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Policy analysis

Habitat loss, extinction predictability and conservation efforts in the terrestrial ecoregions

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ABSTRACT

The destruction of natural habitats is causing loss of biodiversity and ecosystem services. Although a "zero deforestation" is targeted, agriculture expansion caused by increasing human population and per capita consumption might boost the destruction of natural habitats in the coming decades. Here, we estimated the current and future extinction crisis in terrestrial ecoregions caused by habitat destruction and related this pattern with the current conservation efforts. We applied an Endemics-Area Relationship to assess vertebrates' potential extinctions in 513 ecoregions based on current land cover data and a future scenario of habitat loss. We compared our predictions to the proportion of the ecoregions' area formally protected, testing the concordance between threat distribution and conservation efforts. Finally, we evaluated how the distribution of threat relates to the biodiversity hotspots delimitation. We found that 2134 endemic vertebrates are currently threatened due to accumulated habitat loss, which is consistent with the assessment of the IUCN Red List. Further, this threat could overtake 4209 species when considering habitat loss projections to 2040. Our findings indicate a high concentration of threat in a few megadiverse localities, some of them outside the biodiversity hotspots. We found little overlap between our predictions of extinction and current protected areas distribution. This study supports current biodiversity crisis diagnoses and the expected recrudescence of Anthropocene defaunation in the future when considering scenarios of further habitat destruction. Our analysis also contributes to the definition of global priorities to prevent further biodiversity loss.

1. Introduction

An accelerated biodiversity loss is under way on Earth (Balmford et al., 2003). For instance, the abundance of terrestrial vertebrates reduced by 60% since 1970 (Grooten and Almond, 2018), and 198 vertebrates' extinctions have been recorded since 1900, which is at least 100 times more than what is naturally expected (Ceballos et al., 2015). This crisis is the consequence of human enterprises that resulted in a new age on Earth, the Anthropocene (Lewis and Maslin, 2015). Among the anthropic changes on Earth, habitat conversion represents the leading cause of species extinctions, being agricultural activities the drivers of the majority of the destruction of natural areas (Foley et al., 2005). Furthermore, the growth of the human population and the change in consumption patterns have been causing an increasing demand for food, fuel, fiber, and livestock feed (Tilman et al., 2011). As a result, several studies have projected an accentuated agricultural expansion in the next decades (Asselen and Verburg, 2013; Laurance et al., 2014) which might require further modification on natural areas,

causing more impact on species populations (but see Dobrovolski et al., 2013).

In this scenario of increasing destruction of natural vegetation and, consequently, species' population decline, it is essential to quantify and understand the effects of habitat loss across space. One of the main approaches to quantify the "biodiversity crisis" is the species-based monitoring, synthesized on the IUCN Red List (IUCN; https://www.iucnredlist.org/). The IUCN Red List is a valuable tool for conservation, assembling a large amount of data of species under the supervision of experts, yielding in a comprehensive and accessible conservation database (Rodrigues et al., 2006). However, the individual assessment of the extinction risk of species requires considerable effort and only addresses the risk retroactively. Thus, finding alternative, theory-based approaches that allow complementary assessments of the current and future state of biodiversity can help the understanding of this crisis and guide efforts to overcome it. The species-area relationship (SAR) and endemics-area relationship (EAR) are examples of this approach. More specifically, the backward kind of SAR/EAR (i.e., an area decrease

