Title: Functional Connectivity of the World's Protected Areas

Authors: A. Brennan*[1,2,3], R. Naidoo[2,3], L. Greenstreet[2], Z. Mehrabi[2,4], N. Ramankutty[2,4] and C. Kremen[1,2,5]

Affiliations:

[1]Biodiversity Research Centre, University of British Columbia; Vancouver, Canada.

[2]Institute for Resources, Environment and Sustainability, University of British Columbia; Vancouver, Canada.

[3]World Wildlife Fund; Washington, DC, USA.

[4]School of Public Policy and Global Affairs, University of British Columbia; Vancouver, Canada.

[5]Department of Zoology, University of British Columbia; Vancouver, Canada.

*Corresponding author. Email: angela.brennan@ubc.ca

Abstract

Rapid environmental change threatens to isolate the world's wildlife populations and intensify biodiversity loss. Global policies have called for expanding and connecting the world's protected areas (PAs) to curtail the crisis, yet how well PA networks currently support wildlife movement, and where connectivity conservation or restoration is most critical, have never been mapped globally. Here, we map the functional connectivity (how animals move through landscapes) of the world's terrestrial PAs for the first time. Also, going beyond existing global connectivity indices, we quantify national PA-connectedness using an approach that

meaningfully represents animal movement through anthropogenic landscapes. We find that reducing the human footprint may improve national PA-connectivity more than adding new PAs; however, both strategies are critical for improving and preserving connectivity in places where the predicted flow of animal movement is highly concentrated. We show that the majority of critical connectivity areas (CCAs) (defined as globally important areas of concentrated animal movements) remain unprotected. Of these, 72% overlap with previously-identified global conservation priority areas, while 3% of CCAs occur within moderate to heavily modified lands. Conservation and restoration of CCAs could safeguard connectivity of the world's PAs, and dovetail with previously identified global conservation priorities.

Keywords: connectivity, biodiversity conservation, human footprint, protected areas, prioritization, mammal movement, post-2020 Global Biodiversity Framework, connectivity indicator, circuit theory

Our current global system of protected areas (PAs) has been unable to slow biodiversity loss[1,2] or provide adequate coverage for many threatened species and ecosystems[1,3–7]. PAs are constrained in size, ecological representation and governance[8], and 90% or more exist within a matrix of human-dominated, fragmented land[9] that is rapidly eroding[10,11], endangering animal movement[12,13] and survival[14]. As a result, PAs and the animal populations they contain can become isolated, interrupting the flow of vital ecological (e.g., migration, dispersal) and evolutionary (e.g., gene flow) processes that maintain populations, ecosystems and adaptive capacity[14–17]. For these reasons, the Aichi Target 11 of the Convention on Biological Diversity's 2020 Strategic Plan for Biodiversity stipulated expanding the global PA network not only to cover 17% of terrestrial areas but also to ensure connectivity among PAs[18], to facilitate the flow of individuals, genes and processes[19]. While these targets remained unmet by the end of 2020, post-2020 global biodiversity framework discussions continue to champion the importance of connectivity, both as a stand-alone target and integrated into other relevant targets[20,21]. To date, only a few evaluations of the connectedness of the world's PAs exist[9,22,23] and none explicitly map the functional connectivity of PAs. This research gap prevents the identification of globally important areas for wildlife connectivity and the spatially explicit assessment of potential threats to connectivity.

Here, we modelled the functional connectivity of terrestrial PAs (excluding Antarctica) to quantify the connectedness of each PA and map the world's most critical areas for connectivity conservation. Our analysis focuses on the following questions relevant to global conservation practice and policy: (1) Where are the most and least functionally connected PAs in the world located? (2) How does the functional connectivity of national PA-networks compare to previous estimates of national connectivity, and what mechanisms exist for national governments to improve the functional connectivity of their PA-networks? (3) Where are the world's most

important connectivity landscapes? and (4) How do these vulnerable connectivity landscapes overlap with existing global prioritization schemes for biodiversity conservation? To answer these questions we first generated a global resistance-to-movement surface from empirical estimates of animal movement (624 individuals of 48 mammalian species) in response to the human footprint index (HFI)[12,24], which describes the combined effects of infrastructure, land use and human access across the planet. By incorporating observed animal movements, our analysis permits a first-ever assessment of global functional connectivity, reflecting the predicted flow of mammal movement between the world's PAs.

We applied circuit theory[25–27] to the resistance-to-movement surface using two distinct approaches that relate the flow of animal movement across a landscape to the flow of electrical current across a circuit. First, we quantified the 'effective resistance'[26–29] – previously shown to predict gene flow[27,30] – between each terrestrial PA and all other PAs on the same landmass (i.e., continent or island). Effective resistance relates the total resistance between nodes in a circuit to the degree that each node (in our case, each PA) is isolated from all others. PAs with high effective resistance are therefore further away from other PAs and/or are more difficult to travel to, based on the resistance-to-movement surface; we thus use effective resistance as an index of PA isolation (hereafter referred to as PAI). Second, we mapped the flow of electrical current across continents. For each continent we used the center grid cell of each PA as a 'ground' to which electrical current flowed from all other PAs[28], proportional to PA size, with current flowing in greater density in regions of lower resistance. We summed the results from all PAs to produce a global map of relative electrical current densities that reflects the net movement probabilities of randomly moving individuals (i.e., mammal movement probability [MMP]) across all possible land-based travel routes between all terrestrial PAs. To validate our results,

83 we compared our global map of MMP against independent GPS data from 366 individuals
84 representing 7 species of mammals (see Methods).

85 **Protected Area Isolation**

86 Does our PA isolation (PAI) index reveal new information about the connectedness of the
87 world's PAs? While our results agree with the expectation that the least isolated PAs occur
88 within the world's two most intact biomes – boreal forest and tundra[31,32] (Figs. 1 and S1) – we
89 nonetheless found stark contrasts between our PAI index and several global connectivity
90 indicators previously developed for monitoring progress towards post-2020 targets[33] (Fig. 2).
91 Key to these contrasts is that each global indicator employs a different methodological approach
92 to assess a different component of connectivity (Fig. S2). For example, we found that PAI, used
93 to assess functional connectivity, varied considerably among countries that were assigned a
94 connectivity value of zero by the ConnIntact indicator[9], which is used to assess the contiguity of
95 intact natural land between PAs irrespective of animal movement (i.e., structural connectivity)
96 (Fig. 2). Indeed, PAI was only weakly correlated with all existing global connectivity indicators
97 (Pearson's r ranged from 0.36 – 0.55; Fig. 2) and it identified a different set of countries as most
98 connected (Table S1). For example, our PAI index identified Canada, which has the second-
99 largest area of wilderness after Russia[34], as the 2nd most connected country, while the other three
100 indicators identified Canada as only the 15th, 52nd or 111th most connected country. Our results
101 suggest that the PAI index we present here provides a new view of connectivity that
102 complements how connectivity is evaluated by the existing global indicators.

103 What potential mechanisms exist for national governments to improve their PAI value?
104 Because restoration[35] and PA expansion[36] are both recognized strategies for biodiversity
105 conservation, we compared effects on national PAI from decreasing the human footprint (e.g.,

106 via the restoration of degraded habitats[37]) and increasing PA coverage, using a linear mixed
107 effects model with continent as a random intercept. We found that reducing a country's
108 aggregate human footprint would reduce PAI more strongly than would increasing a country's
109 PA estate (Fig. S3). Although these strategies do not entail equal costs or effort, we found that on
110 average a 50% reduction in the human footprint would decrease national PAI by 24% (95% CI:
111 17-45%), whereas a 50% increase in PA coverage would decrease national PAI by only 11%
112 (95% CI: 9-21%). Utilizing both strategies in combination, however, has the greatest benefit,
113 decreasing PAI by 42% (95% CI = 27-73%). These results suggest that habitat restoration, and
114 favorable land management practices that improve the permeability of anthropogenic landscapes
115 to animal movement[35,37,38], can complement formal protection efforts to improve connectivity.

