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Intense human pressure is widespread across terrestrial vertebrate ranges



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ABSTRACT

The United Nation's Strategic Plan for Biodiversity 2011–2020 calls for reducing species extinctions, as it is increasingly clear that human activities threaten to drive species to decline. Yet despite considerable scientific evidence pointing to the detrimental effects of interacting threats on biodiversity, many species lack information on their exposure to cumulative human pressures. Using the most comprehensive global dataset on cumulative human footprint, we assess the extent of intense human pressures across 20,529 terrestrial vertebrate species' geographic ranges. We consider intense human pressure as areas where landscapes start to be significantly modified (a summed Human Footprint value at or above three on the index), which is where land uses such as pastureland appear. This threshold has been correlated with extinction risk for many species. We show that 85% (17,517) of the terrestrial vertebrate species assessed have >half of their range exposed to intense human pressure, with 16% (3328) of the species assessed being entirely exposed to this degree of pressure. Threatened terrestrial vertebrates and species with small ranges are disproportionately exposed to intense human pressure. Our analysis also suggests that there are at least 2478 species considered 'least concern' that have considerable portions of their range overlapping with these pressures, which may indicate their risk of decline. These results point to the utility of assessing cumulative human pressure data across species ranges, which may be a useful first step for measuring species vulnerability.

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1. Introduction

A key goal of the United Nation's Strategic Plan for Biodiversity 2011-2020 is to reduce species extinctions. There is growing evidence that land-use change such as pastureland, agriculture, and urbanization, and human activities like over-harvesting threaten to drive species to decline (Newbold et al., 2015; Tilman et al., 2017; Di Marco et al., 2018). Yet previous efforts to study species habitat availability have primarily focused on vegetation intactness (Andrén and Andren, 1994; Betts et al., 2007; Maron et al., 2012), but this does not capture cumulative threats that can impact species (e.g. Maxwell et al., 2016) even when their habitat appears to be intact (Barlow et al., 2016; Betts et al., 2017). By taking advantage of recently available human footprint data, we capture cumulative pressures (Di Marco et al., 2018; Allan et al., 2019), not only providing an initial understanding of how much low-pressure geographic range is available for species, but also delivering necessary results that can inform the urgency and specificity of conservation actions needed to avert species' declines.

We use the updated Human Footprint (Venter et al., 2016a), a cumulative human pressure assessment that includes data on roads, built environments, human population density, railways, navigable waterways, pasturelands, and croplands, at a 1-km² resolution globally (Venter et al., 2016a, 2016b). The Human Footprint is the most comprehensive global human pressure dataset available (McGowan, 2016), and given the nature of the input data, captures the greatest number of drivers of species declines (e.g. agricultural activity, urban development, transportation, energy production, and system modification; Maxwell et al., 2016), and has been shown to explain extinction risk in globally threatened vertebrates (Safi and Pettorelli, 2010; Yackulic et al., 2011; Beans et al., 2012; Seiferling et al., 2014; Hand et al., 2014; Di Marco et al., 2018). We identify intense human pressure as areas on the Human Footprint index that are composed of pressures at or above an index value of three, which is the equivalent to pastureland (Venter et al., 2016a), a land use where habitat is considered functionally unavailable for many terrestrial vertebrate species that have been assessed (Fleischner, 1994; Newbold et al., 2015). Recently, Di Marco and colleagues found that a value greater than or equal to three on the index was correlated with extinction risk in terrestrial mammals globally, and similar values held true across regions, even when compared to other factors such as species' traits, environmental conditions, and individual pressure layers (Di Marco et al., 2018).

We first quantify the proportion of species ranges facing intense human pressure across 10,745 birds (Birdlife International and Handbook of the Birds of the World, 2017), 4592 mammals, 5000 amphibians, and 192 reptiles, with 4610 of the total being threatened (IUCN, 2017). We focus on these taxa, as they are the only major terrestrial taxonomic groups that have been comprehensively assessed for their distribution and extinction risk (with the exception of reptiles, see Methods). We then investigate the extent of intense human pressure across taxonomic classes, species level of endangerment, and species range size. Lastly, we quantify changes in the extent of intense human pressure within species ranges between 1993 and 2009.

2. Methods

2.1. Species distribution data

We focused our analysis on terrestrial vertebrate classes (mammals, birds, reptiles, and amphibians). Spatial data on mammal, amphibian, and reptile distributions were obtained from the IUCN Red List of Threatened Species (IUCN, 2017), and bird distributions from BirdLife International (Birdlife International and Handbook of the Birds of the World, 2017). We excluded species that were considered data deficient ("DD") on the Red List, and removed individual range polygons that were considered extinct, thought to be extinct, or presence uncertain. We only included the remaining extant species' distributions that overlapped with the extent of the terrestrial Human Footprint datasets (Venter et al., 2016b). We note that for reptiles, only chameleons, crocodilians, and sea snakes had been assessed comprehensively by the IUCN at the time of our analysis; as such, we only included reptiles when reporting on all species or on all threatened species, and do not report on reptiles for class-specific metrics.

