Only ten percent of the global terrestrial protected area network is connected via intact land

**Authors:** Michelle Ward*[1,2], Santiago Saura[3,4], Brooke Williams[1,2], Juan Pablo Ramírez-Delgado[5], Nur Arafeh-Dalmau[1,2], James R. Allan[2,6], Oscar Venter[5], Grégoire Dubois[3], James E.M. Watson[1,2,7]

**Affiliations:**

[1]*School of Earth and Environmental Sciences, University of Queensland, St Lucia 4072, Australia.*

[2]*Centre for Biodiversity and Conservation Science, School of Biological Sciences, The University of Queensland, Brisbane 4072, Queensland, Australia.*

[3]*European Commission, Joint Research Centre (JRC), Via E. Fermi 2749, I-21027 Ispra, VA, Italy.*

[4]*ETSI Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid, Ciudad Universitaria s/n, 28040, Madrid, Spain.*

[5]*Natural Resource and Environmental Studies Institute, University of Northern British Columbia, Prince George, Canada.*

[6]*Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94240, 1090 GE, Amsterdam, The Netherlands.*

[7]*Wildlife Conservation Society, Global Conservation Program, Bronx, NY 20460, USA.*

*Correspondence to: m.ward@uq.edu.au

**Abstract**

Land free of direct anthropogenic disturbance is considered essential for achieving biodiversity conservation outcomes but is rapidly eroding. In response, many nations are increasing their protected area estates but little consideration is given to the context of the surrounding landscape. This is despite the fact that connectivity between protected areas is critical in a changing climate and mandated in international protected area targets. By utilizing the latest human pressure assessment, which shows that ~40% of the terrestrial planet is still intact, and a connectivity method, we found just 9.7% of Earth's terrestrial protected network can be considered 'connected'. On average, 11% of each nation's protected area estate is connected via intact land. As the global community commits to bolder action on abating biodiversity loss, only an increased focus on landscape-scale habitat retention and restoration efforts will ensure those critical areas safeguarded for conservation outcomes will remain (or become) connected.

**One Sentence Summary**

Only 9.7% of the global protected area network can be considered 'connected' by intact land.

**Short Title**

Global protected areas are not connected

**Main Text**

Protected areas (PAs) are a core tool in abating the biodiversity crisis (*1*), and their importance is reflected in the 2020 Strategic Plan for Biodiversity (*2*). This international agreement calls for the expansion of the global PA network to cover 17% of terrestrial areas and

5      10% of marine areas by 2020. Crucially, the Strategic Plan stipulates that PA networks must be well-connected, effectively and equitably managed, and also cover ecologically representative areas of particular importance for biodiversity (*2*). Due to their extraordinary importance for biodiversity outcomes, PAs have received substantial research attention in global conservation policy discussions, with recent assessments focusing on how well they are representing species

10     (*3*), their overall management effectiveness (*4*), and how well are they abating key threatening processes (*5*). Yet, to date, reporting has been almost completely blind to how well connected the expanding global PA estate is, with the only substantive research considering connectivity solely through protected land (*6*), disregarding the condition of the wider landscape context.

15     High levels of landscape connectivity is seen as critical for species adaptation under anthropogenic climate change as it allows individuals and populations to track their preferred climatic conditions (*7*). Under projected climate scenarios, it is predicted that many species will need to move further and more rapidly in the 21st century and connected landscapes that facilitate this movement is one of the best conservation responses (*8*, *9*). Connected landscapes allow

20     fundamental ecological mechanisms to operate unimpeded, such as meta-population retention (*10*) and successful dispersal and migration (*11*). Landscape connectivity allows for increased ecosystem function and resilience (*12*) by ensuring nutrient cycling can continue unabated, as well as other important abiotic conditions such as radiation, wind, light regimes, humidity, and

3

key hydrological regimes (*13*, *14*). It is well known that land use activities such as farming,

urbanization, mining, and unsustainable forestry disrupt the connectivity of landscapes to various

degrees (*11*). The retention, and where necessary, restoration of connectivity across a landscape

matrix between protected areas (PAs) is therefore vital for achieving biodiversity goals clearly

5      outlined in the Strategic Plan for Biodiversity (*2*).


Here, we analyze the connectivity of the global terrestrial PA system using measures of

contiguity of intact land (areas largely devoid of high anthropogenic pressures that significantly

alter natural habitat) as a favorable movement pathway between PAs. We determined the

10    connectivity of the global network of PAs by quantifying intact continuous pathways between

PAs. To map intactness, we used the human footprint dataset (HFP), which, at a $1km^2$ resolution,

is the most comprehensive, fine-scale human pressure map available as it takes into account

agricultural lands, roads, railways, human population density, built environments, night-time

lights, and navigable waterways, all of which are driving the species extinction crisis (*15*). We

15    used an updated version of the HFP updated to 2013, which supersedes the published version

dated for 2009 (*16*). Following other studies (*5*, *17*), we defined intact land as that with a human

footprint value <4 out of 50, as this threshold is where anthropogenic activities have significantly

changed the state of land from largely natural in extent to highly modified (*18*). Moreover, this

human pressure threshold is associated with the sharpest declines in mammal movement (*11*) and

20    is one of the strongest predictors of mammal species extinction risk (*19*). For these reasons, we

argue that areas with human pressure above this threshold are unlikely to hold sufficient

connectivity value for many key elements of biodiversity. However, recognizing that there is no

one true level of pressure that prohibits connectivity for all biodiversity (as ecological responses

to human pressure are idiosyncratic), we conducted several sensitivity analyses around this human footprint threshold and found our results were robust to lower and higher human footprint values (table S1 and table S2).

5      Globally, while 41.6% of terrestrial land is intact, only 9.7% of the area under protection can be considered connected through intact landscapes (Fig. 1 and fig. S1). This means that very few PAs have a fully continuous pathway through intact lands, connecting their demarcated edges. At a continental scale, PAs in Oceania are the most connected across all continents (16.7%), followed by the Americas (14.8%). In contrast, Asia (3.3%), Africa (0.4%), and Europe