116 **Global Connectivity Conservation Priorities**

117 Beyond the connectedness of each of the world's PAs, can we also identify where
118 connectivity is most vulnerable and in need of protection or restoration around the world? We
119 focused on identifying critical concentrations of MMP that typically occur through corridors and
120 pinch points (Fig. 3). Because these areas have few or no alternative paths for animal movement,
121 they can have disproportionate impacts on connectivity if further restricted or destroyed[27]. We
122 identified concentrated flows using MMP grid cells in the 90th percentile, hereafter referred to as
123 critical connectivity areas (CCAs). We further divided CCAs into two categories based on a
124 threshold HFI value of 4 previously used by others[9,11,31]: "modified" CCAs where HFI $\geq$ 4, and
125 "intact" CCAs where HFI < 4. We found that 97% of CCAs occur in intact areas and 3% are
126 modified (i.e., 9.7% and 0.3% of the terrestrial realm, respectively). Modified CCAs thus
127 represent small but critical pinch points that if conserved or managed to limit further
128 modification (e.g., through conservation easements, payments for ecosystem services, or
129 community-based conservation[38]) could achieve gains in safeguarding connectivity through

anthropogenic landscapes. The vast majority of these modified CCAs are in sub-Saharan Africa, Europe and South America, with the greatest total coverage occurring in the Bolivia, Tanzania, Democratic Republic of Congo and Poland (Fig. S4). The greatest total coverage of intact CCAs on the other hand, are in Russia, Brazil, Australia and Canada (Fig. S5).

Where are CCAs unprotected and thus vulnerable to further land-use conversion? We found that two-thirds of all CCAs are currently unprotected (Fig. 4) and that this lack of formal protection is particularly widespread for intact CCAs. We found small but important clusters of unprotected modified-CCAs in parts of Europe, sub-Saharan Africa and North and South America, where wide-ranging species, such as red deer *Cervus elaphus*, African wild dog *Lycaon pictus* and jaguar *Panthera onca*, can occur. Further, roughly 24% of all CCAs are both unprotected and occur on land suitable for future agricultural expansion[39] (Fig. S6). The potential for rapid land conversion to agriculture highlights the need to act quickly to secure these regions for long term connectivity, either via formal protection measures or, with working lands conservation practices that focus on managing for permeable agricultural landscapes[37,38]. Such working lands, managed using strategies to enhance biodiversity conservation (e.g., silvo-pastoral, agroforestry and other agroecological management practices) and benefits to humans (e.g., pollination services and pest control), could also represent an important other effective area-based conservation measure (OECM) and as such could provide important contributions to global conservation policy targets[18,21].

Which of the world's continents, biomes and ecoregions contain the greatest proportion of CCAs? We found that the tropical moist forests of South America, the tropical grasslands and deserts of Africa, and the boreal forests of Asia contain > 80% more CCAs than other biomes (Fig. 4). Globally, these four biomes contain 41% of the world's ecoregions and a majority of the world's species, 50% of which are contained within tropical moist forests[40]. Of the world's 846

154 ecoregions, the 50 that were recently identified as having the greatest potential to protect
155 biodiversity[36] also contribute disproportionately to connectivity; unprotected portions of these
156 priority ecoregions contain on average two times greater MMP than all other unprotected
157 ecoregions (Fig. S7) and contain > 42% of the unprotected CCAs. Thus, conserving movement
158 corridors and restoring degraded habitat around pinch points in the unprotected portions of these
159 priority ecoregions is likely to benefit biodiversity conservation *and* safeguard the connectivity
160 of currently established PAs, a key goal in the post-2020 global biodiversity framework[21].

161 **Connectivity-Biodiversity Conservation Synergies**

162 Where can we further maximize conservation effectiveness by identifying landscapes that
163 simultaneously enhance connectivity and biodiversity? We examined the proportion of CCAs
164 that overlap with the Global Safety Net (GSN) – a proposed global conservation scheme that
165 identifies new priority areas for expanded protection that would boost the world's terrestrial PA
166 coverage to ~ 50%[36]. We found that roughly 72% of unprotected CCAs, and a majority of CCAs
167 suitable for future agricultural expansion, overlap with the GSN priority areas for expanded
168 conservation (Figs. 4 and S7). Thus, the GSN would protect key biodiversity elements as well as
169 more than 81% of the world's most important areas for connectivity. Of the remaining CCAs not
170 covered by the GSN, many are vulnerable to potential disturbance, degradation and/or land-
171 conversion (9% are modified and roughly 30% have the potential for agricultural development;
172 Fig. S7).

173 We also examined CCA overlap with other global conservation prioritization schemes
174 that were not explicitly incorporated into the GSN, including Frontier Forests[41], Global 200
175 Ecoregions[42] and High-Biodiversity Wilderness Areas[43]. We found that > 60% of the CCAs
176 overlap with currently-unprotected portions of these global conservation schemes, and that the

Global 200 Ecoregions covered the highest percentage of CCAs (~30%; Fig. S8). This overlap between CCAs and global conservation priorities highlights potential synergies that conservation efforts in these areas could deliver via maintaining globally-significant areas for connectivity, while also preserving rare species and assemblages, biologically outstanding ecoregions and intact habitats critical for biodiversity and ecosystem function.

Conclusions

Our study identifies key opportunities for conserving globally important areas for connectivity and for monitoring national PA connectivity using circuit theory methods adapted to the global scale. Our results show that the functional connectivity approach substantially changes the view of national PA connectivity compared to the existing global-policy indicators that are more geared towards assessing other aspects of connectivity. A key difference is that our approach specifically incorporates observed animal responses to attributes of natural and human-dominated landscapes, which is lacking in the other global indicators. Our global application of circuit theory also makes it possible for the first time to assess the permeability of both intact and human-modified landscapes to mammal movement across the terrestrial realm. With this approach, we identified small areas of modified but still permeable lands, representing only 0.3% of the terrestrial world, where timely conservation is of utmost importance to prevent further impediments to the flow of mammals between PAs.

Our study specifically evaluates the functional connectivity of protected areas at the global scale, and therefore we do not explicitly consider the connectedness of other potential sources and destinations of movement (e.g., OECMs or other natural areas), nor do we portray connectivity for more localized movements (e.g., inter-patch movement). In addition, our connectivity model is informed only by mammal movements, and therefore may not capture

connectivity for other taxa. Indeed, our results illustrate that differences in national PA connectivity can occur even among mammalian species; we found that PAs appear more isolated from the perspective of larger mammals (see Methods and Fig. S9). While this suggests that larger mammals are more sensitive to higher HFI levels, we found that patterns of flow – that is, where the flow of mammal movement is dispersed versus constricted – remain consistent across mammalian body sizes. Finally, although our approach is based on mammalian movement, our results illustrate how CCAs spatially overlap with global conservation priorities that aim to protect a variety of taxonomic groups.