resulting in species richness decrease) has been used extensively as a way of quantifying biodiversity loss due to habitat destruction (e.g., Thomas et al., 2004; Pereira et al., 2010; Bellard et al., 2014). To specifically address the potential biodiversity loss at highly vulnerable and irreplaceable areas, Brooks et al., 2002 applied a backward EAR and predicted the number of vertebrates and plants at extinction risk due to accrued habitat loss. However, the analysis was restricted to the biodiversity hotspots (BH). Although BH represents probably the most successful global priority scheme, they cover only 16% of the global terrestrial area, being most of the land bypassed in this analysis. More recently, after the delimitation of ecoregions (Olson et al., 2001), the use of ecoregions as biogeographic units has become more common in global analysis on conservation topics (e.g., Hoekstra et al., 2005; Jenkins and Joppa, 2009). Therefore, using a simple tool as the EAR, there is an opportunity to conduct a global analysis in the ecoregions of the effect of habitat loss on biodiversity and modeling scenarios for the future considering the land-use change. Alongside, evaluating the spatial correlation between the distribution of protected areas and the threats to biodiversity is a crucial task. Such analysis can improve the knowledge of the main elements that compose the biodiversity crisis, thereby allowing more informed conservation actions.

Here, we used EAR to quantify extinction risk in the terrestrial ecoregions, predicting the threat of extinction of endemic vertebrates due to accumulated habitat loss. The risk assessment had two steps. In the first step, we evaluated the risk of extinction of endemic vertebrates on the ecoregions due to the historical habitat loss that occurred until the present time. This step also worked as a model validation since we compared our assessment with independent risk assessment of extinction risk of the IUCN Red List. The second step was the risk assessment of extinction for the future, using for this the historical habitat loss coupled to a future land use scenario. Moreover, we could assess the vulnerability of the protected areas network by confronting the possible upcoming habitat loss and species extinction with the protected areas coverage. Finally, we explore the concordances and novelties of our results with the BH to evaluate the merits and shortfalls of this approach.

2. Methods

2.1. EAR

The SAR is a well-documented empirical model that infers that, the increase in available area is accompanied by an increase in the number of species (Rosenzweig, 1995). The elementary form of SAR is the power function as proposed by Arrhenius (1921):

$$S = cA^z$$

where the S is the number of species in a given area, A, and c and z are constants. Harte and Kinzig (1997) argued that the relationship is also valid for endemic species. On the endemics-area relationship (EAR), considering an area *a* that is part of a larger area *A*, the number of species that occurs exclusively in the area *a* increases alongside the area of *a*. Therefore:

$$E = c'a^{z'}$$

where the *E* is the number of endemic species of a given area *a* and c' and z' are constants, being z' dependent of and always greater than z.

To predict the number of endemic species threatened with extinction in the ecoregions in the present and the future, we used a backward derivation of the EAR power function:

$$E_{original} - E_{new} = E_{original} - E_{original} (a_{new}/a_{original})^{z'}$$

In this function, assuming that an initial ecoregion area $a_{original}$ is reduced to an area a_{new}, the initial number of endemic species found on that ecoregion $E_{original}$ declines to E_{new}. The value of z commonly used on SAR is 0.25. (Brooks et al., 2002; Thomas et al., 2004). However, the

EAR value of z' is always greater than its value on SAR (Harte and Kinzig, 1997), and has been reported to vary around 0.75 and 1.5 for vertebrates on a continental scale (Storch et al., 2012). Here, we use the intermediate value of 1 for z. (see Appendix A for further discussion).

To assess our EAR model, we fitted a linear regression of the number of the predicted endemic extinctions in each ecoregion considering the habitat loss that occurred until 2015 with the number of endemics that are currently considered threatened or extinct by IUCN in the same ecoregion. The expectation is that, in each ecoregion, our predictions are approximately the number of endemic species threatened or already extinct (i.e., a regression with a slope of 1). We estimated the confidence intervals for the coefficient intervals using the profile likelihood method.

2.2. Ecoregions

We used terrestrial ecoregions as primary biogeographic units to assess the risk of extinction of endemic vertebrates. The ecoregions map used here (TNC, 2009) consists of 814 ecoregions divided into 14 different biomes. We excluded ecoregions in Antarctica and those classified as Rock and Ice or Inland Water.