10    (0.3%) have extremely low levels of PA connectivity provided by intact lands.
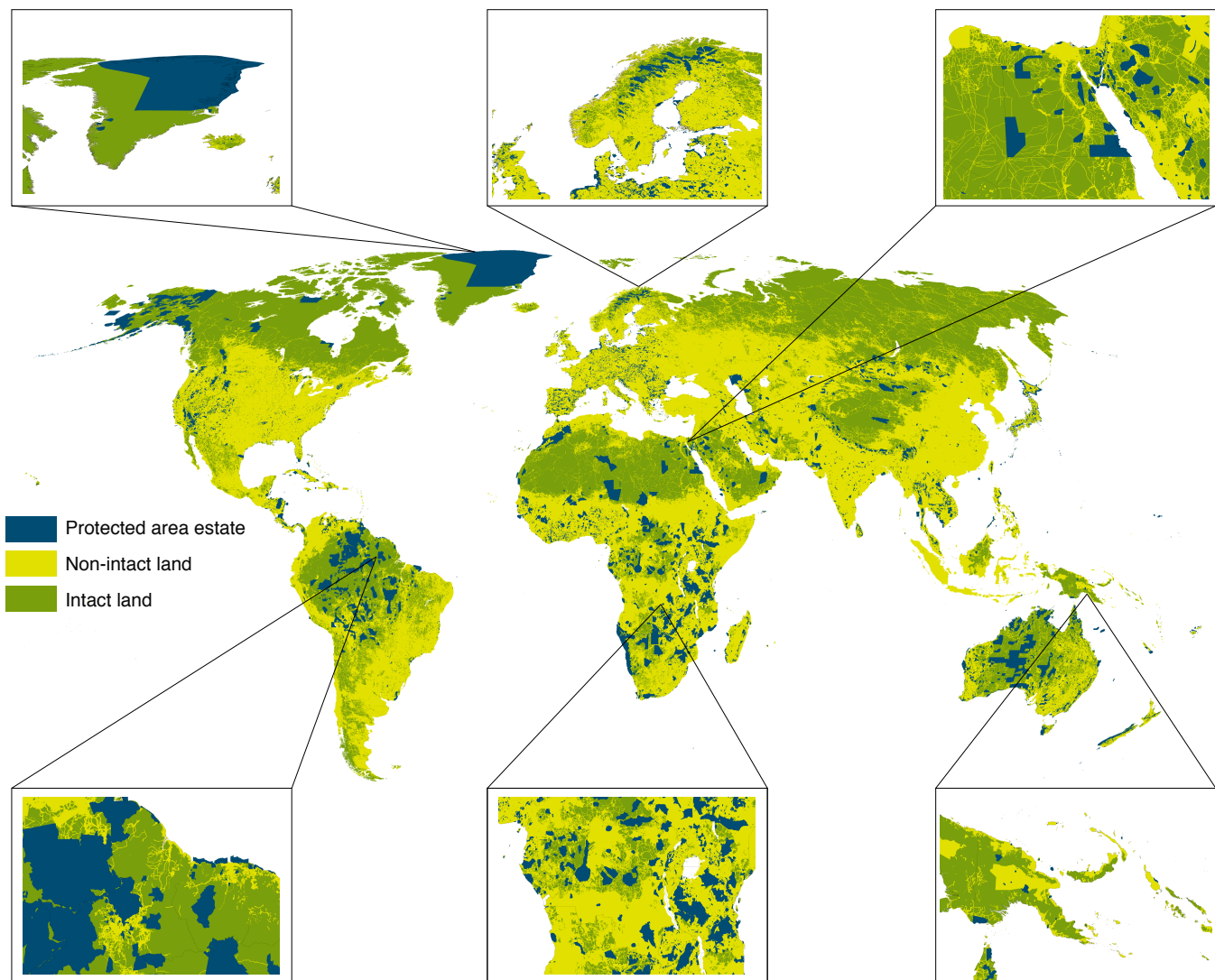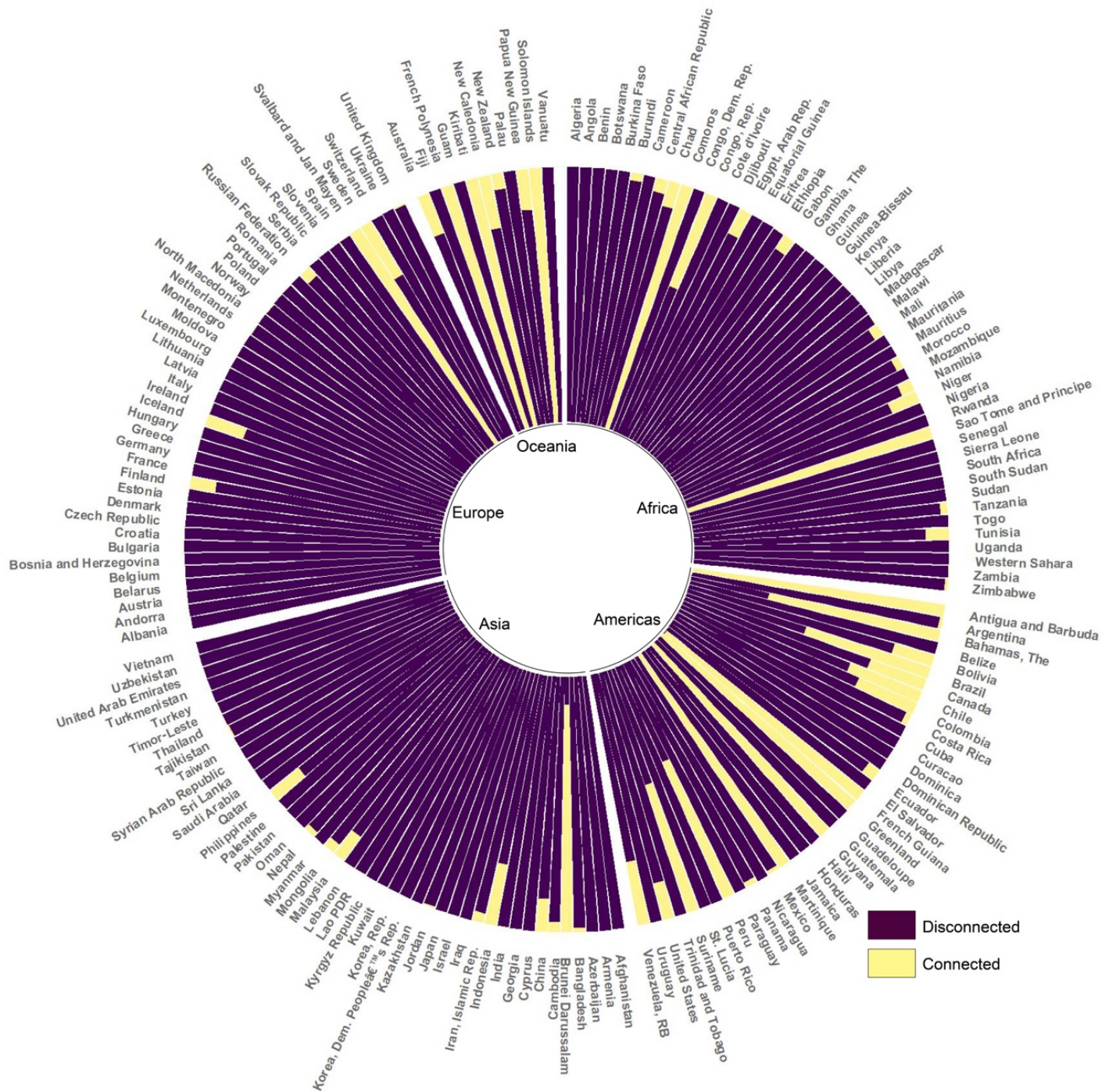
**Fig. 1. Human pressure compromises protected area connectivity.** The spatial distribution of the protected area estate (blue) littered throughout non-intact (yellow) and intact land (green). We provide six fine-scale examples, starting top left and moving clockwise, Greenland, Finland, Egypt, Papua New Guinea, Democratic republic of Congo, and Guyana.

