



Short communication

# Current overlapping distribution of megaherbivores and top predators: An approach to the last terrestrial areas with ecological integrity

Jose María Gil-Sánchez<sup>a,\*</sup>, Mariola Sánchez-Cerdá<sup>b</sup>

<sup>a</sup> Departamento de Zoología, Universidad de Granada, Avda. de Fuente Nueva, s/n, 18071 Granada, Spain

<sup>b</sup> Conservation and Evolutionary Genetics Group, Estación Biológica de Doñana (EBD-CSIC), Avda. Americo Vespucio 26, 41092 Seville, Spain

## ARTICLE INFO

## Keywords:

Ecosystem functionality  
Extinction  
Key species  
Wildlife conservation  
Wildlife mapping

## ABSTRACT

The Earth's wildlife is facing a new, fast and huge extinction process due to the impact of humans. This scenario not only affects the biodiversity itself but also the capacity of the ecosystems to retain their structure and functions. The roles of megaherbivores and top predators are crucial for ecosystem ecological integrity and key in many eco-evolutionary processes. We provide a global overview of the current ecological integrity of terrestrial surfaces, built through an inventory of the areas that still preserve their integral community of megaherbivores and top predators. The targeted species were the taxa present during the upper Holocene, which represents the ecological scenario before the current biodiversity crisis caused by humans. We established the ecosystem's ecological integrity by mapping the areas where all targeted taxa are currently present. We used the maps provided by the Red List of the International Union for Conservation of Nature and the information obtained through a bibliography review for the former distribution ranges to build the cartography. We identified 81 areas with a full community of megaherbivores and top predators, most of which are very small in size (<10,000 km<sup>2</sup>). Only eco-regions that have the lowest species diversity have large patches of ecological integrity, mostly overlapping with large areas of Intact Forest Landscapes. Overall, 15.8 % of the Earth's terrestrial surfaces currently retain their target taxa. Our results are an important complement for the available maps of ecosystem ecological integrity, since we offer a detailed global inventory of key areas for conservation of functional wildlife.

## 1. Introduction

The Earth's biodiversity is facing a new, fast, and huge extinction process due to human development. Conservation Biology is a scientific discipline that aims to equilibrate human needs and wildlife conservation. Its key goal is to preserve not only the biodiversity itself (i.e. the species richness) but also the evolutionary scenarios that rule the ecosystems. Unfortunately, global ecosystems are severely impacted by human activities and, for many countries, only scattered well-preserved small patches are present in the best cases (Plumptre et al., 2019, 2021). This scenario severely affects the ecosystem's ecological integrity, which is defined as the capacity of the system to retain the structure and functions through processes and elements characteristic for its eco-region (Dorren et al., 2004). Some maps of the global conservation status of Earth's eco-regions are available, being the most recent approaches built on the number of extinct faunal species or on intact habitat estimates, specifically "Intact Forest Landscapes" and "Last of the Wild" areas (Plumptre et al., 2019, 2021), based on the overlay of

the latest human footprint map (Venter et al., 2016) on the most recent map of the world's eco-regions (Dinerstein et al., 2017). However, to our knowledge, there is a lack of a global map of the ecosystem ecological integrity, specifically based on the persistence of some key faunal elements for the ecological functions and the evolutionary processes, as is the case of megaherbivores and top predators. Megaherbivores (e.g. elephants) are capable of transforming the vegetation at the landscape level as engineer species (Barnosky et al., 2015), whereas top predators (e.g. lions) can regulate herbivore populations and play a crucial role in several evolutionary processes (Ripple et al., 2014; a synthesis of the main eco-evolutionary roles of present and past (Pleistocene) megafauna can be consulted in Galetti et al., 2018). In fact, the role of both groups of fauna is essential for the understanding of the Green World Hypothesis postulated in 1960 by Hairston, Smith and Slobodkin (Hairston et al., 1960), which "may be the ecologist's only parallel to Albert Einstein's thought experiments in physics" (Steneck, 2005). The relevance of megaherbivores and top predators in this hypothesis, and in its alternative Plant Self-Defense Hypothesis (Murdoch, 1966), is so

\* Corresponding author.