2.2. Spatial data on human pressure

Recent advances in remote sensing coupled with bottom-up survey data have facilitated the development of a spatially explicit, high-resolution global dataset on human pressures across time steps (Allan et al., 2017), which enables the quantification of the extent of human pressures on individual species (Di Marco and Santini, 2015; Allan et al., 2019). We obtained data on the distribution of terrestrial human pressure for 1993 and 2009 from the global Human Footprint maps (Venter et al., 2016b, 2016a). These maps are comprised of a cumulative spatial index of eight key human pressures at a 1 km² resolution including 1) built environments, 2) population density, 3) electric infrastructure, 4) crop lands, 5) pasture lands, 6) roads, 7) railways, and 8) navigable waterways. These eight individual pressures are scaled based on their estimated environmental impact and summed in 1 km² grid cells. Some pressures can co-occur while others are mutually exclusive; resulting in a combined global scale between zero and fifty where zero is little to no human pressure and fifty is extreme urban conglomerates.

2.3. Analyzing human pressure on species distributions

We intersected individual species ranges with both the 1993 and 2009 Human Footprint (Venter et al., 2016a,b) maps under a World Mollweide projection in a geographic information system using the tabulate area tool in model builder of ArcGIS (ESRI, 2017), and outputs were managed in R statistical software (R Core Team, 2017). This intersection resulted in a dataset with each species having the area of their range composed of each individual Human Footprint index value (index values of 0–50 as mentioned above). We then calculated the proportion of the species' range that is composed of each index value of the Human Footprint by dividing the area of a species' range for the respective index value by the total range size (with the sum of all proportions equalling one). We then sum the resulting proportions for each species starting at the Human Footprint value of three and above, as this is where landscapes start to be considered significantly modified. This threshold (a summed Human Footprint value at or above three on the index) has been used in previous studies for evaluating human pressure in ecosystems (Watson et al., 2016; Jones et al., 2018). Additionally, Di Marco and colleagues (Di Marco et al., 2018) recently found that the same threshold was a strong indicator of extinction risk in mammals globally, even when compared to other factors such as species' traits, environmental conditions, and individual pressure layers, and similar values held true across regions. We also assessed the proportion of a species' range containing summed Human Footprint index values of seven and above, which are considered to be areas where intense industrial agriculture and urbanization appear (Venter et al., 2016a), for comparison.

3. Results

Of the 20,529 terrestrial vertebrate species assessed, we found that 85.3% (17,517) have >50% of their range exposed to intense human pressures and that 16.2% (3328) have no portion of their range free from intense human pressure (Table S1). We also found that all taxonomic classes are experiencing intense human pressure across the majority of their range, with 39.6% (1980) of amphibians having no portion of their range free from intense human pressure (Fig. 1A), compared to mammals (15.2% [698]; Fig. 1B) and birds (11.6% [1250]; Fig. 1C).

Threatened species (those classified as vulnerable, endangered, and critically endangered on the IUCN Red List) are disproportionately exposed to intense human pressure compared to non-threatened species, even when comparing across range sizes (Fig. 2). Threatened species have, on average, less than 12 percent of their range free from intense human pressure (Table S2), with only 0.87% (40) of threatened species having their entire range free from intense human pressure (Table S1). Of the 4610 threatened species assessed, 90.8% (4185) have more than half of their range under intense human pressures, with 53.3% (2457) having no portion of their range free from this pressure (Fig. 1D). We found that 70.9% (1453) of threatened amphibians have no portion of their range free from intense human pressure (Table S1), with 39.4% (441) of threatened mammals and 37.5% (510) of threatened birds having no portion of their range free from this pressure (Table S1).

We found that species with small ranges have more of their distribution overlapping with intense human pressure compared to species with large ranges (Fig. 2). This pattern is expected by random chance, since species with small ranges are the most likely ones to be fully covered by spatially aggregated regions of human pressure. However, we found that species with a median range size less than 100,000 km² have their entire distribution under intense human pressure (Fig. 2). That is, 100% of range with intense human pressure for a species with range size less than or equal to the area of South Korea (larger than the area of 45% of countries). Therefore, intense human pressure is widespread even for species with moderately large range sizes.

Over the last two decades, intense human pressure has increased in extent by 4.5% across Earth's terrestrial surface (Venter et al., 2016a) (Table S3). For the terrestrial vertebrates assessed however, we found that intense human pressure has increased within their ranges by 6.1% on average (Table S2). This may indicate that the global increase in human pressure is occurring in species-rich areas (likely containing species with already restricted ranges, as shown above), with the number of species entirely exposed to intense human pressure in 2009 being 44.1% higher than it was in 1993, and the number of species entirely free from intense human pressure 37.6% lower (Table S1). Additionally, threatened species have experienced a 3.9% average increase in the proportion of their range exposed to intense human pressure over the two decade study period (Table S2).