5

At a national scale, the percentage of connected PAs varies enormously (Fig. 2A and fig. S2 to fig. S5). The majority of nations maintain the lowest level of connectivity possible (median connectivity = 0%). These countries are found not just concentrated in Europe (where one would expect minimal presence of low human pressure matrix between PAs) but also across Asia and

5    Africa (table S3) where landscapes are rapidly changing through large-scale infrastructure projects such as roads and agriculture (*20, 21*). This has significant ramifications for international conservation agendas, as many Asian and African countries are megadiverse when it comes to biodiversity (*22, 23*). For example, Vietnam – one of Earth's most biologically diverse countries (*24*), has ~8% protection and no connected PAs based on our analysis, (Fig.

10    2B) yet PA connectivity is likely vital for the persistence of critically endangered species such as saola (*Pseudoryx nghetinhensis*) and Indochinese tiger (*Panthera tigris corbetti*) (*25, 26*). Similarly, Madagascar is home to some of the most genetically-diverse species on Earth, including the black and white ruffed lemur *(Varecia variegata)*, aye-aye *(Daubentonia madagascariensis)*, and fossa *(Crytoprocta forex)*. These genetically-unique species, being

15    predominately arboreal, require contiguous intact landscapes to fulfill their important ecological roles (*27*), yet we found Madagascar only has 4.2% intact land remaining and no fully connected PAs.
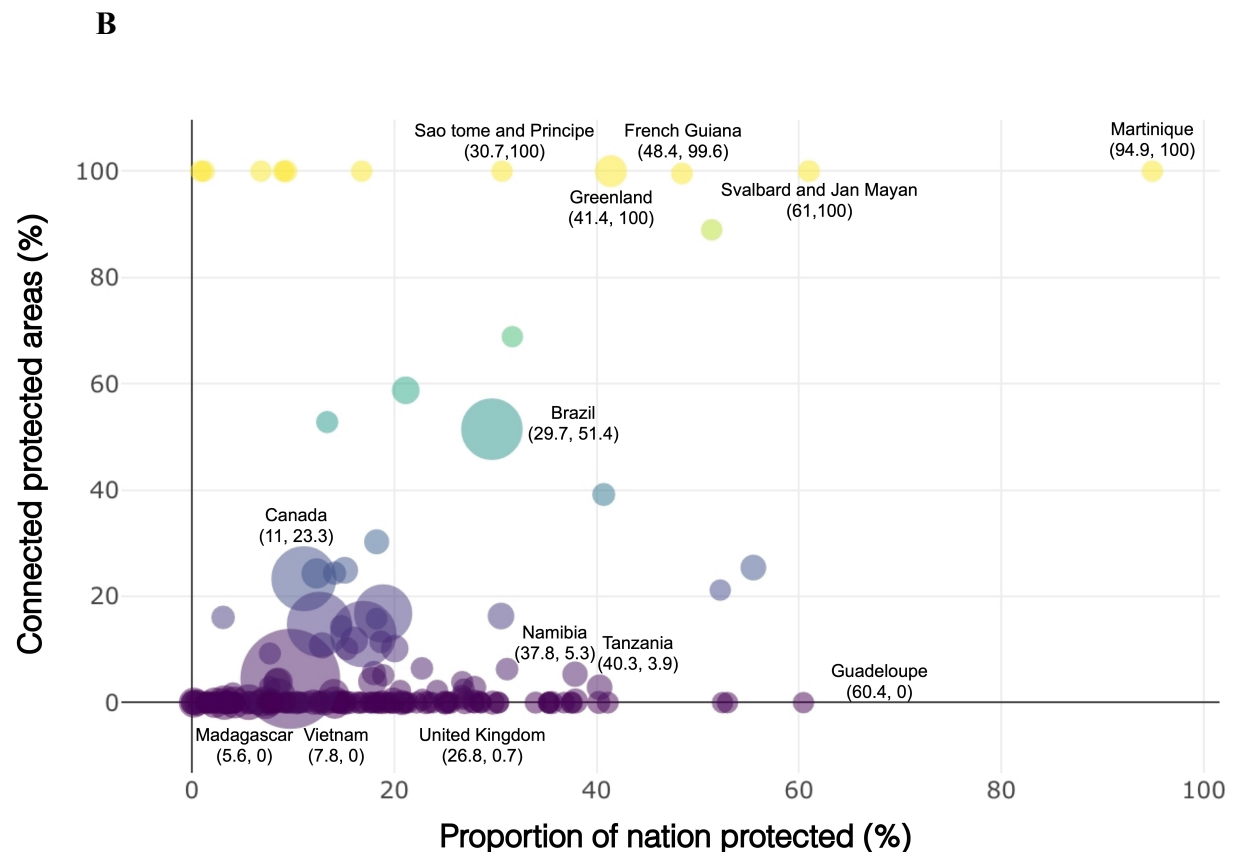
**A**

**Fig. 2. Few nations maintain a connected protected network through intact land. (A)** Proportion of connected and disconnected protected areas for each nation. Countries are grouped per continent. **(B)** The relationship between the proportion of land under protection (x-axis) and the proportion of connected protected areas (y-axis) per country (less connected countries are purple while more connected countries are yellow). The size of the bubble indicates the size of the country.

