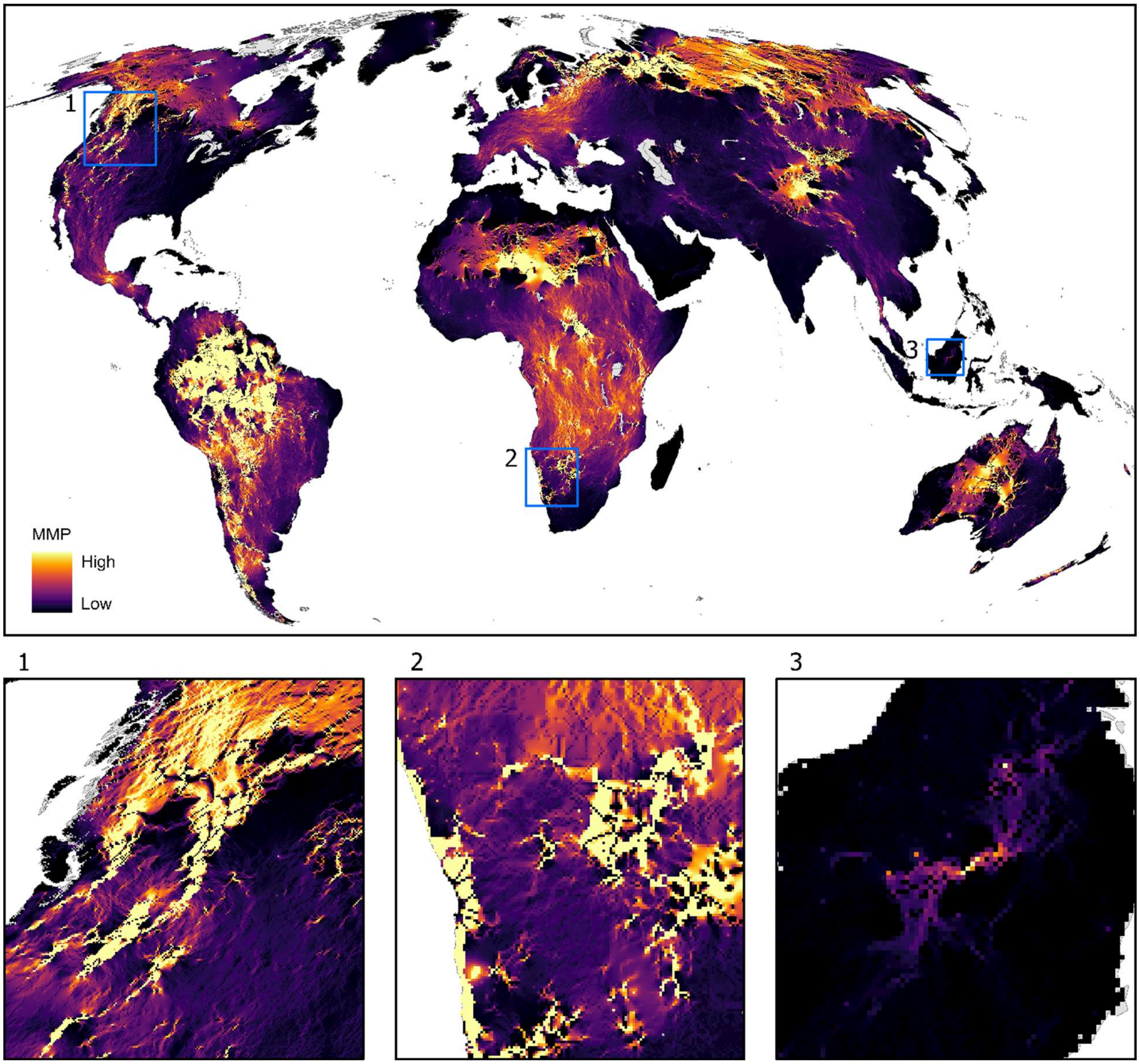

Fig. 2. Global mammal movement probability (MMP) between terrestrial PAs. High MMP depicts concentrated movements, typically within corridors that funnel movement between less permeable land or within large blocks of intact land nestled within a network of large PAs (e.g., Amazon Basin). Areas in orange and purple reflect areas where MMP is dispersed across many pathways. Both concentrated and dispersed flow are important to connectivity, but with many pathways, dispersed areas have a lower risk of total loss of connectivity. Black regions, which are not devoid of connectivity (fig. S15), depict areas of lower flow relative to the global scale.