We found that the vast majority of the world's CCAs currently under threat (i.e., unprotected or located on modified land), or likely to be threatened in the future (i.e., located on land suitable for future food production), would be protected by expanded conservation under the proposed Global Safety Net (GSN)[36]. If protected, these areas of GSN-CCA overlap could result in important conservation synergies that slow or prevent biodiversity loss. Since many of these areas of overlap are also predicted to be suitable for future agricultural expansion, where formal protections could be contested over livelihoods or food supply needs, alternative strategies for conserving or restoring connectivity may be needed. Our results suggest that managing the matrix for more permeability to animal movement (e.g., habitat restoration) can be a better single strategy for improving connectivity than adding protected areas alone. However, formal protection and habitat restoration together generated the largest improvements to connectivity, supporting the need for holistic approaches that combine working lands conservation[37,38] with protected areas. Such combined strategies can also provide significant benefits to humans[37,38,44], thus advancing the post-2020 global biodiversity framework vision of "living in harmony with nature"[21].

Methods

We modelled connectivity using Circuitscape, an open-source program implemented in Julia[45] and widely used in research and conservation planning[25,27,46–51] that relies on principles from circuit theory to relate the flow of animal movement across a heterogeneous landscape to the flow of electrical current across a circuit[27]. This approach treats a gridded resistance-to-movement surface as a conductive layer where neighboring grid cells are connected by resistors, whose level of resistance represents the friction of the landscape to animal movement (i.e., low-resistance grid cells are most likely to be traversed). Electrical current, injected at a source node representing a source of animal movement, flows across all neighboring landscape grid cells (resistors) in the circuit to a ground node representing the destination of animal movement. Connectivity is then evaluated in two distinct ways: (1) from the effective resistance of the circuit, measuring the degree to which the source node is isolated from the ground node and (2) from the pattern of electrical current flow (i.e., animal movement probabilities) across the resistance-to-movement surface[27], as outlined below and illustrated as a workflow in Fig. S10.

Two inputs are required for this analysis: the resistance-to-movement surface describing the friction of the landscape to animal movement and the layer specifying sources and destinations of animal movement. To model functional connectivity (Fig. S3), we generated a resistance-to-movement surface using the data and linear mixed effects model of 0.95 quantile displacement distances from 10-day intervals presented in Tucker et al. (2018)[12] for 624 GPS-collared individuals from 48 species of mammals. This movement model included as predictor variables the human footprint index (HFI)[24], normalized difference vegetation index (NDVI), body weight and dietary guild, and species as a random effect. We focused on the long-distance, long-time scale movements as those more likely to represent the scale of movement occurring

between protected areas, thus representing movements promoting gene flow, rescue effects or climate adaptation.

Using the model above, we predicted mammal movement for all values of HFI across Earth's terrestrial surface after resampling the HFI layer from 1 km^2 to ~70 km^2 (in Mollweide equal area projection) to reduce computation time in our Circuitscape analysis from months to days (using a Google virtual machine with 96 CPUs and 360 GB memory). We rescaled these predicted movements to between 0 and 1 to represent the landscape's permeability to mammal movement across the globe. We then used an inverse linear function (e.g., 1-permeability) to convert the permeability surface to a resistance-to-movement surface[52–54]. Following other studies, we further modified resistance-to-movement, M, by percent slope to reflect the energetic costs of moving in steep terrain[28,50,55] using the equation $\widehat{M} = M^{1-\left(\frac{s}{max(s)}\right)}$, where s = terrain slope.

We used all terrestrial PAs from the May 2020 World Database on Protected Areas (WDPA)[56] as the sources and destinations of mammal movement (i.e., source and ground of electrical current). We combined this WDPA layer with PAs in China from the April 2018 WDPA[56], because China removed all its national PAs from the WDPA after this date. As recommended in the WDPA best practices guide, we removed any PA that did not report its area, or with a 'Proposed' status or 'UNESCO-MAB Biosphere Reserve' designation (https://www.protectedplanet.net/en/resources/calculating-protected-area-coverage). We used PA centroids as the source and ground of electrical current, rather than entire PA polygons, because this allowed for estimates of electrical current flow within PAs, rather than assuming flow is equally good within PA boundaries[28]. We rasterized PA-centroids to match the resolution and extent of the resistance-to-movement surface. We excluded PA-centroid grid cells for which the sum total of PA area was less than half the grid cell resolution, 35 km^2, to ensure that electrical

source grid cells are primarily represented by a probable source or destination of mammal movement. By excluding these small PAs (similar to[28,57]), we also avoided overestimating connectivity from using source and destination nodes much smaller than the resolution of our analysis and the home ranges of many of the mammals that we examined. Excluded PAs represented 90% of the total number of individual PAs but, with a mean area of 2.4 km^2, they comprised only ~2% of the total area of the global PA estate (Fig S11 and Table S2). Included PAs were on average 420 times larger than excluded PAs. Note also that excluded PA-centroids were removed only as sources and destinations of mammal movement in the model; importantly their benefits to connectivity were fully incorporated into the resistance-to-movement surface as areas of lower resistance (i.e., lower HFI). We modelled connectivity by continent, excluding Antarctica, islands < 2,500 km^2 and islands with < 2 PAs. We also combined Europe and Asia to avoid boundary effects where the two continents meet.

Protected Area Isolation

To obtain a value of effective resistance for all terrestrial PAs (steps 4-5 in Fig. S10), we applied Circuitscape's one-to-all mode[58] to the input layers. This mode connects a focal PA-centroid to an electrical current source and connects all remaining PA-centroids to ground, thereby generating one circuit where electrical current flows from the focal PA source to all other PAs within the continent. When the circuit is connected, effective resistance, R_{eff}, is calculated as $1/R_{eff} = 1/R_1 + 1/R_2 + 1/R_3 \ldots 1/R_n$, where each R_i represents a pathway (i.e., summed grid cell 'resistors' connected in series) between PAs. Following this central equation of circuit theory, effective resistance decreases, and thus connectivity increases, as more connections (i.e., redundant pathways, R_i) are added to the circuit[27]. For this process we maintain the default current injection of 1 Amp, because each grid cell 'resistor' in the landscape has an assigned resistance value, effective resistance does not vary with the amount of current injected.

295 We repeated this procedure for each PA and mapped the resulting PA isolation (PAI) values for
296 all qualified terrestrial PAs (i.e., with summed area within a grid cell of > 35 km^2) and evaluated
297 PAI within the world's biomes[42] and continents.

298 We calculated the median PAI for each country's PA network. Because measures of PAI
299 were generated from connecting PAs across entire continents, national PAI may be affected by
300 connections with neighboring cross-border PAs. To ensure that national PAI was not unduly
301 sensitive to the location and extent of PAs outside the country's borders, we repeated the steps to
302 model PAI at the country level for 25 randomly selected countries. To do so, we clipped the
303 resistance-to-movement surface and PA layer to each of the 25 countries, re-applied circuit
304 theory using the one-to-all approach and re-computed median PAI by country. National PAI
305 from the continent and country analyses were highly correlated (Pearson's $r = 0.92$; Fig. S12),
306 suggesting that metrics from our global analysis are suitable proxies for country-level PAI.

307 We evaluated how hypothetical changes to mean-national HFI and proportion of PA
308 would affect national PAI. We used a linear mixed effects model with mean HFI and % PA area
309 as predictor variables scaled by subtracting the mean and dividing by the standard deviation to
310 evaluate the relative effects of each, with continent as a random intercept. We then used the
311 estimated coefficients to simulate the effects of changing the proportion of protected area
312 (including PAs of all sizes) and mean HFI on national PAI.