4. Discussion

The extent and condition of species ranges are some of the most important components of species' conservation status (Boakes et al., 2018), and are key elements for determining extinction risk (IUCN, 2017). Our results suggest that 85% of all terrestrial vertebrates assessed have more than half of their range exposed to intense human pressure (Table S1), and that this pressure has increased since 1993. We note that although the presence of intense human pressure is detrimental to many species (Di Marco et al., 2018), some species can still persist in these areas (for example in agricultural and managed forestry lands [Phalan et al., 2011; Homyack et al., 2014; O'Bryan et al., 2016]) and urban areas (McPherson et al., 2016; Braczkowski et al., 2018; O'Bryan et al., 2018). However, many species that live in human modified habitats will do so at lower population density, with lower reproductive rates, and with drastic changes to behaviour than would be otherwise in more natural habitats. These changes can result in extinction debts for many species (Essl et al., 2015; Chen and Peng, 2017; Semper-Pascual et al., 2018). Yet as a further exploration of the intensity of human pressure on species, we adjusted the lower bounds of what

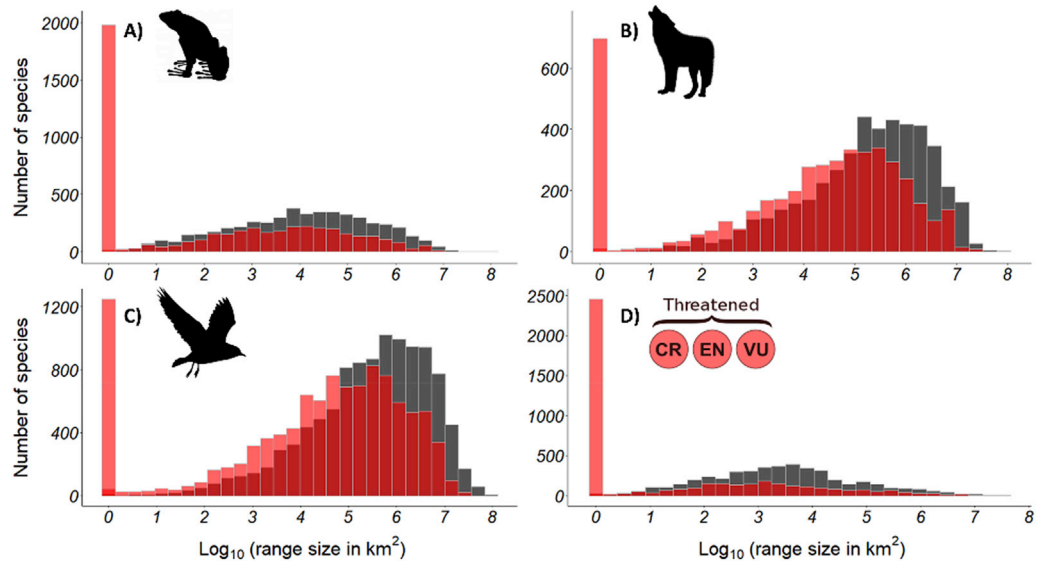


Fig. 1. Hypothetical range size with and without intense human pressure (Human Footprint value of ≥ 3) for all species assessed. Range size frequencies for the entire known geographic range of species (dark grey bars) and range size frequencies of the same species after excluding areas of intense human pressure (red bars) for (A) amphibians, (B) mammals, (C) birds, and (D) threatened species (including vulnerable, endangered, and critically endangered species). The first column for each plot represents the number of species that have their entire range exposed to intense human pressure. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