E-mail address: [jmgilsanchez@yahoo.es](mailto:jmgilsanchez@yahoo.es) (J.M. Gil-Sánchez).

<https://doi.org/10.1016/j.biocon.2022.109848>

Received 9 July 2022; Received in revised form 28 November 2022; Accepted 3 December 2022

Available online 26 December 2022

0006-3207/© 2022 Elsevier Ltd. All rights reserved.

central in science that it led J. Terborgh to write: “If humans complete the process of exterminating these guilds worldwide, ecology will irrevocably become the science of human artifacts” (Terborgh, 2005).

Here, we offer a global view of the current terrestrial surfaces that preserve ecological integrity, through mapping of the areas where both guilds, megaherbivores and top predators, are still fully complete, at both continent and country levels. Our result brings, therefore, a comprehensive overview, not only for the scientific community, but also for the politicians and practitioners that manage the conservation of wildlife in practice.

## 2. Methods

We have studied the modern mammalian communities that resulted after the post-glacial extinctions. Therefore, we selected the taxa present during the upper Holocene, in particular along the Meghalayan age (4200 BP), which includes one extinct species in the XVII century, the auroch (*Bos primigenius*). Following Owen-Smith (1989), as megaherbivores we have included the mammal species weighing >1000 kg (nine species). For the eco-regions lacking taxa within this size class, we selected the largest herbivores (twelve species ranging 90 to 850 kg; Wilson and Mittermeier, 2009) due to their ecological role as “apex herbivores” (a variant of the concept of functional megafauna proposed by Moleón et al., 2020), resulting in a total of twenty-nine species in this guild (see Fig. 1). We have followed the list of the World's largest carnivores (>15 kg) provided by Ripple et al. (2014), in the case of top predators (thirteen species), excluding Ursidae species (except the brown bear *Ursus arctos*) that are mainly herbivorous or frugivorous. The Antarctic, Australasia, and island systems including Madagascar, Sulawesi and Philippines, were not included, since these areas lack the targeted guilds (the Australasian dingo *Canis lupus dingo* is a canid introduced by humans and the thylacine *Thylacinus cynocephalus* is extinct).

Second, we established the current ecosystem integrity by looking for the areas where all targeted taxa that should be present from the upper Holocene are currently present. The maps provided by the Red List of the International Union for Conservation of Nature (IUCN, 2021) were used to build a cartography of these areas, through the distribution areas with the confirmed presence of each species. Note that our maps could be considered conservative e.g. the case of areas within the puma (*Puma concolor*) range, whose current limits are imprecise (IUCN, 2021). Contractions in distribution ranges were determined from former distributions taken both from the IUCN Red List and from bibliography searching (Appendix S1). We sourced the current distribution data from IUCN Red List shapefiles, and created new shapefiles of historic distribution when necessary (e.g. for auroch and rhinos), from the bibliography information. The detailed current distribution of rhinos is not available due to security reasons to avoid severe poaching (IUCN, 2021), but we were able to obtain the data on the current presence within the areas with the remaining potential sympatric megaherbivores; we then deleted those areas where rhinos were vanished. The area of current ecosystem integrity resulted from the superposition of the layers of the global distribution of megaherbivores and the global distribution of top predators. We classified the size of the resulting areas in four categories, following a logarithmic scale, and the percentage of preserved ecosystem integrity was calculated at the continent level. Vector, geospatial processing, and area calculations were run in QGIS v.3.16.6 using WG84 World Mercator (EPSG: 4326) projected shapefiles (QGIS Development Team, 2021).