Only nine (4.6%) countries have >17% of their land protected (which many nations

define as their contributions to the CDB PA target) (*28*) and maintain >50% connectivity across

their PA network (Fig. 3). These countries with high proportions of land under protection have

statistically significant correlations with higher proportions of connected PAs ($\rho=0.28$, n=183,

5        p<0.05). We found no significant relationship between countries with high proportions of the

protected land connected and the number of PAs ($\rho=0.00$, n=183, p>0.05) or the size of the

country ($\rho=0.04$, n=183, p>0.05). This indicates that connectivity may not be considered when

nations are adding to their PA estates. For the more intact countries, it may be because they

declare fewer but larger PAs, while more human-modified countries (such as those in Europe)

10       declare many small PAs that are usually surrounded by a non-intact matrix.
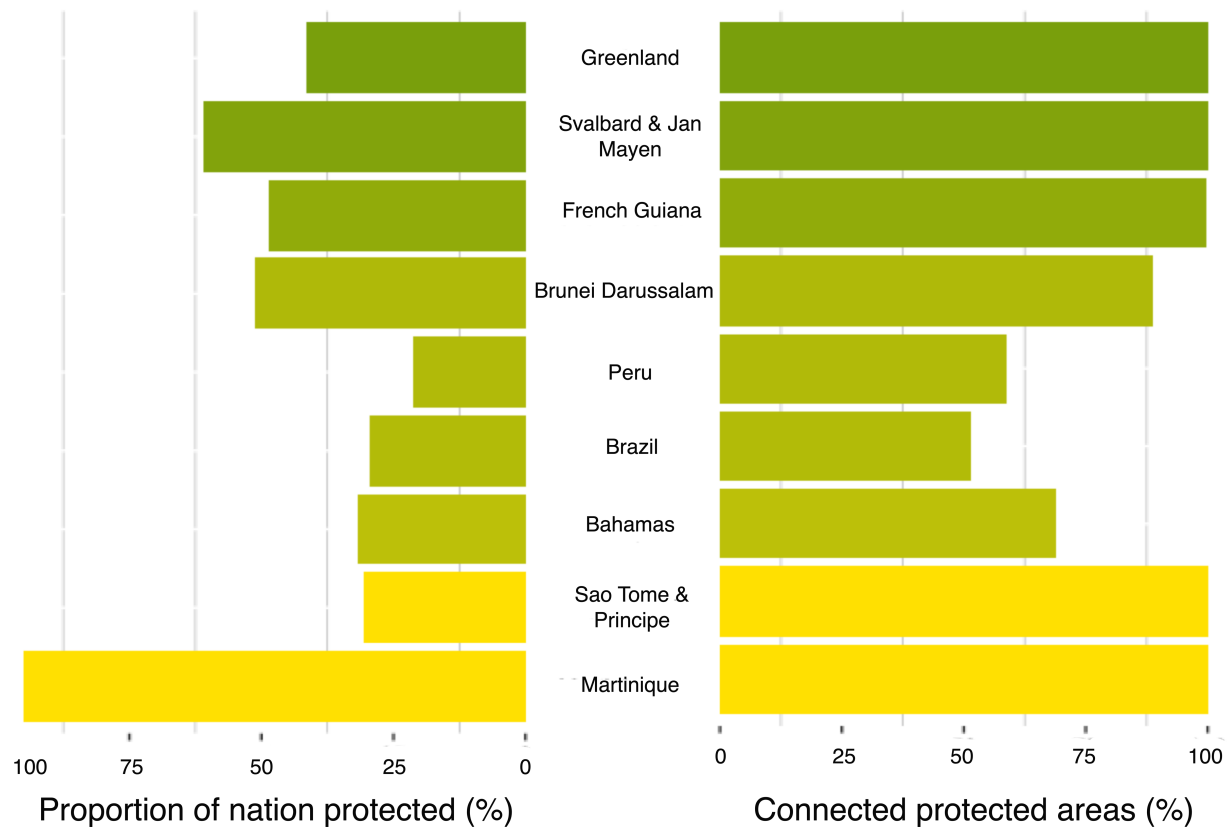
**Fig. 3. Examples of countries with high proportions of land protected and connected protected areas.** Only nine countries protect >17% of land (left) and maintain >50% connected protected areas (right). Countries are ordered based on the highest proportion of remaining intact land (less intact countries are yellow, while more intact countries are green).

Eighteen countries have >50% of their land that can be considered intact, yet have very low connectivity between their PAs (Fig. 4 and fig. S6 to fig. S7). For example, our analysis revealed that Egypt has 77.1% intact land, but only 10.7% of its PA network is connected. Even though there are large PAs within this nation, including El-Gelf El-Keber (48,523km$^2$) and Elba (36,600km$^2$), major roads, agriculture, and urban sprawl are increasingly fragmenting the landscapes (*29*).
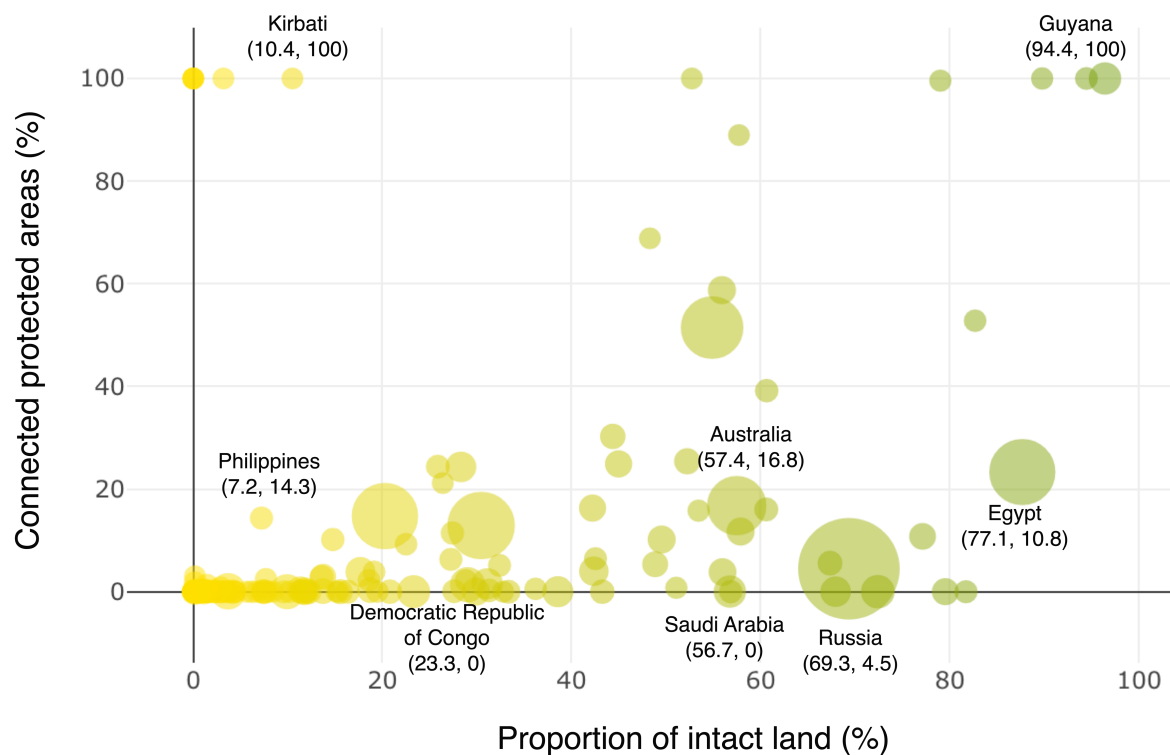
5

10

**Fig 4. The relationship between the proportion of land that can be considered intact per country and the proportion of connected protected areas.** Scatterplot showing the relationship between proportion of intact land (less intact countries are yellow, while more intact countries are green) and proportion of connected protected areas per country. The size of the bubble indicates the size of the country.