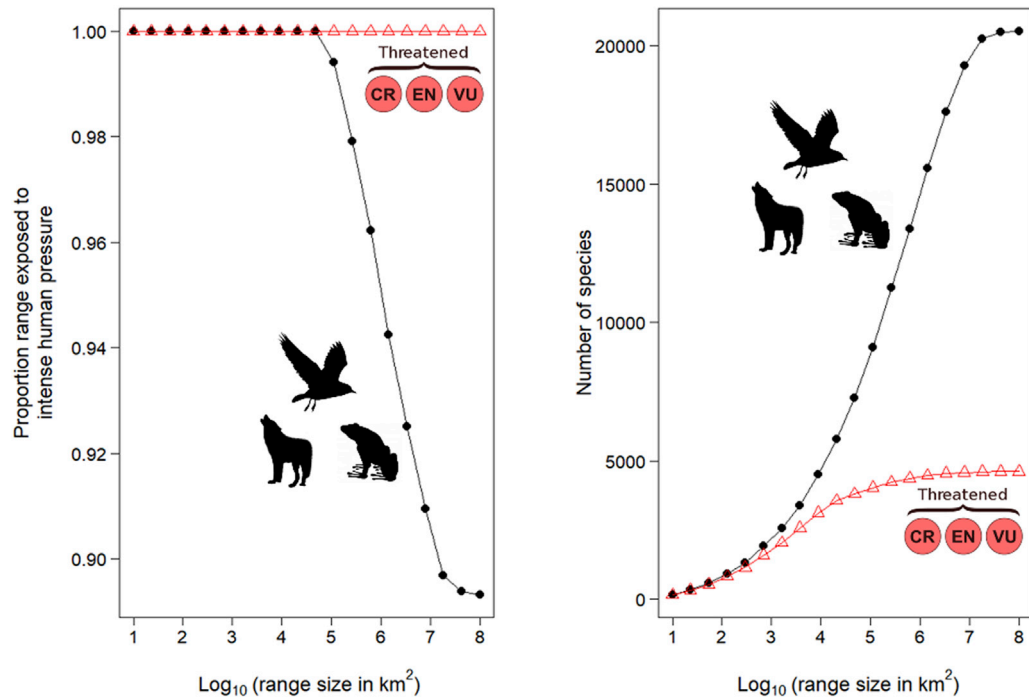


Fig. 2. Relationship between range size and proportion overlapping with intense human pressure for both threatened (red triangles) and non-threatened (black dots) terrestrial vertebrate species assessed. The plot on the left shows the median proportion of a species' range under intense human pressure for all species assessed with the specified median range size on the x-axis or smaller. For example, this shows that species with median range sizes around or below $100,000 \text{ km}^2$ ($10^{5.0} \text{ km}^2$) have 100% of their range exposed to intense human pressure, and that threatened species are 100% exposed regardless of median range size. The plot on the right shows the total number of species in the dataset with the specified median range size or smaller for both threatened and non-threatened species. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

is considered intense human pressure for many vertebrates (i.e. pastureland) to start at industrial-level agriculture (pressures at or above a value of seven; Venter et al., 2016a). We found that, even when shifting the lower limit to a more intense human pressure score, 40.5% (8308) of all species assessed and 50.7% (3230) of threatened species have more than half of their range under this intense human pressure (Table S4). This means that species able to persist in areas with some level of intense human pressure, such as pastureland, but not in areas where land is almost completely cleared for industrial agriculture and urbanization, may be at risk of decline. We recommend future research delve into the 'winners' and 'losers' at different levels of human footprint, perhaps by assessing whether habitat specialists are impacted more than habitat generalists by intense human pressure.

An important caveat to our work is that the Human Footprint data do not incorporate all pressures affecting biodiversity directly, such as anthropogenic climate change (e.g. Pecl et al., 2017), pollution (e.g. Oita et al., 2016), infectious diseases (e.g. Bower et al., 2017), overexploitation (e.g. Brackzkowski et al., 2019) and invasive species (e.g. Bankovich et al., 2016), making it a conservative estimate of pressure (Jones et al., 2018). However, some pressures such as invasive species and over-exploitation are closely associated with pressures represented in the Human Footprint dataset, such as presence of roads and population density (Spear et al., 2013). As such, while our results encompass well-established pressures that are partly driving the global extinction crisis (Maxwell et al., 2016), additional refinement will be necessary to insure all ancillary pressures are included, as this is particularly important for taxonomic groups that are known to be sensitive to pressures that are not easily quantified. Furthermore, although human pressures may occur within species' ranges, these pressures may not evenly affect species, partially because individuals are not always evenly distributed throughout their geographic ranges and intense human pressure may not affect the majority of individuals and species in an assemblage. Lastly, the process of indexation that has been done with the Human Footprint does not allow us to point to direct actors of change (e.g. agriculture or urbanization) at local and global scales. Capturing the nuances of species use within their distributions and their sensitivity to interacting threats will be particularly helpful in enhancing the utility of cumulative human pressure data.

Range size and range reduction are two of the main values used to assess species extinction risk in the IUCN Red List, representing restricted population size and population decline over time (Visconti et al., 2016; Tracewski et al., 2016; IUCN Standards and Petitions Subcommittee, 2017; Ceballos et al., 2017; Santini et al., 2019). Overestimating range size fundamentally undermines the assessment of species extinction risk and efficacy of conservation planning and action (Jetz et al., 2008; Di Marco et al., 2017). Our approach may be useful as a first pass to assess range availability, assuming areas exposed to intense human pressure are functionally unavailable to the species in question. For example, 832 (42.9%) vulnerable species would have a potential Area of Occupancy (AOO) smaller than the 500 km² threshold that classifies endangered species under Red List sub-criterion B2 (Mace et al., 2008), if AOO is inferred from the extent of range free from intense pressure (Fig. 3A). Thus, if these 832 species already show evidence of population decline, fragmentation, or extreme fluctuations (at least two of these attributes must verify in order for criterion B to be applicable), then they could be deemed as endangered (Mace et al., 2008). The same logic might apply to species that are not currently acknowledged as threatened on the IUCN Red List (Bland et al., 2015). For example, 2478 (17.5%) least concern species could be considered threatened under the range-loss criteria B2 of the IUCN (2000 km²) if incorporating intense human pressure (Fig. 3B). This has implications for how we view species' vulnerability, and also for efforts aimed at prioritizing funding and conservation action for currently acknowledged threatened species (Di Marco et al., 2018).