313 We compared our national PAI index, which explicitly accounts for mammal movement,
314 to three proposed indicators of progress towards post-2020 global connectivity targets that lack
315 measurements of animal movement (Fig. S3): (1) the proportion of country protected, (2)
316 ConnIntact[9] – an updated version of Protconn[22], the currently proposed global indicator – and (3)
317 the PA connectedness index (PARC)[59]. ConnIntact is a network-based structural connectivity
318 approach that accounts for the number of PAs, total area of PAs, total country area and the

contiguity of intact land between PAs. Specifically, this approach assumes PAs are perfectly connected whenever there is a contiguous pathway of 1 km^2 grid cells of intact natural land directly connecting PA edges or indirectly connecting PAs through connecting intermediate PAs as stepping stones. PAs are assumed to be completely disconnected when there is no contiguous pathway of intact land. The PARC index accounts for connectivity between ~1 km^2 grid PA grid cells and between these PA grid cells and ~1 km^2 grid cells containing primary vegetation using a cost-distance approach where the cost of moving between grid cells is assumed to be negatively related to the proportion of primary vegetation (i.e., the more primary vegetation in a grid cell, the lower the cost). We used Pearson's *r* to evaluate the correlations between national PAI and the three global indicators of connectivity.

Mapping Global Connectivity

To map patterns of mammal movement probability (MMP) using electrical current density (steps 6-10 in Fig. S10) we applied Circuitscape's all-to-one mode[58] to the input layers. Similar to the pairwise mode[58], the all-to-one mode produces patterns of electrical current flow between each source-ground pair but with greater computational efficiency. It does this by generating many circuits simultaneously; in our application, one PA-centroid is designated as ground while all remaining PA-centroids are current sources. At each source, we injected an electrical current amount proportional to PA area (e.g., we injected 100 Amps into any PA centroid that represented a 100-km^2 PA), to account for the effect of PA size on the number of animals potentially moving from each PA (i.e., assuming that all else equal, large PAs have a greater abundance of wildlife and thus more dispersing animals than small PAs[60]). To account for the size of the destination PA (i.e., all else equal, large PAs will receive more immigrating animals than small PAs[60]), we multiplied the output electrical current density map – depicting electrical current flow from all source PAs to one ground PA – by the area of the corresponding

343 ground PA. We repeated this process for each PA-centroid connected to ground and summed all
344 maps to obtain a map of cumulative electrical current density (i.e., MMP) per continent.
345 We found that electrical current densities increased with land mass area. To correct for
346 this effect and 'normalize' electrical current densities into a common scale – using current
347 density/km^2 – we divided electrical current densities by the area of their corresponding land
348 mass. Finally, we merged all electrical current density/km^2 maps together to generate a
349 comparable global map.

350 ***Validation and Sensitivity Analyses***

351 We validated our global map of electrical current density (MMP) using two different
352 approaches. First, we used independent GPS movement data (> 1.5 million locations) from 366
353 individuals and 7 mammal species, combined with GPS movement data (> 220,000 locations)
354 from another 88 individuals and 4 species included in the Tucker et al. (2018)[12] analysis, to
355 evaluate whether connectivity values were higher where animals were observed moving (see
356 Table S3 for details and list of data providers; see Fig. S13 for dataset locations). We obtained
357 known range data for each species (https://www.iucnredlist.org/). Then for each species-dataset
358 we (1) generated a 95% utilization distribution (UD) (i.e., 95% kernel home range) from the GPS
359 data using the adehabitatHR package[61] in the R statistical computing environment[62] version
360 3.6.3, (2) randomly selected 1000 points within that UD to represent locations where those
361 individuals were likely to occur and (3) extracted electrical current density values for those
362 points. To compare these values to electrical current density values where the collared
363 individuals could have been but were not observed, we (4) calculated max displacement distance
364 using the adehabitatHR package[61] in R and buffered the UD by this distance, (5) clipped the
365 species range data to that buffer, (6) randomly selected points within that clipped range outside
366 of the UD and (7) extracted electrical current density values from those random points.

367 We used a Bayesian hierarchical approach to evaluate the differences in electrical current
368 density extracted from points inside and outside the UDs. We used the package brms[63] in R to
369 construct the model, with log electrical current density as the response variable, inside or outside
370 UD as a categorical predictor variable, and a random intercept and slope by species. We used
371 uninformative prior distributions, ran 4 iterations of the model with 400 chains per iteration, and
372 confirmed that all parameters converged with R-hat values < 1.1. Using the predicted posterior
373 distributions, we calculated the percentage that electrical current densities were higher inside the
374 UDs and provide strong evidence for species moving within areas of higher predicted movement
375 probability (Fig. S14).

376 Second, using the same data, we evaluated whether animals were selecting for critical
377 connectivity areas (CCAs) (i.e., grid cells having electrical current density values in the 90th
378 percentile). Using a raster of CCAs and the GPS datasets described above, we extracted the
379 number of unique CCA grid cells that were used by each species. We calculated the proportion
380 of used grid cells that were CCAs. We also calculated the proportion of unused grid cells that
381 were CCAs, within the same buffered areas described previously. From this, we calculated the
382 percent that CCAs were used (i.e., inside UDs) relative to what was available and found strong
383 evidence that 9 of the 11 species preferred to move within CCAs (Table S4).

384 We also evaluated the sensitivity of effective resistance (PAI) and electrical current
385 density (MMP) to species body size[12,64] and continent-specific species attributes. We first created
386 three different resistance-to-movement surfaces using a similar linear mixed effects model that
387 was used in Tucker et al. (2018)[12] and our previous analysis, but instead fitted to: (1) 10-day
388 displacement distances recorded by species whose mean body mass was greater than the mean
389 body mass, ~ 53 kg, of the 48 species considered in our full model, (2) 10-day displacement
390 distances recorded by species whose mean body mass was less than the mean body mass of the

391 48 species, and (3) 10-day displacement distances recorded by African species only. We repeated
392 the steps in the workflow described for our main analysis (Fig. S10) and compared effective
393 resistances and electrical current densities between our full model and the sensitivity test models
394 (Fig. S9). Effective resistances increased with body size and electrical current densities were
395 highly correlated across models ($R^2 > 0.9$), suggesting that while larger mammals are more
396 sensitive to high HFI, the patterns of flow remain consistent across mammalian body sizes.

397 ***Areas of Overlap for Priority Connectivity and Biodiversity Sites***

398 We summarized the total area of both modified and intact categories of critical
399 connectivity areas (CCAs) by country and identified countries with the largest area (95th
400 percentile) of CCAs. To assess the protection status of CCAs, we quantified CCA overlap with
401 PAs using the May 2020 World Database on Protected Areas (WDPA) and the April 2018
402 WDPA for PAs in China[56]. We used both WDPA polygons and WDPA points files to generate
403 our PA layer. We converted WDPA points to polygons using circular buffers with areas equal to
404 their corresponding reported PA area (https://www.protectedplanet.net/en/resources/calculating-
405 protected-area-coverage), and then we spatially intersected these buffers with their country of
406 origin to exclude parts of the buffer that occurred in other countries. We compared MMP in
407 protected and unprotected portions of the 50 ecoregions recently identified as contributing most
408 to enhancing biodiversity protection[36] and in protected and unprotected portions of all other
409 ecoregions (https://ecoregions2017.appspot.com/). We also summarized the total area of CCAs
410 within continents, ecoregions[40] and biomes[42].

411 We quantified the amount of unprotected CCAs that overlapped with lands where future
412 agricultural expansion is predicted using a global land-systems (GLS) map describing crop
413 suitability as determined by agro-climatic and agro-edaphic conditions[39]. The crop suitable areas
414 in the GLS map included those that were categorized as very high to marginally suitable for high

415 intensity cropland along with low intensity cropland, and thus may overpredict cropland
416 expansion in some cases[39]. However, suitable areas for tree plantation and livestock expansion
417 were not included in the GLS map, potentially resulting in an underprediction of CCA overlap
418 with future agricultural areas.