## 3. Results

We were able to detect eighty-one areas that fully conserved all the targeted species (Fig. 1), most of them very small in size (Fig. 2). Boreal forests and tundra (twenty-seven areas), Neotropic (nineteen areas), Tibetan Plateau and central Asia mountains (seven areas), and Southern

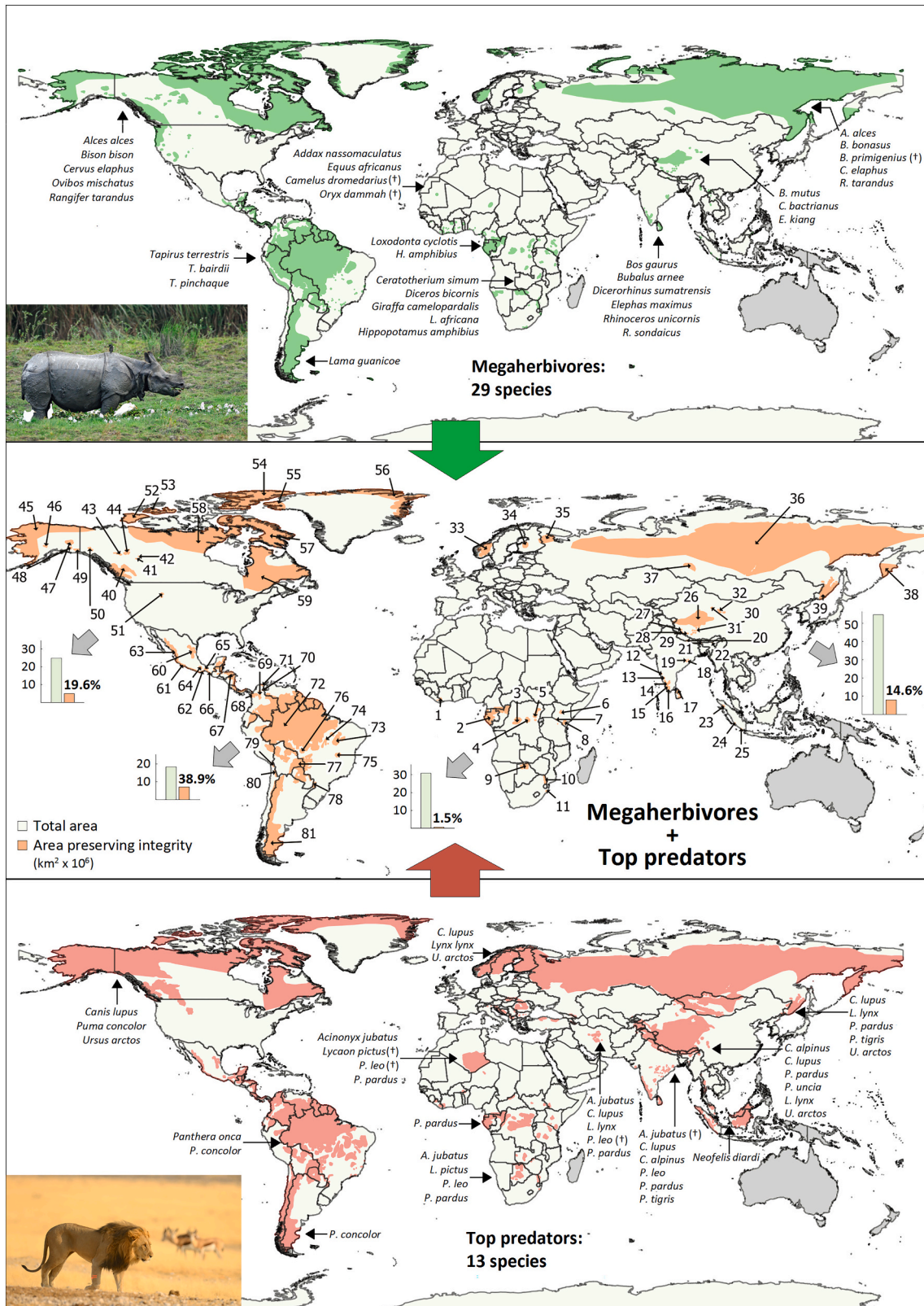
Andean range – Patagonian complex (three areas), are the eco-regions with the largest preserved areas (Fig. 1). However, they were the areas with the lowest species richness (Fig. 1). Temperate forests (one remaining area, to the Far East) and Eurasian grasslands, the Sahara Desert (with no preserved patches) and South-eastern Asia (only fourteen diminutive patches) are the most heavily impacted areas (Fig. 1). In Africa, only scattered and small areas with taxon integrity remain, with the largest areas preserved in evergreen forests (five areas), and the smallest in savannah landscapes (six areas) (Fig. 1). Overall, 15.8 % of the Earth's terrestrial surface currently retains the targeted taxa, with South America largely conserving the best percentage of integrity, followed by North America, Eurasia and, in a very bad situation, Africa (Fig. 1).