5. Conclusion

We show that considering cumulative human pressures has the potential to improve how we assess species' vulnerability, with subsequent benefits for many other areas of conservation. For example, our approach could be used as an initial examination of pressure within known species' geographic ranges, especially when resources are limited. This information could also inform necessary species and ecosystem-specific habitat retention and restoration targets (Maron et al., 2018). It can highlight areas where species are substantially exposed to intense human pressure (thus prioritizing habitat restoration and threat abatement in order to reopen viable space for species persistence [Allan et al., 2017, 2019; Newmark et al., 2017]) and areas where species still have large swaths of their range free from intense human pressure (thus prioritizing the protection of existing quality habitat, but could also be under threat from future human actions [Noss et al., 2012; Venter et al., 2014; Watson et al., 2014]). This information can aid current assessments of progress against the 2020 Aichi Targets (especially Target 12, which deals with preventing extinctions and Target 5, and deals with preventing the loss of natural habitats), and for conversations around post-2020 targets.

As intense human activities spread, habitat becomes lost to many species, and their populations will likely decline (Di Marco et al., 2014; Di Marco and Santini, 2015). Our work suggests that intense human pressure is widespread within the ranges of the terrestrial vertebrates assessed. For a clearer picture on the status of species, we advocate for utilizing cumulative human pressure data, alongside other measures such as species habitat preferences and abundance (e.g. Santini et al., 2019), to identify areas within their ranges that are at a higher risk from cumulative anthropogenic threats, and where conservation action is imminently needed to ensure they have enough range to persist. Given the growing human influence on the planet, time and space are running out for biodiversity, and we need to prioritize actions against these intense human pressures.

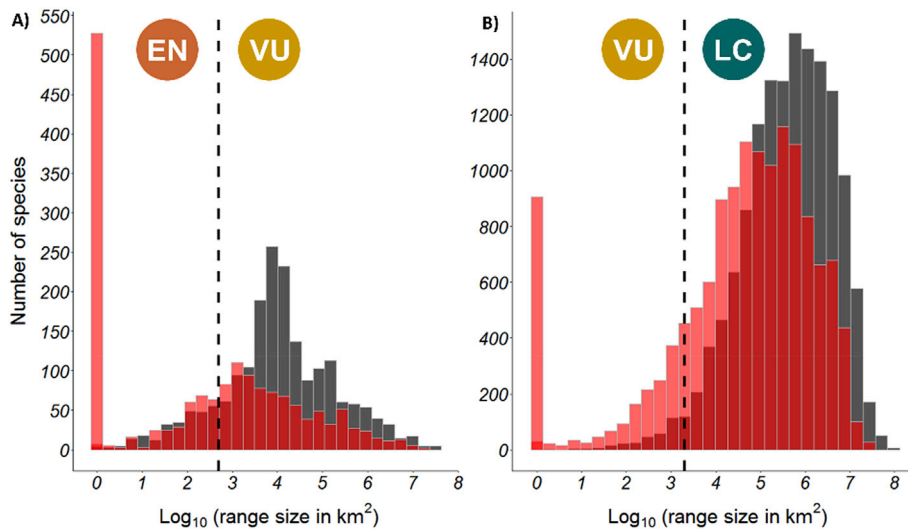


Fig. 3. Hypothetical range change after removing areas with intense human pressure for species listed as 'vulnerable' and 'least concern'. (A) Range size frequency for species considered 'vulnerable' by the IUCN (IUCN, 2017) (dark grey bars) against the range size frequency for the same species after removing areas with intense human pressure (red bars). We find that 832 (42.9%) vulnerable species could be considered for being listed as endangered if areas with intense human pressure were removed from the range (using sub-criterion B2 of the IUCN (IUCN, 2017), a 500 km² threshold denoted by the vertical dashed line). (B) For species considered 'least concern' by the IUCN, 2478 (17.5%) could be considered for listing as threatened (using sub-criterion B2 of the IUCN (IUCN, 2017), a 2000 km² threshold denoted by the vertical dashed line). The first column for both (A) and (B) represents the number of species that have their entire range exposed to intense human pressure. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00882>.