The vast majority (76.4%) of countries have very few intact landscapes remaining and low proportions of connected PAs. These include surprising examples such as the Democratic Republic of Congo (DRC), which we found to have 23% intact land and no connected PAs. Much of the PA network within the DRC is scattered across the country, disconnected by

5 agricultural lands, urban areas, and mines. In addition to the 149 countries that have low proportions of both intact landscapes and few connected PAs, there are also 13 countries that do not have any remaining intact landscapes and therefore no connectivity between PAs. Statistically, countries with low proportions of intact land also have significantly lower connected PAs (Spearman's p=0.40, n=183, p<0.05; Eigenvalue 1.37, Eigenvalue 0.62).

10

Our results show that while many countries are meeting the areal component of global PA targets, much of this PA estate is not connected through non-modified habitat pathways. This suggests that the overall strategic goal of overcoming biodiversity loss will be likely compromised without increased focused on wider land-use efforts to retain and restore habitats

15 beyond PA boundaries. Any plan for maintaining and restoring ecosystem connectivity between protected areas must include a clear focus on retention strategies for the remaining ecosystems that are currently not degraded because these places are, by definition, areas of high connectivity and known to hold exceptional value (*11*, *30*). It is also well accepted that avoiding degradation of habitat (and hence loss of connectivity) is a far better strategy than attempting restoration after

20 it is lost. Restoration is more costly, riskier, and unlikely to lead to a full recovery of connectivity values (*31*). For Earth's remaining intact, connected ecosystems to be retained, they must be formally recognized, prioritized in spatial plans, then placed under effective management so they are protected from human impacts. Opportunities to recognize and conserve intact lands that help

retain connectivity are expanding beyond areas in strict protected areas. For example, a definition for 'other effective area-based conservation measures' (OECMs) was agreed by nations in November 2018, with the objective to "…achieve positive and sustained long-term outcomes for the in-situ conservation of biodiversity, with associated ecosystem functions and

5     services and where applicable, cultural, spiritual, socio–economic, and other locally relevant values" (*32*). The global extent of OECMs is expected to increase rapidly over the coming years (*33*). As such, their use, if planned and implemented well, could play an enormous role in keeping connectivity between PAs.

10    But our findings show that even if humanity was successful in halting the degradation of all remaining intact ecosystems, there would be many PAs isolated given their surrounding matrix has already been highly altered. As such, there is also the need for a broad, transboundary restoration agenda to rapidly increase connectivity between those lands set aside for conservation. There is clearly appetite for such bold restoration action, with the UN recently

15    declaring the 'Decade on Ecosystem Restoration' (*34*), by which 350 million hectares of degraded land will be restored between now and 2030. We argue that these types of restoration goals should be framed within a broader connectivity agenda and specifically planned to maximize the quality of the landscape matrix between those PAs essential to biodiversity outcomes. As restoration of less degraded natural ecosystems presents some of the most cost-

20    effective restoration opportunities (*35*) and lowest potential for conflicts with other priorities (such as agriculture), it is essential to incorporate the cost of such restoration to other societal goals when planning for restoration action.

Our results highlight the need for a far more comprehensive reporting framework on area-based conservation that captures not just the extent and overall effectiveness of local implementation of conservation activities but also how connected these PA networks are within the wider landscape. As the relationship between the placement of area-based conservation activities, how they are managed, and the wider landscape context is nuanced, simple metrics on connectivity must be integrated with other assessments of PA effectiveness. For example, while Venezuela is currently achieving 55.5% protection, we found very little connectivity between PAs. This may not be a poor result, as the PA estate within Venezuela seem to be extremely large, well-managed, and representative (*36*). Other nations may have low proportional connectivity because their PAs have been established in human-dominated landscapes, which are often where much conservation action must occur. This type of reactive conservation strategy is clearly necessary for countries that have degraded, but ecologically important, landscapes (*37*). In contrast, some nations that have good connectivity scores could be hiding inherent biases in PA placement. For example, Australia is achieving ~17% connectivity via our assessment and has ~19% of its land under protection, which could be considered a relatively good outcome. Yet upon closer inspection, most new PAs have been placed in the desert ecosystems, which do not adequately represent all taxonomic groups and are already over-represented in the nation's PA estate (*38*). In addition, most Australian PAs are also not effectively managed, with 1,390 threatened species continuing to lose critical threatened species habitat inside and outside PAs (*39*, *40*). The numbers around PA connectivity alone can hide important issues but there are now methodologies that capture quality, extent, and connectedness of landscapes (*17*) and it should be possible for nations to transform these into a framework that holistically assesses the overall effectiveness of area-based conservation action.

We note that in some cases, a low proportional connectivity score between PAs may be a reasonable outcome. This is likely the case in some parts of Europe, where small-scale efforts to create corridors between PAs may not be captured at the $1km^2$ resolution of our analysis. In

5    addition, areas of high pressure in the matrix between PAs may be acceptable for some species that have co-existed with human-modified landscapes for centuries. But as most species, especially those that are endangered, cannot persist in human-dominated landscapes (*11, 19*), our results provide a sobering assessment.

10    Well managed PAs and retaining and restoring intact landscapes that surround them are critical to abating the biodiversity crisis. Right now, the majority of PAs are isolated by a matrix of rapidly eroding intact habitat and are unlikely to be effective, especially in a time of anthropogenic climate change. Our results show that urgent change in how nations protect and restore landscape-scale habitat is crucial as the international community gears up to embrace a

15    new global biodiversity framework post-2020.

20

**Materials and Methods:**

We determined the connectivity of the global network of protected areas by quantifying

intact continuous pathways (areas largely devoid of high anthropogenic pressures) between

protected areas.