Only four countries (Russia, Brazil, Canada, and Argentina) compile the 90.4 % of the global integrity, representing four eco-regions (tundra, taiga, Amazonian forests, and Patagonian grasslands) with low natural diversity of megaherbivores and top predators (Fig. 1). On the opposite scenario, nine African countries (Côte d'Ivoire, Gabon, Congo, Equatorial Guinea, Democratic Republic of the Congo, Kenya, Tanzania, Botswana, and South Africa) and five Asian countries (India, Sri Lanka, Nepal, Malaysia, and China) compile 86.6 % of taxa (sixteen megaherbivores and ten top predators), including the last of the Holocene's giants, like elephants, giraffes and rhinos, which are mainly restricted to very small and isolated areas (Fig. 1).

## 4. Discussion

Unsurprisingly, our evaluation describes a bleak global situation. Only eco-regions with a lower natural diversity of species have large patches of integral ecosystems, considering our assessment approach, and are located in large areas of Intact Forest Landscapes (the Neotropic and the taigas, Plumptre et al., 2019). The regions of maximum richness of the targeted species (including the biggest terrestrial mammals: elephants, rhinos and giraffes) show an even worse scenario where the situation is somewhat kept in check thanks to the positive effects of the protected areas network. In fact, most of the populations of African and Asian megaherbivores and top predators are currently relegated to national parks or other wildlife reserves, the case of rhinos being an extreme example (IUCN, 2021). It is well known that overhunting and habitat destruction through agriculture and cattle raising are the main forces extirpating megaherbivores and top predators (IUCN, 2021). At the eco-region level, a paradigmatic example is the dramatic case of the Sahara Desert, where there is still a huge well-preserved habitat availability (Plumptre et al., 2021) but the largest wildlife taxa have literally vanished due to poaching (Durant et al., 2014).

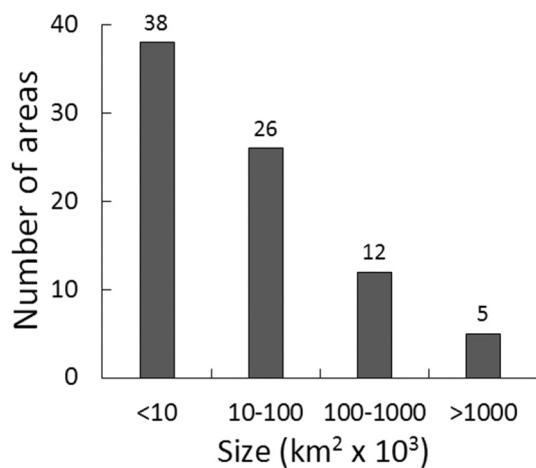
Megaherbivores of Eurasia, North America and Sahara (auroch, bison *Bison* sp., wild horse *Equus ferus*, dromedary *Camelus dromedarius* and scimitar-horned oryx *Oryx dammah*) represent the most severely impacted megafauna, most of them extinct in the wild (some wild horses have been re-introduced in Mongolia, IUCN, 2021). The five rhino species, Bactrian camel *C. bactrianus* and addax *Addax nasomaculatus* are represented, at best, by very small populations at abundance and distribution levels, some of them the result of recent reintroduction programs (IUCN, 2021). Indeed, most of their current populations are likely not functional due to their small numbers, and in consequence, our atlas likely offers an optimistic scenario for some patches (i.e. eastern and south Africa and southeastern Asia, where rhinos are very scarce in most of the areas). In this sense, we recognize that our results are constrained by a lack of information on the extent of the abundance of the targeted species within its overall distributional range, which is required for the persistence of fully functional ecosystems. Unfortunately, for most of the species, there is a total lack of reliable data on population size (IUCN, 2021) or information to define the population levels needed to reach functionality. Interestingly, no top-predator placental species have become extinct in the wild, but viable populations are on the verge of extinction, such as tigers *Panthera tigris*,