References

- Allan, J.R., Venter, O., Maxwell, S., Bertzky, B., Jones, K., Shi, Y., Watson, J.E.M., 2017. Recent increases in human pressure and forest loss threaten many Natural World Heritage Sites. *Biol. Conserv.* 206, 47–55.
- Allan, J.R., Watson, J.E.M., Di Marco, M., O'Bryan, C.J., Possingham, H.P., Atkinson, S.C., Venter, O., 2019. Hotspots of human impact on threatened terrestrial vertebrates. *PLoS Biol.* 17, e3000158. Public Library of Science. Available from: <http://dx.plos.org/10.1371/journal.pbio.3000158>.
- Andrén, H., Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355. WileyNordic Society Oikos. Available from: <https://www.jstor.org/stable/3545823?origin=crossref>.
- Bankovich, B., Boughton, E., Boughton, R., Avery, M.L., Wisely, S.M., 2016. Plant community shifts caused by feral swine rooting devalue Florida rangeland. *Agric. Ecosyst. Environ.* 220, 45–54.
- Barlow, J., et al., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* 535, 144–147. Nature Publishing Group. Available from: <http://www.nature.com/articles/nature18326>.
- Beans, C.M., Kilkenny, F.F., Galloway, L.F., 2012. Climate suitability and human influences combined explain the range expansion of an invasive horticultural plant. *Biol. Invasions* 14, 2067–2078. Springer Netherlands. Available from: <http://link.springer.com/10.1007/s10530-012-0214-0>.
- Betts, M., Forbes, G., Diamond, A., 2007. Thresholds in songbird occurrence in relation to landscape structure. *Conserv. Biol.* 21, 1046–1058. <https://doi.org/10.1111/j.1523-1739.2007.00723.x>. Wiley/Blackwell (10.1111). Available from.
- Betts, M.G., Wolf, C., Ripple, W.J., Phalan, B., Millers, K.A., Duarte, A., Butchart, S.H.M., Levi, T., 2017. Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* 547, 441–444. Available from: https://www.researchgate.net/profile/Matthew_Betts/publication/318562419_Global_forest_loss_disproportionately_erodes_biodiversity_in_intact_landscapes/links/597caaa7aca272d568fe2958/Global-forest-loss-disproportionately-erodes-biodiversity-in-intact-land.