5

Protected areas

Data on protected area location and boundary were obtained from the May 2019 World

Database of Protected Areas (WDPA) (*41*). We only considered protected areas that had a land

area of at least 10 km$^2$. As China removed most of its protected areas from the public May 2018

10    WDPA version, we used the April 2018 WDPA for China only, which contained the full set of

Chinese protected areas at the time. It is important to note that our statistics may differ from

those reported by countries due methodologies and datasets differences used to measure

terrestrial area of a country or territory.

15    Measure of human pressure

We used the latest global terrestrial human footprint maps – a cumulative index of eight

variables measuring human pressure on the global environment – to calculate the average human

pressure between protected areas. The Human Footprint 2013 map uses the following variables:

1) the extent of built human environments, 2) population density, 3) electric infrastructure, 4)

20    crop lands, 5) pasture lands, 6) roads, 7) railways, and 8) navigable waterways. Each human

pressure is scaled from 0-10, then weighted within that range according to estimates of their

relative levels of human pressure following Sanderson et al., 2012. The resulting standardized

pressures were then summed together to create the standardized Human Footprint maps for all non-Antarctic land areas *(16)*.

Within the main manuscript, we defined intact land as any 1km$^2$ pixel with a human footprint value not higher than 4, not including the value 4. Within this threshold, all areas with a human footprint score higher than 4 are defined as non-intact. While previous analyses showed that a >4 score is a key threshold above which species extinction risk greatly increases *(19)*, we recognized that there is no one true threshold which impacts all species equally. Some species may require no human pressure to successfully disperse, while others might successfully navigate through more intensively modified landscapes. Therefore, we conducted out analyses for two additional human footprint thresholds. The first used a human footprint score <1 and the second incorporated all areas with a human footprint <10.

Probability of Connectivity

The Probability of Connectivity network-based metric underlies the analysis performed *(6)*, with adaptations to account for connectivity provided by intact lands. Probability of Connectivity is given by the following formula:

$$PC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j p_{ij}^*}{A_L^2} \qquad (1)$$

where n is the total number of protected areas (PAs) in the study area (i.e. continent or country), $a_i$ is the total area of PA i, $p_{ij}^*$ is the maximum product probability between protected areas i and j, and $A_L$ is the total area of the study area. The maximum product probability ($p_{ij}^*$) considers both direct connections (movement from i to j without using any other intermediate PA in the network) and indirect connections (movement from i to j facilitated by one or several other

19

intermediate PAs). The maximum product probability ($p^*_{ij}$) is calculated through network analysis using the values of the direct dispersal probabilities between nodes ($p_{ij}$). It holds that $p^*_{ij} \geq p_{ij}$. Both probabilities will be equal when the direct movement is the most favorable (probable) pathway between i and j. $p^*_{ij}$ will be larger than $p_{ij}$ when intermediate stepping stones increase the connectivity between i and j beyond what possible by using only the direct connection between them (*42,43,44*). In this analysis, $p_{ij}$=1 when protected area i and j are connected (edge to edge) by a continuous pathway of intact land and $p_{ij}$=0 if not. Two protected areas may not be directly connected by intact lands (hence having $p_{ij}$=0), but may be connected through an intermediate stepping-stone protected areas, which would give $p^*_{ij}$=1.

## Connectivity between protected areas

The Probability of Connectivity (PC) metric accounts for both intra-PA (i=j) and inter-PA area (i≠j) connectivity, which is respectively given by the intra-PA (PCintra) and inter-PA (PCinter) components of PC as follows:

$$PC = PCintra + PCinter$$

$$PCintra = \frac{\sum_{i=1}^{n}\sum_{j=1,i=j}^{n} a_i a_j p^*_{ij}}{A_L^2} = \frac{\sum_{i=1}^{n} a_i^2}{A_L^2} \qquad (2)$$

$$PCinter = \frac{\sum_{i=1}^{n}\sum_{j=1,i\neq j}^{n} a_i a_j p^*_{ij}}{A_L^2}$$

We focused on the inter-PA connectivity, given by PCinter. PCinter is defined as the probability that two points randomly located in two different PAs within the study area (therefore considering only the cases where i≠j) are connected to each other via intact habitat. We

calculated PCinter using two scenarios: PCinter_ intact and PCinter_all. PCinter_intact is the value when considering that only the intact lands provide connectivity between PAs. PCinter_all is the value when any land (all land, intact, or not) provides connectivity between PAs, i.e. considering that two protected areas are connected when they are located in the same land mass

5          or island. This analysis (PCinter_all) provided us with the maximum terrestrial protected area connectivity that could be theoretically achieved in a country or continent if all of its land was intact.  In both scenarios, an 8-neighbouhood rule between land cells was used when defining the continuity of land (using the 1 km$^2$ resolution of the human footprint layer).


10          Connectivity provided by intact lands: ConnIntact

We combined PCinter_intact and PCinter_all, as defined above, to obtain ConnIntact, which quantifies the percentage of the protected are system that is connected through intact pathways. It is calculated using the following ratio:

$$\text{ConnIntact} = 100\frac{\text{PCinter\_intact}}{\text{PCinter\_all}} \qquad (3)$$

15

Which, given the equation for PCinter above, can be expressed as:

$$\text{ConnIntact} = \frac{\sum_{i=1}^{n}\sum_{j=1,i\neq j}^{n} a_i a_j p_{\text{INTACT}ij}^*}{\sum_{i=1}^{n}\sum_{j=1,i\neq j}^{n} a_i a_j p_{\text{ALL}ij}^*} \qquad (4)$$

20          where $p_{\text{INTACT}}$ refers to the maximum product probabilities when only the intact lands provide connectivity between protected areas, and $p_{\text{ALL}}$ refers to the maximum product probabilities when all land would be intact and hence would provide the highest possible connectivity between protected areas. As noted above, n is the total number of protected areas in the study

21

area (e.g. a country or continent), and $a_i$ is the attribute of protected area i. ConnIntact provides

the percentage of the protected area network that is connected by intact lands. This metric is

expressed as percentage of the total area under protection.

5

**References and Notes:**

1. C. L. Gray, S. L. L. Hill, T. Newbold, L. N. Hudson, L. Boïrger, S. Contu, A. J. Hoskins, S. Ferrier, A. Purvis, J. P. W. Scharlemann, Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nat. Commun.* **7**, 12306 (2016).

2. Convention on Biological Diversity, "COP 10 Decision X/2. Strategic plan for biodiversity 2011–2020," 10th Meeting of the Conference of the Parties to the Convention on Biological Diversity, Nagoya, Japan, 18 to 19 October 2010.