(caption on next page)

**Fig. 1.** Global map of the integrity of terrestrial surfaces through the current presence of the full community of top predators and megaherbivores. (†) extinct or locally extinct. In grey are shown the non-evaluated eco-regions.

1, Tai NP; 2, West African jungles; 3, Salonga-ud; 4, Yangolo area; 5, Maiko NT region; 6, Samburu region; 7, Mara & Serengeti Complex; 8, TsavoNP region; 9, Okavango region; 10, Kruger NP; 11, Hluhluwe–Imfolozi Game Reserve; 12, Anshi NP area; 13, BhadraWLS; 14, Nagarghole NP and Bandipur NP; 15, Anamalai; 16, Periyar; 17, Eastern Sri Lanka; 18, Kothgarh WLS area; 19, Tikarpada WLS – Satkosia Tiger Reserve area; 20, Chitwan NP; 21, Jaldapara NP; 22, Kaziranga NP; 23, Leuser mountains; 24, Barisan mountains; 25, Bukit Barisan Selatan NP; 26, Northern Tibetan Plateau; 27, Sagge Zangba basin; 28, Kunggyso Co lake; 29, Maquan He basin; 30, Zhari Nanco lake and Siling lake region; 31, Har Hu lake region; 32, Altun mountains; 33, Southern Norway; 34, Southern Finland; 35, White sea coast; 36, Eurasian taiga and tundra; 37, Novosibirsk and Kemerovo region; 38, Southern Kanchatka; 39, Sikhote-Alin region; 40, Northern Rocky Mountains; 41, Milligans Hills; 42, Hay river; 43, Liard river; 44, Fort Liard; 45, North and west Alaska; 46, Western Denali NP; 47, Tanana river basin; 48, West Wrangell St. Elias NP; 49, East Wrangell St. Elias NP; 50, Aishihik lake; 51, Yellowstone area; 52, Banks Island; 53, Melville Island; 54, Ellesmere Island; 55, Northwestern Greenland (Narsaq); 56, Northern Greenland; 57, Baffin Island; 58, Northwest territories; 59, Labrador Peninsula; 60, Sierra Madre Oriental; 61, Western Sierra Madre del Sur; 62, Eastern Sierra Madre del Sur; 63, Sierra Madre Occidental; 64, Sierra de Juárez; 65, Tehuantepec's isthmus; 66, Sierra Madre de Chiapas; 67, Yucatan-Panamá's isthmus complex; 68, Cordillera Occidental-Panamá's isthmus; 69, Serranías San Mateo & San Lucas; 70, Catatumbo Bari NP; 71, Sierra Nevada de Santa Marta; 72, Amazonian basin; 73, Upper Parnaíba river basin; 74, Tocantins river and Araguaia river area; 75, Grande Sertao Veredas NP area; 76, Mato Grosso Plateau; 77, Gran Chaco and Pantanal; 78, Iguazú NP area; 79, Lauca NP and Las Vicuñas NP; 80, Northern Chilean Andes; 81 Southern Andes and Patagonia.