419 We examined the proportion of unprotected CCAs that overlapped with four areas
420 prioritized for expanded conservation under the Global Safety Net (GSN)[36], the most recent
421 global prioritization scheme for biodiversity conservation. These areas are prioritized in the GSN
422 because of their disproportionate contribution to (1) important rare and threatened species, (2)
423 distinct species assemblages, (3) intact assemblages of large mammals and (4) wilderness or
424 other macrorefugia for wildlife. Conservation of these additional four priority areas, plus climate
425 stabilization sites, would extend coverage of the PA estate to ~50% of the terrestrial realm.

426 We also quantified the proportion of unprotected CCAs that overlapped with three other
427 global conservation prioritization schemes that target other critical ecological conditions or
428 regions important to biodiversity (which may be partially overlapping with the GSN), including
429 Frontier Forests[41], Global 200 Ecoregions[65] and High-Biodiversity Wilderness Areas[43]. Frontier
430 forests represent large contiguous wilderness areas that specifically encompass forests and
431 conditions important to forest integrity. The Global 200 Ecoregions is based on representation
432 and biologically outstanding character, and is thus meant to encompass the most biologically
433 outstanding ecoregions in every biome-realm combination. High Biodiversity Wilderness Areas
434 are the complement of Biodiversity Hotspots, thus encompassing non-threatened areas of high
435 biodiversity.
436

437 **References**

438 1. Maxwell, S. L. *et al.* Area-based conservation in the twenty-first century. *Nature* **586**,
439 217–227 (2020).
440 2. Butchart, S. H. M. *et al.* Shortfalls and Solutions for Meeting National and Global
441 Conservation Area Targets. *Conserv. Lett.* **8**, 329–337 (2015).
442 3. Pimm, S. L. *et al.* The biodiversity of species and their rates of extinction, distribution,
443 and protection. *Science* **344**, (2014).
444 4. Venter, O. *et al.* Bias in protected-area location and its effects on long-term aspirations of
445 biodiversity conventions. *Conserv. Biol.* **32**, 127–134 (2018).
446 5. Venter, O. *et al.* Targeting Global Protected Area Expansion for Imperiled Biodiversity.
447 *PLoS Biol.* **12**, (2014).
448 6. Rodrigues, A. S. L. *et al.* Global gap analysis: Priority regions for expanding the global
449 protected-area network. *Bioscience* **54**, 1092–1100 (2004).
450 7. Terraube, J., Van doninck, J., Helle, P. & Cabeza, M. Assessing the effectiveness of a
451 national protected area network for carnivore conservation. *Nat. Commun.* **11**, 1–9 (2020).
452 8. Visconti, B. P. *et al.* Protected area targets post-2020. *Science* **364**, 239–241 (2019).
453 9. Ward, M. *et al.* Only ten percent of the global terrestrial protected area network is
454 connected via intact land. *Nat. Commun.* 1–10 (2020) doi:10.1101/2020.01.28.920488.
455 10. Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S. & Kiesecker, J.
456 Managing the middle: A shift in conservation priorities based on the global human
457 modification gradient. *Glob. Chang. Biol.* **25**, 811–826 (2019).
458 11. Watson, J. E. M. *et al.* Persistent Disparities between Recent Rates of Habitat Conversion
459 and Protection and Implications for Future Global Conservation Targets. *Conserv. Lett.* **9**,
460 413–421 (2016).

461 12. Tucker, M. A. *et al.* Moving in the Anthropocene: Global reductions in terrestrial
462 mammalian movements. *Science* **359**, 466–469 (2018).
463 13. Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P. G. M. & Berger, J. Global
464 decline in aggregated migrations of large terrestrial mammals. *Endanger. Species Res.* **7**,
465 55–76 (2009).
466 14. Haddad, N. M. *et al.* Habitat fragmentation and its lasting impact on Earth's ecosystems.
467 *Sci. Adv.* **1**, 1–10 (2015).
468 15. Pacifici, M., Di Marco, M. & Watson, J. E. M. Protected areas are now the last
469 strongholds for many imperiled mammal species. *Conserv. Lett.* **13**, 1–7 (2020).
470 16. UNEP. Ecological connectivity: a bridge to preserving biodiversity. *Front. 2018/19*
471 *Emerg. Issues Environ. Concern. United Nations Environ. Program.* 24–37 (2019).
472 17. Schmidt, C., Domaratzki, M., Kinnunen, R. P., Bowman, J. & Garroway, C. J. Continent-
473 wide effects of urbanization on bird and mammal genetic diversity. *Proc. R. Soc. B Biol.*
474 *Sci.* **287**, 20192497 (2020).
475 18. CBD. *Strategic Plan for Biodiversity 2011-2020*. https://www.cbd.int/sp/ (2011).
476 19. Taylor, P. D., Fahrig, L., Henein, K. & Merriam, G. Connectivity Is a Vital Element of
477 Landscape Structure Author(s): *Oikos* **68**, 571–573 (1993).
478 20. CMS. Ecological Connectivity in the Post-2020 Global Biodiversity Framework.
479 https://go.nature.com/38GB6Nf (2019).
480 21. Secretariat of the United Nations Convention on Biological Diversity. *First Draft of the*
481 *Post-2020 Global Biodiversity Framework*. *Cbd/Wg2020/3/3* (2021).
482 22. Saura, S. *et al.* Protected area connectivity: Shortfalls in global targets and country-level
483 priorities. *Biol. Conserv.* **219**, 53–67 (2018).
484 23. Saura, S. *et al.* Global trends in protected area connectivity from 2010 to 2018. *Biol.*

485 *Conserv.* **238**, 108183 (2019).
486 24. Venter, O. *et al.* Sixteen years of change in the global terrestrial human footprint and
487 implications for biodiversity conservation. *Nat. Commun.* **7**, 1–11 (2016).
488 25. Dickson, B. G. *et al.* Circuit-theory applications to connectivity science and conservation.
489 *Conserv. Biol.* **33**, 239–249 (2019).
490 26. McRae, B. H. Isolation By Resistance. *Evolution (N. Y).* **60**, 1551 (2006).
491 27. McRae, B. H., Dickson, B. G., Keitt, T. H. & Shah, V. B. Using circuit theory to model
492 connectivity in ecology, evolution, and conservation. *Ecology* **89**, 2712–2724 (2008).
493 28. Dickson, B. G. *et al.* Informing Strategic Efforts to Expand and Connect Protected Areas
494 Using a Model of Ecological Flow , with Application to the Western United States.
495 *Conserv. Lett.* **10**, 564–571 (2017).
496 29. Keeley, A. T. H., Beier, P. & Jenness, J. S. Connectivity metrics for conservation planning
497 and monitoring. *Biol. Conserv.* **255**, 109008 (2021).
498 30. Garroway, C. J., Bowman, J. & Wilson, P. J. Using a genetic network to parameterize a
499 landscape resistance surface for fishers, Martes pennanti. *Mol. Ecol.* **20**, 3978–3988
500 (2011).
501 31. Riggio, J. *et al.* Global human influence maps reveal clear opportunities in conserving
502 Earth's remaining intact terrestrial ecosystems. *Glob. Chang. Biol.* **26**, 4344–4356 (2020).
503 32. Watson, J. E. M. *et al.* Catastrophic Declines in Wilderness Areas Undermine Global
504 Environment Targets. *Curr. Biol.* **26**, 2929–2934 (2016).
505 33. Secretariat of the United Nations Convention on Biological Diversity. *Zero Draft of the*
506 *Post- 2020 Global Biodiversity*. (2020).
507 34. Morales-Hidalgo, D., Oswalt, S. N. & Somanathan, E. Status and trends in global primary
508 forest, protected areas, and areas designated for conservation of biodiversity from the

Global Forest Resources Assessment 2015. *For. Ecol. Manage.* **352**, 68–77 (2015).