Boxes highlight several landscapes. Box A: corridors through mountains of western North America (e.g., Yellowstone to Yukon corridor). Box B: corridors and dispersed flow across sub-Saharan Africa's Kavango-Zambezi Transfrontier Conservation Area and coastal deserts of Namibia. Box C: flows through rainforests of Indonesia and Malaysia (e.g., Heart of Borneo conservation area).

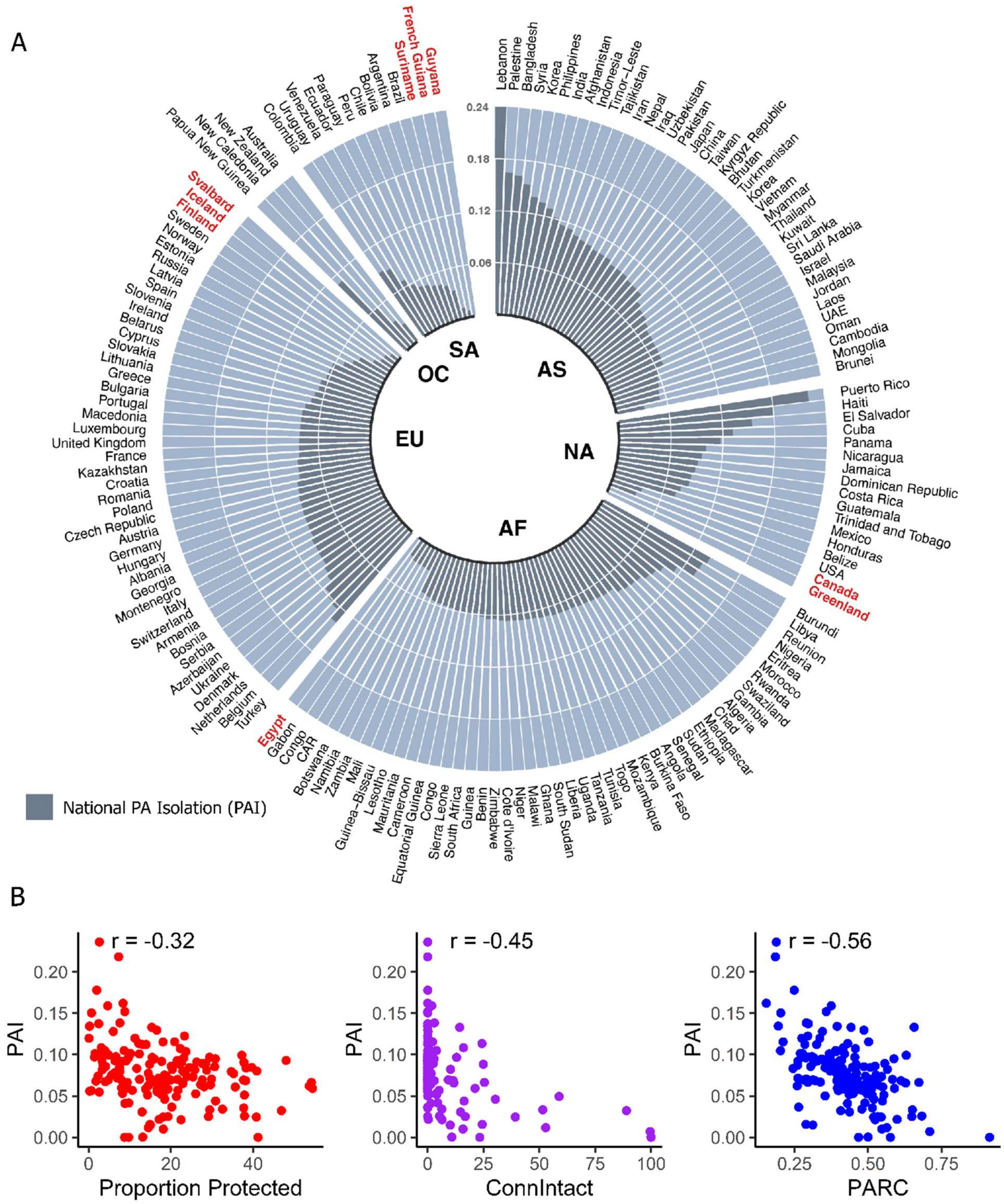

Fig. 3. National PA isolation (PAI). (A) PAI aggregated to the national level. Bars are organized by continent. Red-labeled countries have the most connected national PA networks (95th percentile). (B) Comparisons of national PAI to three existing global indicators of

connectivity. ConnIntact (*4*) is a recently updated version of the protected-connected index (*15*); PARC is the PA connectedness index (*29*). Correlations were measured using Pearson's *r* (an *r* equal to -1 would reflect perfect correlation).