- Birdlife International, Handbook of the Birds of the World, 2017. Bird species distribution maps of the world. Available from: <http://datazone.birdlife.org/species/requestdis>.
- Bland, L.M., Collen, B., Orme, C.D.L., Bielby, J., 2015. Predicting the conservation status of data-deficient species. *Conserv. Biol.* 29, 250–259. <https://doi.org/10.1111/cobi.12372>. Wiley/Blackwell (10.1111). Available from.
- Boakes, E.H., Isaac, N.J.B., Fuller, R.A., Mace, G.M., McGowan, P.J.K., 2018. Examining the relationship between local extinction risk and position in range. *Conserv. Biol.* 32, 229–239. <https://doi.org/10.1111/cobi.12979>. Wiley/Blackwell (10.1111). Available from.
- Bower, D.S., Lips, K.R., Schwarzkopf, L., Georges, A., Clulow, S., 2017. Amphibians on the brink. *Science* 357, 454–455. American Association for the Advancement of Science. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/28774916>.
- Braczkowski, A., Ruzo, A., Sanchez, F., Castagnino, R., Brown, C., Guynup, S., Winter, S., Gandy, D., O'Bryan, C., 2019. The ayahuasca tourism boom: an undervalued demand driver for jaguar body parts? *Conserv. Sci. Pract.* Available from <https://onlinelibrary.wiley.com/doi/abs/10.1111/csp2.126>.
- Braczkowski, A.R., O'Bryan, C.J., Stringer, M.J., Watson, J.E., Possingham, H.P., Beyer, H.L., 2018. Leopards provide public health benefits in Mumbai, India. *Front. Ecol. Environ.* 16, 176–182.
- Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. In: *Proceedings of the National Academy of Sciences of the United States of America* 114, pp. E6089–E6096. National Academy of Sciences. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/28696295>.
- Chen, Y., Peng, S., 2017. Evidence and mapping of extinction debts for global forest-dwelling reptiles, amphibians and mammals. *Sci. Rep.* 7, 44305. Nature Publishing Group. Available from: <http://www.nature.com/articles/srep44305>.
- Di Marco, M., Buchanan, G.M., Szantoi, Z., Holmgren, M., Grottole Marasini, G., Gross, D., Tranquilli, S., Boitani, L., Rondinini, C., 2014. Drivers of extinction risk in African mammals: the interplay of distribution state, human pressure, conservation response and species biology. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 369, 20130198. The Royal Society. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/24733953>.
- Di Marco, M., Santini, L., 2015. Human pressures predict species' geographic range size better than biological traits. *Glob. Chang. Biol.* 21, 2169–2178. <https://doi.org/10.1111/gcb.12834>. Available from.
- Di Marco, M., Venter, O., Possingham, H.P., Watson, J.E.M., 2018. Changes in human footprint drive changes in species extinction risk. *Nat. Commun.* 9, 1–9. <https://doi.org/10.1038/s41467-018-07049-5>. Springer US. Available from.
- Di Marco, M., Watson, J.E.M., Possingham, H.P., Venter, O., 2017. Limitations and trade-offs in the use of species distribution maps for protected area planning. *J. Appl. Ecol.* 54, 402–411. <https://doi.org/10.1111/1365-2664.12771>. Available from.
- ESRI, 2017. *ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.*
- Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Pyšek, P., Wilson, J.R.U., Richardson, D.M., 2015. Delayed biodiversity change: no time to waste. *Trends Ecol. Evol.* 30, 375–378. Elsevier Current Trends. Available from: <https://www.sciencedirect.com/science/article/pii/S016953471500124X>.
- Fleischner, T.L., 1994. Ecological costs of livestock grazing in Western North America. *Conserv. Biol.* 8, 629–644. <https://doi.org/10.1046/j.1523-1739.1994.08030629.x>. Wiley/Blackwell (10.1111). Available from.
- Hand, B.K., Cushman, S.A., Landguth, E.L., Lucotch, J., 2014. Assessing multi-taxa sensitivity to the human footprint, habitat fragmentation and loss by exploring alternative scenarios of dispersal ability and population size: a simulation approach. *Biodivers. Conserv.* 23, 2761–2779. Springer Netherlands. Available from: <http://link.springer.com/10.1007/s10531-014-0747-x>.
- Homyack, J.A., O'Bryan, C.J., Thornton, J.E., Baldwin, R.F., 2014. Anuran assemblages associated with roadside ditches in a managed pine landscape. *For. Ecol. Manag.* 334, 217–231.
- IUCN, 2017. The IUCN red list of threatened species. Available from: <https://www.iucnredlist.org/>.
- IUCN Standards, Petitions Subcommittee, 2017. Guidelines for using the IUCN red list categories and criteria. Available from: <http://intranet.iucn.org/webfiles/doc/JSSC/RedList/RedListGuidelines.pdf>.
- Jetz, W., Sekercioglu, C.H., Watson, J.E.M., 2008. Ecological correlates and conservation implications of overestimating species geographic ranges. *Conserv. Biol.* 22, 110–119. <https://doi.org/10.1111/j.1523-1739.2007.00847.x>. Wiley/Blackwell (10.1111). Available from.
- Jones, K.R., Venter, O., Fuller, R.A., Allan, J.R., Maxwell, S.L., Negret, P.J., Watson, J.E.M., 2018. One-third of global protected land is under intense human pressure. *Science* 360, 788–791. American Association for the Advancement of Science. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/29773750>.
- Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J., Stuart, S., 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* 22, 1424–1442. <https://doi.org/10.1111/j.1523-1739.2008.01044.x>. Wiley/Blackwell (10.1111). Available from.
- Maron, M., Bowen, M., Fuller, R.A., Smith, G.C., Eyre, T.J., Mathieson, M., Watson, J.E.M., McAlpine, C.A., 2012. Spurious thresholds in the relationship between species richness and vegetation cover. *Glob. Ecol. Biogeogr.* 21, 682–692. <https://doi.org/10.1111/j.1466-8238.2011.00706.x>. Wiley/Blackwell (10.1111). Available from.
- Maron, M., Simmonds, J.S., Watson, J.E.M., 2018. Bold nature retention targets are essential for the global environment agenda. *Nat. Ecol. Evol.* 2, 1194–1195. Nature Publishing Group. Available from: <http://www.nature.com/articles/s41559-018-0595-2>.
- Maxwell, S.L., Fuller, R.A., Brooks, T.M., Watson, J.E.M., 2016. Biodiversity: the ravages of guns, nets and bulldozers. *Nature* 536, 143–145. Available from: <http://www.nature.com/doi/10.1038/536143a>.
- McGowan, P.J.K., 2016. Mapping the terrestrial human footprint. *Nature* 537, 172–173. Nature Publishing Group. Available from: <http://www.nature.com/articles/537172a>.
- McPherson, S.C., Brown, M., Downs, C.T., 2016. Crowned eagle nest sites in an urban landscape: requirements of a large eagle in the Durban Metropolitan Open Space System. *Landsc. Urban Plan.* 146, 43–50.
- Newbold, T., et al., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50. Nature Publishing Group. Available from: <http://www.nature.com/articles/nature14324>.
- Newmark, W.D., Jenkins, C.N., Pimm, S.L., McNeally, P.B., Halley, J.M., 2017. Targeted habitat restoration can reduce extinction rates in fragmented forests. In: *Proceedings of the National Academy of Sciences of the United States of America* 114, pp. 9635–9640. National Academy of Sciences. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/28827340>.
- Noss, R.F., et al., 2012. Bolder thinking for conservation. *Conserv. Biol.* 26, 1–4.
- O'Bryan, C.J., Braczkowski, A.R., Beyer, H.L., Carter, N.H., Watson, J.E.M., McDonald-Madden, E., 2018. The contribution of predators and scavengers to human well-being. *Nat. Ecol. Evol.* 2, 229–236.
- O'Bryan, C.J., Homyack, J.A., Baldwin, R.F., Kanno, Y., Harrison, A.-L., 2016. Novel habitat use supports population maintenance in a reconfigured landscape. *Ecosphere* 7.
- Oita, A., Malik, A., Kanemoto, K., Geschke, A., Nishijima, S., Lenzen, M., 2016. Substantial nitrogen pollution embedded in international trade. *Nat. Geosci.* 9, 111–115. Nature Publishing Group. Available from: <http://www.nature.com/articles/ngeo2635>.
- Pecl, G.T., et al., 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355, 1–9. Available from: <http://science.sciencemag.org/content/355/6332/eaai9214>.
- Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333, 1289–1291. American Association for the Advancement of Science. Available from: <http://www.ncbi.nlm.nih.gov/pubmed/21885781>.
- R Core Team, 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Safi, K., Pettorelli, N., 2010. Phylogenetic, spatial and environmental components of extinction risk in carnivores. *Glob. Ecol. Biogeogr.* 19, 352–362. <https://doi.org/10.1111/j.1466-8238.2010.00523.x>. Wiley/Blackwell (10.1111). Available from.