35. Strassburg, B. B. N. *et al.* Global priority areas for ecosystem restoration. *Nature* **586**, 724–729 (2020).

36. Dinerstein, E. *et al.* A 'Global Safety Net' to reverse biodiversity loss and stabilize Earth's climate. *Sci. Adv.* **6**, 1–14 (2020).

37. Garibaldi, L. A. *et al.* Working landscapes need at least 20% native habitat. *Conserv. Lett.* 1–10 (2020) doi:10.1111/conl.12773.

38. Kremen, C. & Merenlender, A. M. Landscapes that work for biodiversity and people. *Science* **362**, (2018).

39. Kehoe, L. *et al.* Biodiversity at risk under future cropland expansion and intensification. *Nat. Ecol. Evol.* **1**, 1129–1135 (2017).

40. Dinerstein, E. *et al.* An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. *Bioscience* **67**, 534–545 (2017).

41. Bryant, D., Nielsen, D. & Tangley, L. *The Last Frontier Forests: Ecosystems and Economics on the Edge*. (1997).

42. Olson, D. M. *et al.* Terrestrial ecoregions of the world: A new map of life on Earth. *Bioscience* **51**, 933–938 (2001).

43. Mittermeier, R. A. *et al.* Wilderness and biodiversity conservation. *Proc. Natl. Acad. Sci. U. S. A.* **100**, 10309–10313 (2003).

44. Díaz, S. *et al.* Assessing nature's contributions to people. *Science* **359**, 270–272 (2018).

45. Hall, K. R. *et al.* Circuitscape in Julia: Empowering Dynamic Approaches to Connectivity Assessment. *Land* **10**, 301 (2021).

46. McClure, M. L., Dickson, B. G. & Nicholson, K. L. Modeling connectivity to identify current and future anthropogenic barriers to movement of large carnivores: A case study

533 in the American Southwest. *Ecol. Evol.* **7**, 3762–3772 (2017).

534 47. Brennan, A. *et al.* Characterizing multispecies connectivity across a transfrontier
535 conservation landscape. *J. Appl. Ecol.* **57**, 1700–1710 (2020).

536 48. Naidoo, R. *et al.* Evaluating the effectiveness of local- and regional-scale wildlife
537 corridors using quantitative metrics of functional connectivity. *Biol. Conserv.* **217**, 96–103
538 (2018).

539 49. Koen, E. L., Bowman, J., Sadowski, C. & Walpole, A. A. Landscape connectivity for
540 wildlife: Development and validation of multispecies linkage maps. *Methods Ecol. Evol.*
541 **5**, 626–633 (2014).

542 50. Marrec, R. *et al.* Conceptual framework and uncertainty analysis for large-scale, species-
543 agnostic modelling of landscape connectivity across Alberta, Canada. *Sci. Rep.* **10**, 1–15
544 (2020).

545 51. McRae, B. *et al.* Conserving Nature's Stage: Mapping Omnidirectional Connectivity for
546 Resilient Terrestrial Landscapes in the Pacific Northwest. 47 (2016)
547 doi:10.13140/RG.2.1.4158.6166.

548 52. Keeley, A. T. H., Beier, P. & Gagnon, J. W. Estimating landscape resistance from habitat
549 suitability: effects of data source and nonlinearities. *Landsc. Ecol.* **31**, 2151–2162 (2016).

550 53. González-Saucedo, Z. Y., González-Bernal, A. & Martínez-Meyer, E. Identifying priority
551 areas for landscape connectivity for three large carnivores in northwestern Mexico and
552 southwestern United States. *Landsc. Ecol.* **4**, (2021).

553 54. Brennan, A. *et al.* Examining speed versus selection in connectivity models using elk
554 migration as an example. *Landsc. Ecol.* **33**, 955–968 (2018).

555 55. Theobald, D. M., Reed, S. E., Fields, K. & Soulé, M. Connecting natural landscapes using
556 a landscape permeability model to prioritize conservation activities in the United States.

Conserv. Lett. **5**, 123–133 (2012).

56. UNEP-WCMC and IUCN. Protected Planet: the World Database on Protected Areas (WDPA), Cambridge, UK. www.protectedplanet.com.

57. Barnett, K. & Belote, R. T. Modeling an aspirational connected network of protected areas across North America. *Ecol. Appl.* 0–2 (2021) doi:10.1002/eap.2387.

58. McRae, B., Shah, V. & Mohapatra, T. *Circuitscape 4 User Guide*. (2013).

59. CSIRO. *Protected Area Connectedness Index (PARC-Connectedness)*. https://www.bipindicators.net/indicators/protected-area-connectedness-index-parc-connectedness (2019).

60. Hanski, I. & Gyllenberg, M. Uniting two general patterns in the distribution of species. *Science* **275**, 397–400 (1997).

61. Calenge, C. Home Range Estimation in R: the adehabitatHR Package. (2015).

62. R Core Development Team. R: A language and environment for statistical computing. (2020).

63. Bürkner, P. C. brms: An R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, (2017).

64. Pacifici, M. *et al.* Global correlates of range contractions and expansions in terrestrial mammals. *Nat. Commun.* **11**, 1–9 (2020).

65. Olson, D. M. & Dinerstein, E. The global 200: Priority ecoregions for global conservation. in *Annals of the Missouri Botanical Garden* vol. 89 199–224 (2002).