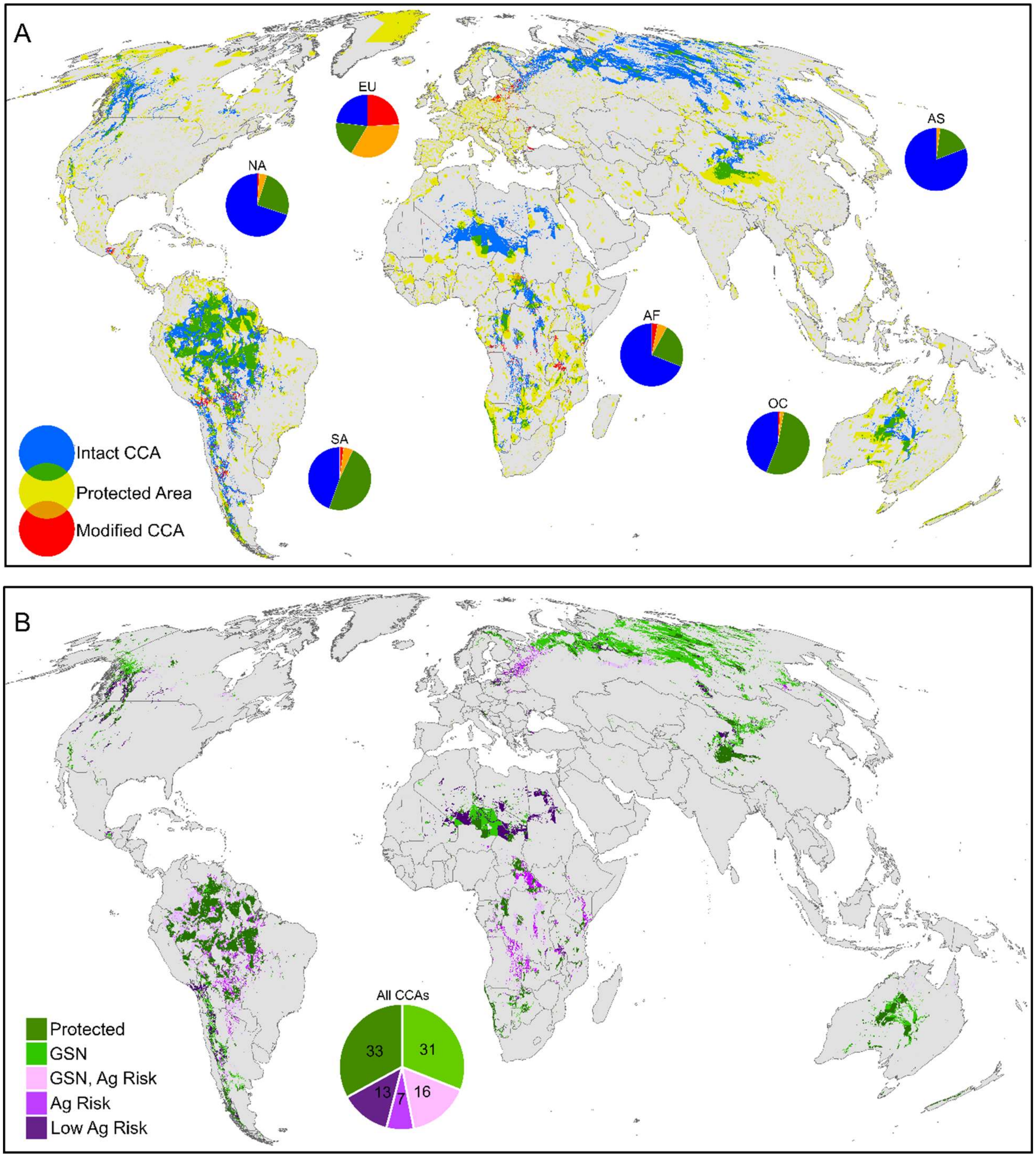

Fig. 4. Mapping critical connectivity areas globally (CCAs). (A) Depicts the current protection status of intact CCAs and modified CCAs. Pie charts indicate the proportion of each CCA type in each continent (B) Depicts the potential future protection and threat status of CCAs. Potential future protection occurs where currently unprotected CCAs overlap with areas

prioritized for expanded conservation under the Global Safety Net (GSN). Future threats were examined where CCAs fall outside the GSN (i.e., remain unprotected) and overlap with areas predicted to be suitable for future agricultural (Ag) expansion (*27*).