- Santini, L., Butchart, S.H.M., Rondinini, C., Benítez-López, A., Hilbers, J.P., Schipper, A.M., Cengic, M., Tobias, J.A., Huijbregts, M.A.J., 2019. Applying habitat and population-density models to land-cover time series to inform IUCN Red List assessments. *Conserv. Biol.* <https://doi.org/10.1111/cobi.13279>. John Wiley & Sons, Ltd (10.1111). Available from.
- Seiferling, I., Proulx, R., Wirth, C., 2014. Disentangling the environmental-heterogeneity–species-diversity relationship along a gradient of human footprint. *Ecology* 95, 2084–2095. <https://doi.org/10.1890/13-1344.1>. John Wiley & Sons, Ltd. Available from.
- Semper-Pascual, A., Macchi, L., Sabatini, F.M., Decarre, J., Baumann, M., Blendinger, P.G., Gómez-Valencia, B., Mastrangelo, M.E., Kuemmerle, T., 2018. Mapping extinction debt highlights conservation opportunities for birds and mammals in the South American Chaco. *J. Appl. Ecol.* 55, 1218–1229. <https://doi.org/10.1111/1365-2664.13074>. John Wiley & Sons, Ltd (10.1111). Available from.
- Spear, D., Foxcroft, L.C., Bezuidenhout, H., McGeoch, M.A., 2013. Human population density explains alien species richness in protected areas. *Biol. Conserv.* 159, 137–147. Elsevier. Available from. <https://www.sciencedirect.com/science/article/pii/S0006320712004909>.
- Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., Packer, C., 2017. Future threats to biodiversity and pathways to their prevention. *Nature* 546, 73–81. Nature Publishing Group. Available from. <http://www.nature.com/doifinder/10.1038/nature22900>.
- Tracewski, Ł., Butchart, S.H.M., Di Marco, M., Ficetola, G.F., Rondinini, C., Symes, A., Wheatley, H., Beresford, A.E., Buchanan, G.M., 2016. Toward quantification of the impact of 21st-century deforestation on the extinction risk of terrestrial vertebrates. *Conserv. Biol.* 30, 1070–1079. <https://doi.org/10.1111/cobi.12715>. John Wiley & Sons, Ltd (10.1111). Available from.
- Venter, O., et al., 2014. Targeting global protected area expansion for imperiled biodiversity. *PLoS Biol.* 12, e1001891. Public Library of Science. Available from. <http://dx.plos.org/10.1371/journal.pbio.1001891>.
- Venter, O., et al., 2016a. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nat. Commun.* 7, 12558. Nature Publishing Group. Available from. <http://www.nature.com/doifinder/10.1038/ncomms12558>.
- Venter, O., et al., 2016b. Global terrestrial human footprint maps for 1993 and 2009. *Sci. Data* 3, 160067. Nature Publishing Group. Available from. <http://www.nature.com/articles/sdata201667>.
- Visconti, P., et al., 2016. Projecting global biodiversity indicators under future development scenarios. *Conserv. Lett.* 9, 5–13. <https://doi.org/10.1111/conl.12159>. John Wiley & Sons, Ltd (10.1111). Available from.
- Watson, J.E.M., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. *Nature* 515, 67–73. Nature Research. Available from. <http://www.nature.com/doifinder/10.1038/nature13947>.
- Watson, J.E.M., Jones, K.R., Fuller, R.A., Marco, M Di, Segan, D.B., Butchart, S.H.M., Allan, J.R., McDonald-Madden, E., Venter, O., 2016. Persistent disparities between recent rates of habitat conversion and protection and implications for future global conservation targets. *Conserv. Lett.* 9, 413–421. <https://doi.org/10.1111/conl.12295>. Available from.
- Yackulic, C.B., Sanderson, E.W., Uriarte, M., 2011. Anthropogenic and environmental drivers of modern range loss in large mammals. In: *Proceedings of the National Academy of Sciences of the United States of America* 108, 4024–9. National Academy of Sciences. Available from. <http://www.ncbi.nlm.nih.gov/pubmed/21368120>.