578 **Acknowledgements**

579 We are grateful to Christina Kennedy for her thoughtful comments on the manuscript.

580

581 **Competing interests**

582 The authors declare no competing interests.

583

584

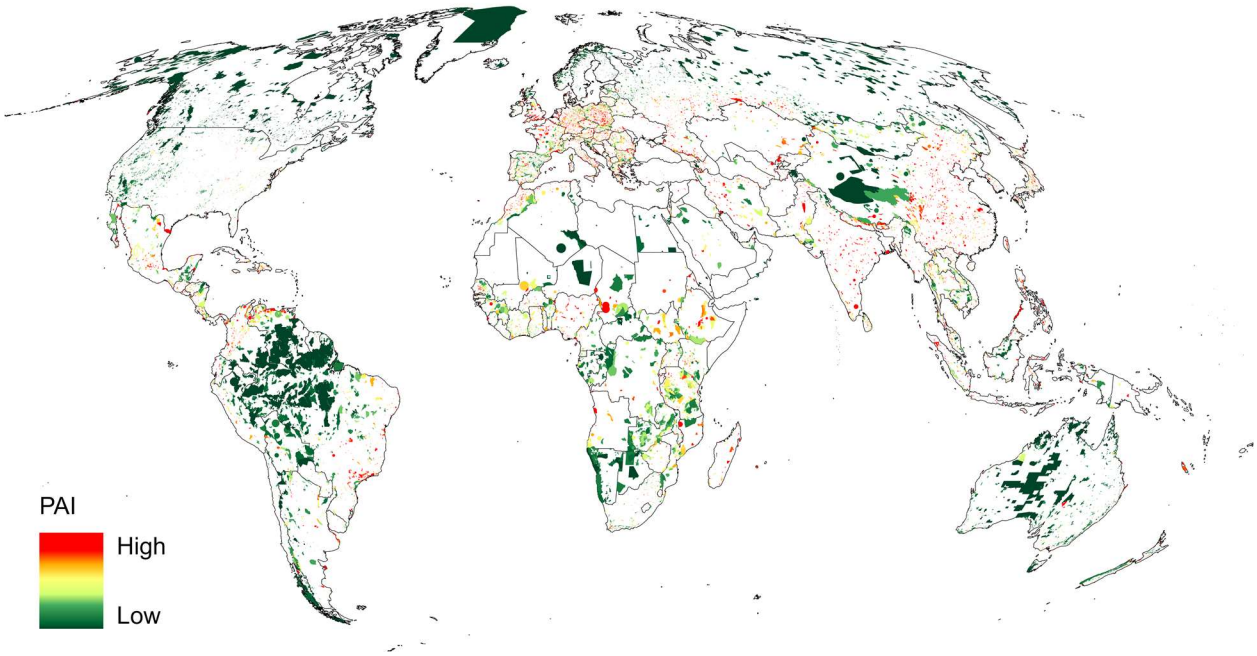

Figure 1. Protected area isolation (PAI). Isolation of the world's terrestrial PAs, as measured by effective resistance to mammal movement. The most connected PAs are those categorized as wilderness areas (i.e., IUCN category Ib) and those that occur within the most intact biomes (boreal forest and tundra), while the most isolated PAs occur in mangroves (a critically endangered biome with few PAs).

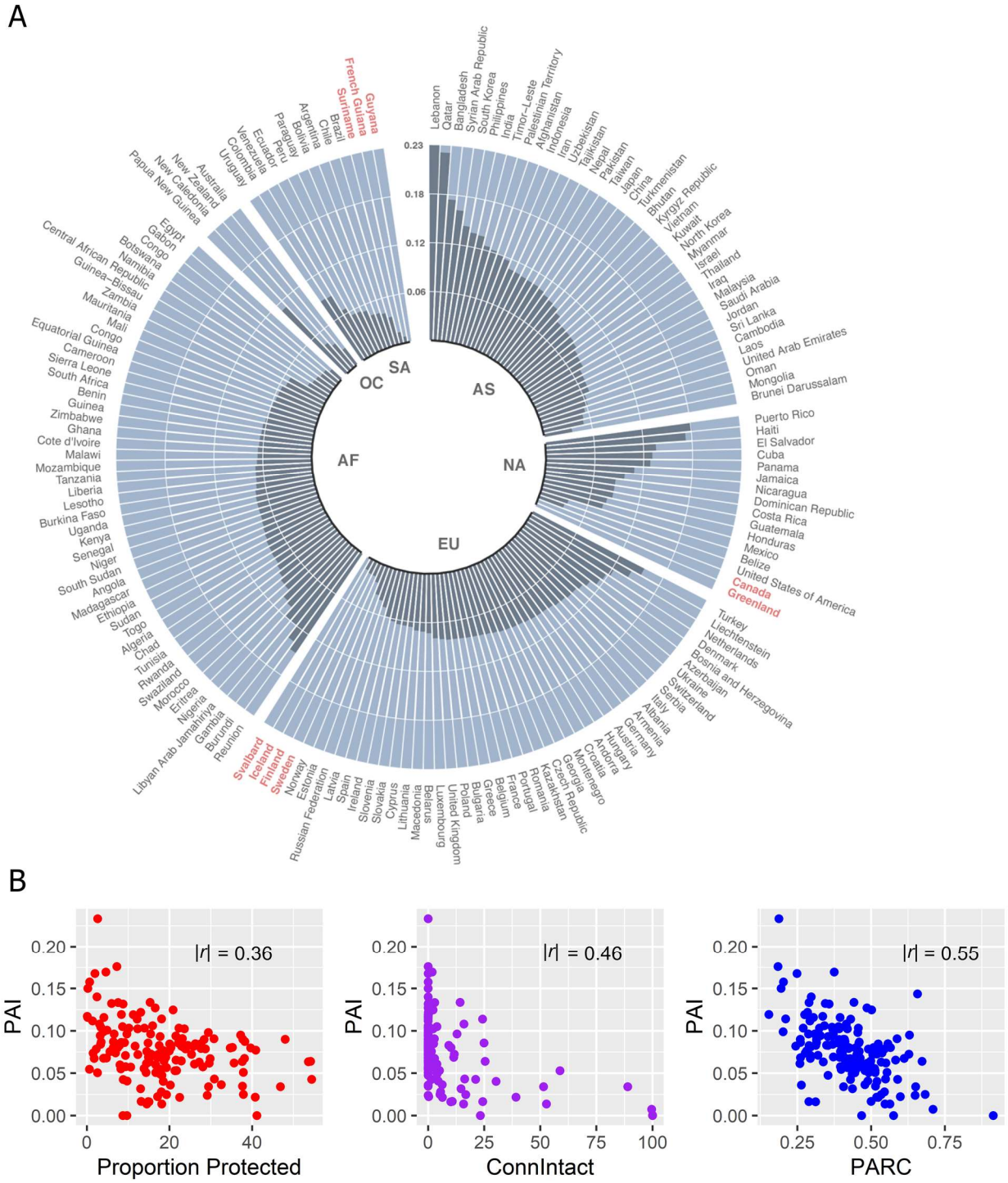

Figure 2. National protected area isolation (PAI). (A) PAI aggregated to the national level (dark grey bars depict PAI values); higher values reflect greater degree of isolation. Bars are organized by continent (AS = Asia; NA = North America; EU = Europe; AF = Africa; SA =

596 South America; OC = Oceania and Australia). Red-labeled countries have the most connected
597 national PA networks (95th percentile). (B) Comparisons of our national PAI index to three
598 existing global indicators of connectivity. ConnIntact[9] is a recently updated version of the
599 protected-connected index[22]; PARC is the PA connectedness index[59]. The PAI and global
600 indicator values were weakly correlated, as evaluated using Pearson's *r*.
601