3. A. S. L. Rodrigues, S. J. Andelman, M. I. Bakarr, L. Boitani, T. M. Brooks, R. M. Cowling, L. D. C. Fishpool, G. A. B. Da Fonseca, K. J. Gaston, M. Hoffmann, J. S. Long, P. A. Marquet, J. D. Pilgrim, R. L. Pressey, J. Schipper, W. Sechrest, S. N. Stuart, L. G. Underhill, R. W. Waller, M. E. J. Watts, X. Yan, Effectiveness of the global protected area network in representing species diversity. *Nature*. **428**, 640–643 (2004).

4. L. Coad, J. E. M. Watson, J. Geldmann, N. D. Burgess, F. Leverington, M. Hockings, K. Knights, M. Di Marco, Widespread shortfalls in protected area resourcing undermine efforts to conserve biodiversity. *Front. Ecol. Environ.* **17**, 259–264 (2019).

5. K. R. Jones, O. Venter, R. A. Fuller, J. R. Allan, S. L. Maxwell, P. J. Negret, J. E. M. Watson, One-third of global protected land is under intense human pressure. *Science.* **360**, 788–791 (2018).

6. S. Saura, B. Bertzky, L. Bastin, L. Battistella, A. Mandrici, G. Dubois, Protected area connectivity: Shortfalls in global targets and country-level priorities. *Biol. Conserv.* **219**, 53–67 (2018).

7. J. F. McLaughlin, J. J. Hellmann, C. L. Boggs, P. R. Ehrlich, Climate change hastens

population extinctions. *Proc. Natl. Acad. Sci. U. S. A.* **99**, 6070–6074 (2002).

8. N. E. Heller, E. S. Zavaleta, Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biol. Conserv.* **142**, 14–32 (2009).

9. C. A. Schloss, T. A. Nuñez, J. J. Lawler, Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 8606–8611 (2012).

10. P. Opdam, Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landsc. Ecol.* **5**, 93–106 (1991).

11. M. A. Tucker, K. Böhning-Gaese, W. F. Fagan, J. M. Fryxell, B. Van Moorter, S. C. Alberts, A. H. Ali, A. M. Allen, N. Attias, T. Avgar, H. Bartlam-Brooks, B. Bayarbaatar, J. L. Belant, A. Bertassoni, D. Beyer, L. Bidner, F. M. van Beest, S. Blake, N. Blaum, C. Bracis, D. Brown, P. J. N. de Bruyn, F. Cagnacci, J. M. Calabrese, C. Camilo-Alves, S. Chamaillé-Jammes, A. Chiaradia, S. C. Davidson, T. Dennis, S. DeStefano, D. Diefenbach, I. Douglas-Hamilton, J. Fennessy, C. Fichtel, W. Fiedler, C. Fischer, I. Fischhoff, C. H. Fleming, A. T. Ford, S. A. Fritz, B. Gehr, J. R. Goheen, E. Gurarie, M. Hebblewhite, M. Heurich, A. J. M. Hewison, C. Hof, E. Hurme, L. A. Isbell, R. Janssen, F. Jeltsch, P. Kaczensky, A. Kane, P. M. Kappeler, M. Kauffman, R. Kays, D. Kimuyu, F. Koch, B. Kranstauber, S. LaPoint, P. Leimgruber, J. D. C. Linnell, P. López-López, A. C. Markham, J. Mattisson, E. P. Medici, U. Mellone, E. Merrill, G. de Miranda Mourão, R. G. Morato, N. Morellet, T. A. Morrison, S. L. Diaz-Muñoz, A. Mysterud, D. Nandintsetseg, R. Nathan, A. Niamir, J. Odden, R. B. O, Hara, L. G. R. Oliveira-Santos, K. A. Olson, B. D. Patterson, R. de Paula, L. Pedrotti, B. Reineking, M. Rimmler, T. L. Rogers, C. M. Rolandsen, C. S. Rosenberry, D. I. Rubenstein, K. Safi, S. Saiid, N. Sapir,

H. Sawyer, N. M. Schmidt, N. Selva, A. Sergiel, E. Shiilegdamba, J. P. Silva, N. Singh, E. J. Solberg, O. Spiegel, O. Strand, S. Sundaresan, W. Ullmann, U. Voigt, J. Wall, D. Wattles, M. Wikelski, C. C. Wilmers, J. W. Wilson, G. Wittemyer, F. Zik eba, T. Zwijacz-Kozica, T. Mueller, Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science.* **359**, 466–469 (2018).

12.    J. Lundberg, F. Moberg, Mobile Link Organisms and Ecosystem Functioning: Implications for Ecosystem Resilience and Management. *Ecosystems*. **6**, 87–98 (2003).

13.    N. M. Haddad, L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D. X. Song, J. R. Townshend, Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, 1–10 (2015).

14.    D. A. Saunders, R. J. Hobbs, C. R. Margules, Biological Consequences of Ecosystem Fragmentation: A Review. *Conserv. Biol.* **5**, 18–32 (1991).

15.    S. L. Maxwell, R. A. Fuller, T. M. Brooks, J. E. M. Watson, Biodiversity: The ravages of guns, nets and bulldozers. *Nature*. **536**, 143–145 (2016).

16.    O. Venter, E. W. Sanderson, A. Magrach, J. R. Allan, J. Beher, K. R. Jones, H. P. Possingham, W. F. Laurance, P. Wood, B. M. Fekete, M. A. Levy, J. E. M. Watson, Global terrestrial Human Footprint maps for 1993 and 2009. *Sci. Data*. **3**, 160067 (2016).

17.    H. L. Beyer, O. Venter, H. S. Grantham, J. E. M. Watson, Substantial losses in ecoregion intactness highlight urgency of globally coordinated action. *Conserv. Lett.*, 1–9 (2019).

18.    J. E. M. Watson, K. R. Jones, R. A. Fuller, M. Di Marco, D. B. Segan, S. H. M. Butchart, J. R. Allan, E. McDonald-Madden, O. Venter, Persistent Disparities between Recent Rates of Habitat Conversion and Protection and Implications for Future Global Conservation Targets. *Conserv. Lett.* **9**, 413–421 (2016).

19.    M. Di Marco, O. Venter, H. P. Possingham, J. E. M. Watson, Changes in human footprint drive changes in species extinction risk. *Nat. Commun.* **9**, 4621 (2018).

20.    W. F. Laurance, M. J. Campbell, M. Alamgir, M. I. Mahmoud, Road expansion and the fate of Africa's tropical forests. *Front. Ecol. Evol.* **5**, 1–7 (2017).

21.    C. Sudhakar Reddy, K. R. L. Saranya, S. Vazeed Pasha, K. V Satish, C. S. Jha, P. G. Diwakar, V. K. Dadhwal, P. V. N. Rao, Y. V. N. Krishna Murthy, Assessment and monitoring of deforestation and forest fragmentation in South Asia since the 1930s. *Glob. Planet. Change*. **161**, 132–148 (2018).