**Fig. 2.** Size distribution of the eighty-one identified areas. The histogram represents the size distribution of the detected areas conserving the current integrity of megaherbivores and top predators.

cheetahs *Acinonyx jubatus* and wild dogs *Lycan pictus*, which are more and more often relegated to too small protection areas (Ripple et al., 2014; IUCN, 2021).

Our results of taxonomic integrity overlap, in general, with the most recent mapping of ecological intactness, provided by Plumptre et al. (2021), who used several approaches to obtain a map that includes extirpated species and a proxy of functional density for some megaherbivores and top predators, particularly African forest elephant *Loxodonta cyclotis*, jaguar *P. onca* and brown bear. However, some important discrepancies between our results and the map by Plumptre et al. (2021) arise. First, it is especially evident in the case of the Sahara Desert, where these authors offer a much more optimistic scenario that includes two large well preserved areas with no extirpated species in Algeria and Libya. However, in both countries the addax antelope (both) and the wild dog (Algeria) are extinct or probably extirpated respectively (IUCN, 2021), or even other species not considered here (like the dama gazelle *Nanger dama* and the ostrich *Struthio camelus*, IUCN, 2021). Indeed, most of the surviving ungulates and top predators (as the Saharan cheetah) are critically endangered (IUCN, 2021). Second, Plumptre et al. (2021) did not register most of the Patagonian region, but it's a well-preserved large region based both on our approach and on habitat intactness (Venter et al., 2016).

## 5. Conclusions

We offer here a detailed GIS database of a number of small key patches that are absent in previous approaches, as an important

complement to the available maps of ecosystem integrity (Venter et al., 2016; Plumptre et al., 2019, 2021). This information may help further studies focused on understanding the patterns and forces that affect the current integral patches and their ecological functionality. Further, conservation applications of the current inventory based on key areas for biodiversity, emphasize the urgent need for its efficient integral conservation, which ideally entails the implementation of a globally designed strategy, funded with the support of all countries in proportion to their resources. In turn, international political agreements and commitments are essential. Finally, it should be highlighted that current distribution information for some species is not updated and/or is imprecise (IUCN, 2021), thus the limits of some areas should be taken with caution. In this context, we need further scientific-based field research in order to improve the necessary basic data on these and other species. To reach this knowledge, fieldwork studies are an essential tool, but unfortunately, nowadays, the progressive decline of fieldwork studies (Ríos-Saldaña et al., 2018) hampers this key goal. Ultimately, the knowledge of what we have lost is the first step in understanding the importance of conserving what we still have left.

## Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

## CRedit authorship contribution statement

Jose María Gil-Sánchez: Conceptualization; Formal analysis; Investigation; Methodology; Supervision; Validation; Visualization; Roles/Writing - original draft, Writing - review & editing.

Mariola Sánchez-Cerdá: Conceptualization; Data curation; Formal analysis; Investigation; Resources; Software; Validation; Visualization; Writing - review & editing.

## Declaration of competing interest

No conflicts of interest to declare.

## Data availability

Data will be made available on request.

## Acknowledgements

The photographs of Fig. 1 were kindly provided by Jesús Rodríguez Osorio. Shapefiles of current taxa distribution were obtained previous authorization by the IUCN Red List.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2022.109848>.