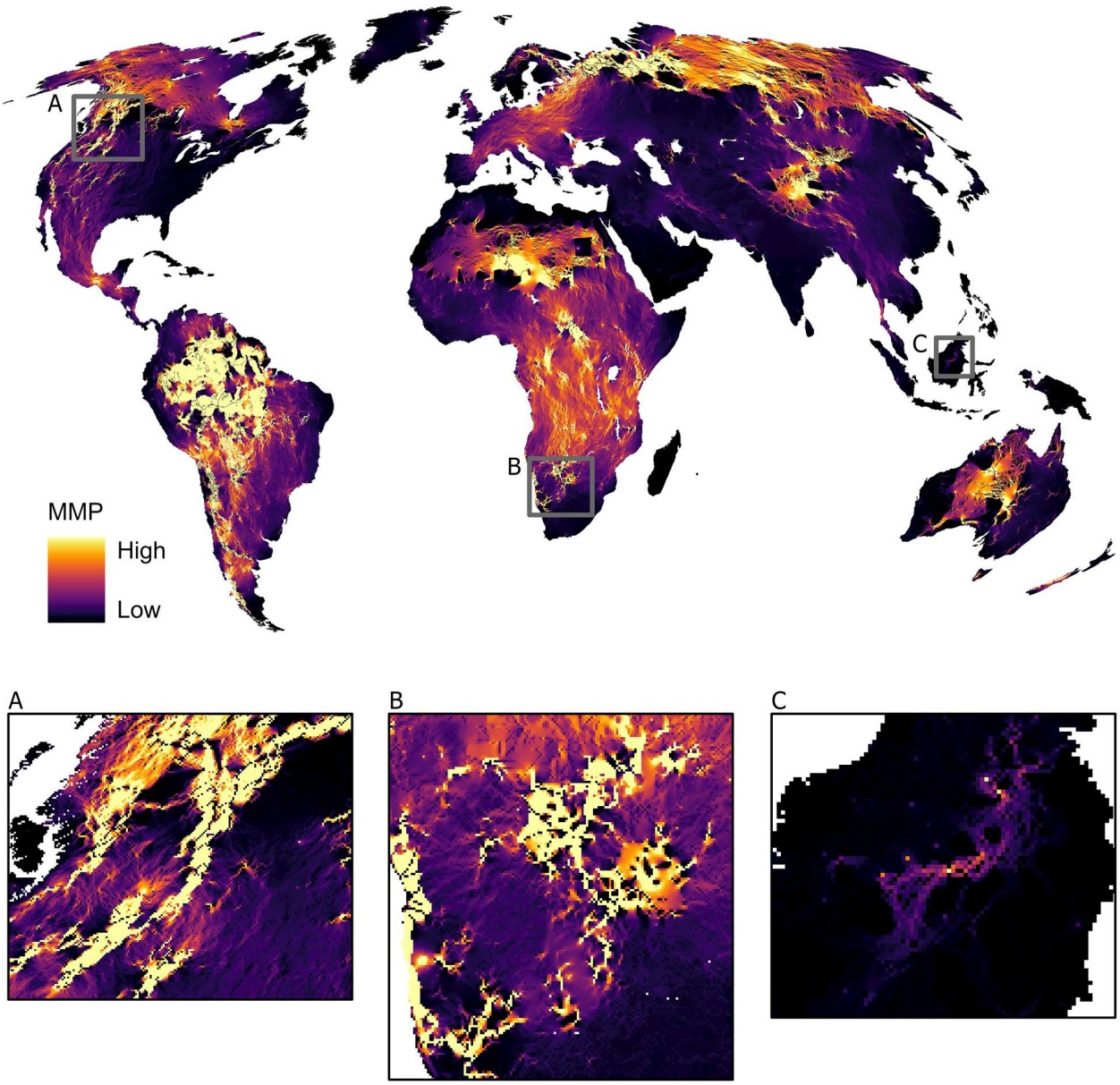

Figure 3. Global mammal movement probability (MMP). Predicted flow of mammal movement between all PAs based on patterns of electrical current flow. Grid cells with the highest MMP reflect areas where mammal movement is predicted to be most concentrated across the globe, flowing through corridors or pinch points (in light yellow) surrounded by less permeable anthropogenic landscape. Areas in orange and purple reflect moderate flows dispersed across many pathways. Areas of concentrated and dispersed flow are both important to connectivity, but with multiple pathways in dispersed areas, there is a lower risk of total loss of

connectivity. Black regions depict areas of lower relative flow (low MMP). Boxes highlight example 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).

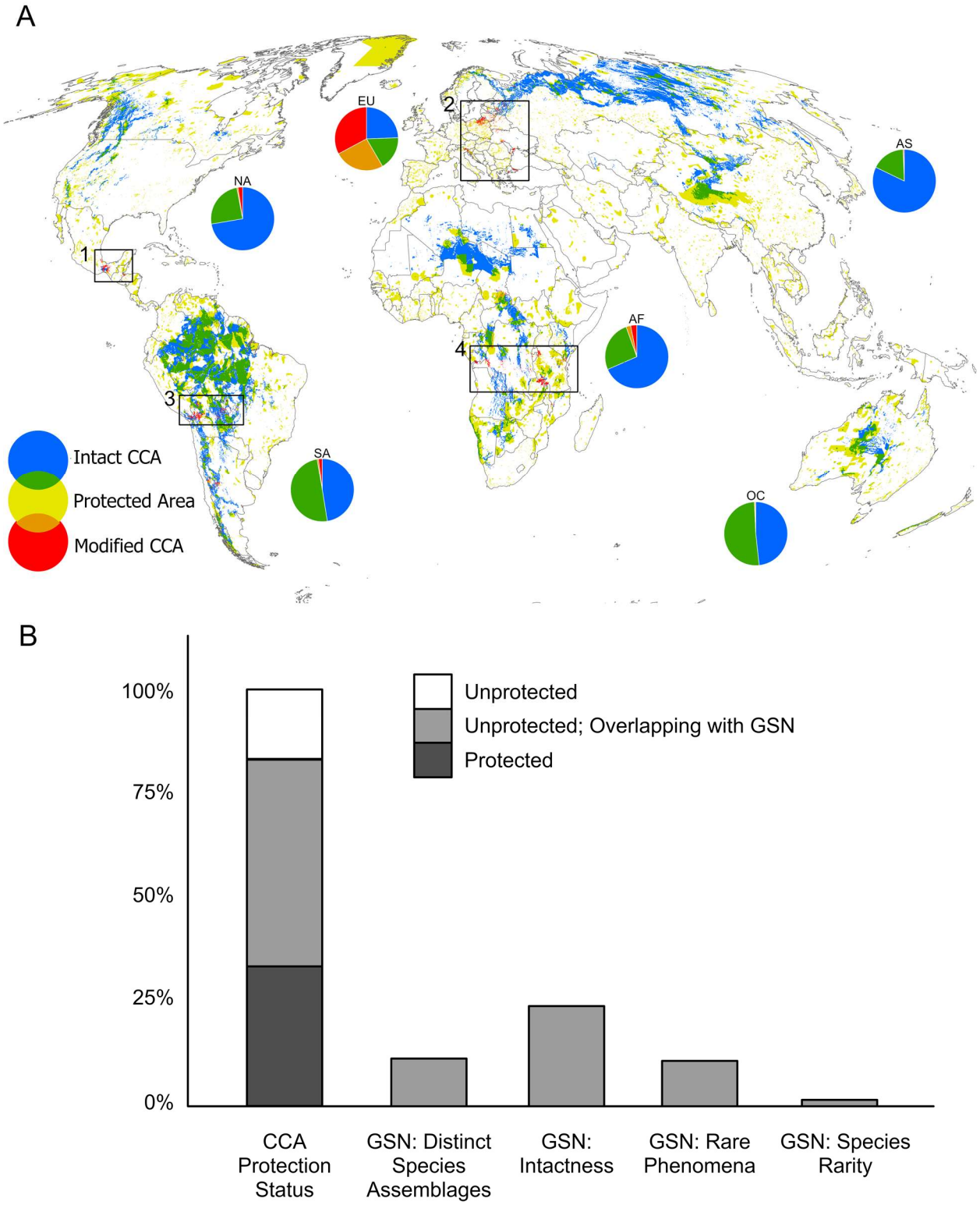

Figure 4. Mapping critical connectivity areas globally (CCAs). (A) Intact CCAs (blue) and modified CCAs (red) were classified based on mammal movement probability (MMP) and

human footprint index values (HFI< 4, HFI ≥ 4, respectively). CCAs in green and orange are covered by protected areas. Black boxes highlight four areas with clusters of modified CCAs, occurring in: (1) Mexico, (2) Poland, Slovenia, Italy, Belarus and Ukraine, (3) Bolivia and Brazil, and (4) Democratic Republic of Congo, Tanzania and Zambia. Pie charts indicate the proportion of each CCA type and protection status in each continent (AS = Asia; NA = North America; EU = Europe [excluding Russia]; AF = Africa; SA = South America; OC = Oceania and Australia) (B) Proportion of CCAs that overlap with expanded conservation areas of the Global Safety Net (GSN). Stacked bars (far left) depict the proportion of protected and unprotected CCAs. Individual bars (right) represent the proportion of CCAs that overlap with each of the priority conservation areas selected for specific purposes under the GSN.