22.    F. Andreone, A. I. Carpenter, N. Cox, L. Du Preez, K. Freeman, S. Furrer, G. Garcia, F. Glaw, J. Glos, D. Knox, J. Köhler, J. R. Mendelson, V. Mercurio, R. A. Mittermeier, R. D. Moore, N. H. C. Rabibisoa, H. Randriamahazo, H. Randrianasolo, N. R. Raminosoa, O. R. Ramilijaona, C. J. Raxworthy, D. Vallan, M. Vences, D. R. Vieites, C. Weldon, The challenge of conserving amphibian megadiversity in Madagascar. *PLoS Biol.* **6**, 0943–0946 (2008).

23.    G. Ceballos, P. R. Ehrlich, J. Soberón, I. Salazar, J. P. Fay, Ecology: Global mammal conservation: What must we manage? *Science.* **309**, 603–607 (2005).

24.    IUCN, Increase connectivity between protected areas: A key solution to conserve biodiversity in Vietnam, (International Union for Conservation of Nature, Switzerland,

2008).

25. A. J. Lynam, Securing a future for wild Indochinese tigers: Transforming tiger vacuums into tiger source sites. *Integr. Zool.* **5**, 324–334 (2010).

26. R. Stone, The Saola's Last Stand. *Nature*. **314**, 1380–1383 (2006).

27. C. Schwitzer, R. A. Mittermeier, S. E. Johnson, G. Donati, M. Irwin, H. Peacock, J. Ratsimbazafy, J. Razafindramanana, E. E. Louis, L. Chikhi, I. C. Colquhoun, J. Tinsman, R. Dolch, M. Lafleur, S. Nash, E. Patel, B. Randrianambinina, T. Rasolofoharivelo, P. C. Wright, Conservation. Averting lemur extinctions amid Madagascar's political crisis. *Science*. **343**, 842–843 (2014).

28. S. H. M. Butchart, M. Clarke, R. J. Smith, R. E. Sykes, J. P. W. Scharlemann, M. Harfoot, G. M. Buchanan, A. Angulo, A. Balmford, B. Bertzky, T. M. Brooks, K. E. Carpenter, M. T. Comeros-Raynal, J. Cornell, G. F. Ficetola, L. D. C. Fishpool, R. A. Fuller, J. Geldmann, H. Harwell, C. Hilton-Taylor, M. Hoffmann, A. Joolia, L. Joppa, N. Kingston, I. May, A. Milam, B. Polidoro, G. Ralph, N. Richman, C. Rondinini, D. B. Segan, B. Skolnik, M. D. Spalding, S. N. Stuart, A. Symes, J. Taylor, P. Visconti, J. E. M. Watson, L. Wood, N. D. Burgess, Shortfalls and Solutions for Meeting National and Global Conservation Area Targets. *Conserv. Lett.* **8**, 329–337 (2015).

29. A. Alfiky, G. Kaule, M. Salheen, Agricultural Fragmentation of the Nile Delta; A Modeling Approach to Measuring Agricultural Land Deterioration in Egyptian Nile Delta. *Procedia Environ. Sci.* **14**, 79–97 (2012).

30. J. E. M. Watson, T. Evans, O. Venter, B. Williams, A. Tulloch, C. Stewart, I. Thompson, J. C. Ray, K. Murray, A. Salazar, C. McAlpine, P. Potapov, J. Walston, J. G. Robinson,

M. Painter, D. Wilkie, C. Filardi, W. F. Laurance, R. A. Houghton, S. Maxwell, H. Grantham, C. Samper, S. Wang, L. Laestadius, R. K. Runting, G. A. Silva-Chávez, J. Ervin, D. Lindenmayer, The exceptional value of intact forest ecosystems. *Nat. Ecol. Evol.* **2**, 599–610 (2018).

31. J. M. Rey Benayas, A. C. Newton, A. Diaz, J. M. Bullock, Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science*. **325**, 1121–1124 (2009).

32. IUCN-WCPA, "Guidelines for Recognizing and ReporƟng Other Effective Area-based Conservation Measures: First Version," (International Union for Conservation of Nature, Switzerland, 2017).

33. N. Dudley, H. Jonas, F. Nelson, J. Parrish, A. Pyhälä, S. Stolton, J. E. M. Watson, The essential role of other effective area-based conservation measures in achieving big bold conservation targets. *Glob. Ecol. Conserv.* **15**, e00424 (2018).

34. United Nations Environment Program, "UN Decade on Ecosystem Restoration (2018)," (United Nations, Switzerland, 2018).

35. R. Maggini, H. Kujala, M. Taylor, J. Lee, H. Possingham, B. Wintle, R. Fuller, "Protecting and restoring habitat to help Australia's threatened species adapt to climate change," (National Climate Change Adaptation Research Facility, 2013).

36. L. Cantú-Salazar, K. J. Gaston, Very Large Protected Areas and Their Contribution to Terrestrial Biological Conservation. *Bioscience*. **60**, 808–818 (2010).

37. M. Schröter, R. Kraemer, S. Ceauşu, G. M. Rusch, Incorporating threat in hotspots and coldspots of biodiversity and ecosystem services. *Ambio*. **46**, 756–768 (2017).

38.   J. E. M. Watson, M. C. Evans, J. Carwardine, R. A. Fuller, L. N. Joseph, D. B. Segan, M. F. J. Taylor, R. J. Fensham, H. P. Possingham, The Capacity of Australia's Protected-Area System to Represent Threatened Species. *Conserv. Biol.* **25**, 324–332 (2011).

39.   C. N. Cook, R. S. Valkan, M. B. Mascia, M. A. McGeoch, Quantifying the extent of protected-area downgrading, downsizing, and degazettement in Australia. *Conserv. Biol.* **31**, 1039–1052 (2017).

40.   M. S. Ward, J. S. Simmonds, A. E. Reside, J. E. M. Watson, J. R. Rhodes, H. P. Possingham, J. Trezise, R. Fletcher, L. File, M. Taylor, Lots of loss with little scrutiny: The attrition of habitat critical for threatened species in Australia. *Conserv. Sci. Pract.*, **1**, e117 (2019).

10   The human footprint data are available for download from

https://datadryad.org/stash/dataset/doi:10.5061/dryad.052q5 , protected-area data (2019 version) are available for download from www.protectedplanet.net by request. All other data needed to evaluate the conclusions in the paper are present in the paper or the supplementary materials.


15   **Supplementary Materials**

Materials and Methods

Table S1 – S3

Fig S1 – S7