## References

- Barnosky, A.D., Lindsey, E.L., Villavicencio, N.A., Bostelman, E., Hadly, E.A., Wanket, J., 2015. Variable impact of late-Quaternary megafaunal extinction in causing ecological state shifts in North and South America. *Proc. Natl. Acad. Sci. U. S. A.* 113 (4), 856–861. <https://doi.org/10.1073/pnas.1505295112e00389>.
- Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., et al., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* 67, 534–545. <https://doi.org/10.1093/biosci/bix014>.
- Dorren, L.K., Berger, F., Imeson, A.C., Marier, B., Rey, F., 2004. Integrity, stability and management of protection forests in the European Alps. *For. Ecol. Manag.* 195, 165–176. <https://doi.org/10.1016/j.foreco.2004.02.057>.
- Durant, S.M., Bashir, R.S., Woodroffe, P.D., Ransom, J.C., Newby, T.A., Abáigar, T., et al., 2014. Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. *Divers. Distrib.* 20, 114–122. <https://doi.org/10.1111/ddi.12157>.
- Galetti, M., Moleón, M., Jordano, P., Pires, M.M., Guimarães, P.R., Pape, T., Nichols, E., Hansen, D., Olesen, J.M., Munk, M., de Mattos, J.S., Schweiger, A.H., Owen-Smith, N., Johnson, C.N., Marquis, R.J., Svenning, Jens-Christian, 2018. Ecological and evolutionary legacy of megafauna extinctions. *Biol. Rev. Camb. Philos. Soc.* 93 (2), 845–862. <https://doi.org/10.1111/brv.12374>.
- Hairton, N.G., Smith, F.E., Slobodkin, B., 1960. Community structure, population control, and competition. *Am. Nat.* 94, 421–425.
- IUCN, 2021. The IUCN red list of threatened species. Version 2021-1. <https://www.iucnredlist.org>.
- Moleón, M., Sánchez-Zapata, J.A., Donazar, J.A., Revilla, E., Martín-López, B., Gutiérrez-Cánovas, C., et al., 2020. Rethinking megafauna. *Proc. R. Soc. B* 287, 20192643. <https://doi.org/10.1098/rspb.2019.2643>.
- Murdoch, W.W., 1966. Community structure, population control, and competition: a critique. *Am. Nat.* 100, 219–226.
- Plumptre, A.J., Baisero, D., Jedrzejewski, W., Kühl, H., Maisels, F., Ray, J.C., 2019. Are we capturing faunal intactness? A comparison of intact forest landscapes and the “last of the wild in each ecoregion. *Front. For. Glob. Chang.* 2, 24. <https://doi.org/10.3389/ffgc.2019.00024>.
- Owen-Smith, R.N., 1989. *Megaherbivores: The Influence of Very Large Body Size on Ecology*. Cambridge Univ. Press, New York.
- Plumptre, A.J., Baisero, D., Belote, R.T., Vázquez-Domínguez, E., Faurby, S., Jedrzejewski, W., et al., 2021. Where might we find ecologically intact communities? *Front. For. Glob. Chang.* 4 <https://doi.org/10.3389/ffgc.2021.626635>.
- QGIS Development Team, 2021. QGIS geographic information system v.3.16.6. Open source geospatial foundation project. [www.qgis.org](http://www.qgis.org).
- Ríos-Saldaña, A.C., Delibes-Mateos, M., Ferreira, C.C., 2018. Are fieldwork studies being relegated to second place in conservation science? *Glob. Ecol. Conserv.* 14, e00389. <https://doi.org/10.1016/j.gecco.2018.e00389>.
- Ripple, W.R., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.U., Hebblewhite, M., et al., 2014. Status and ecological effects of the World's largest carnivores. *Science* 343, 1241484. <https://doi.org/10.1126/science.1241484>.
- Steneck, R.S., 2005. An ecological context for the role of large carnivores in conserving biodiversity. In: Ray, J.C., Redford, K.H., Steneck, S.S. (Eds.), *Large Carnivores and the Conservation of Biodiversity*. Island Press, Washington, pp. 82–99.
- Terborgh, J., 2005. The Green World Hypothesis revised in conserving biodiversity. In: Ray, J.C., Redford, K.H., Steneck, S.S. (Eds.), *Large Carnivores and the Conservation of Biodiversity*. Island Press, Washington, pp. 9–33.
- Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., et al., 2016. Global terrestrial human footprint maps for 1993 and 2009. *Sci. Data* 3, 160067. <https://doi.org/10.1038/sdata.2016.67>.
- Wilson, D.E., Mittermeier, R.A., 2009. *Handbook of the Mammals of the World. In: Carnivores, Vol 1*. Lynx Edicions, Barcelona.