2.3. Species

We quantified the original number of endemics in the ecoregions using the spatial data of 27,319 species of terrestrial vertebrates, available for amphibians, birds, mammals, and reptiles (IUCN, 2017; BirdLife International and NatureServe, 2016). This dataset represents 80% of the amphibians, 99% of the birds, 91.8% of mammals, and 41.2% of reptiles currently described. From this data, grids of 0.1° x 0.1° resolution were derived and then overlaid with the ecoregions in order to identify which species are endemics. We considered as endemic the species that had at least 90% of their distribution area restricted to a single ecoregion. We found endemics in 513 ecoregions.

We obtained the assessment of extinction risk from the IUCN Red List (2018) for the endemic vertebrates we identified. We compared our risk assessment based on current habitat loss with the IUCN assessment. For the risk assessments, we excluded endemics whose habitat preferences included the artificial environments category on IUCN since species that tolerate to human-modified habitats are unlikely to become extinct after habitat loss. As our assessment with the EAR can only identify the number of threatened species, being unable to define their level of threat, we reclassified the categories of IUCN Red List into a binary classification. Therefore, we considered species as threatened with extinction, those categorized as *Vulnerable*, *Endangered*, *Critically Endangered*, *Extinct in the Wild*, and *Extinct*. Species that were listed on threatened categories for fitting the criteria A1 or A2 from subcategories d or e, or from criterion D, were not included since they are threatened by other factors than habitat destruction.

2.4. Habitat loss

To quantify the current habitat loss on the ecoregions, we used the map of land cover from the *Climate Change Initiative Land Cover* (CCI LC) for the year 2015 with a resolution of 0.0028° x 0.0028° (ESA, 2017). For the forecasting into future conditions, we used the *CLUMondo* model of land system change for the year 2040, with a resolution of 0.083° x 0.083°. This model is based on regional economic demands, calculated by integrated assessment models and a dynamic social-environmental context, and presents a probable forthcoming land-use scenario (Asselen and Verburg, 2013). The scenario used in this study is based on the OECD Environmental Outlook scenario, which depicts probable developments in the economic and environmental conditions, being regarded as a baseline scenario. The land system trends captured in this scenario resemble those of the well-known SSP2 scenario (Wolf et al., 2018). We reclassified the classes of land use of both maps in

three categories: anthropic areas, habitat, and a category that embodies bare areas, water bodies, and permanent ice areas (see Appendix A: Table A1 and Table A2 in Supporting Information). To quantify the current habitat loss, we used the CCI LC map and considered the natural formations of vegetation categories as the available habitat for the species. For the original area available for the species, we considered the sum of anthropic areas and habitat areas, assuming that the anthropic areas were formerly habitat. We excluded water bodies, bare areas, and permanent ice areas for the habitat analyses since these areas are not subjected to natural vegetation clearance. For future habitat loss, we overlaid the CCI LC map and the *CLUMondo* land systems map and quantified the pixels that were converted from a natural land cover in 2015 to an anthropic one in 2040. Data for land use for both present and future were available for 775 ecoregions.

2.5. Protected areas

The polygon and point data from the World Database on Protected Areas (UNEP-WCMC and IUCN, 2018; http://www.protectedplanet.net) from May 2018 were rasterized to 0.1° x 0.1° resolution and used to determine the coverage of protection on the ecoregions. The zone of influence of the protection sites from the point data was estimated by generating buffers based on the reported area of each site. We excluded the protected areas with no reported areas from the analyses. Also, we excluded protected sites that were classified as "Not Applicable" by the IUCN criteria from the analyses. We included indigenous lands and PAs of all management categories of IUCN classification because we aimed to measure conservation efforts, rather than the effectiveness of the network of PAs to protect biodiversity. To evaluate the suitability of the current location of conservation sites in safeguarding the species on future agricultural expansion scenarios, we compared our predictions of future extinctions with the proportion of each ecoregion that is under protection. We also made exploratory comparisons with coverage of protection and endemics richness and remaining habitat.

2.6. Biodiversity hotspots

We used the map of the BH (Brooks et al., 2006) to evaluate the relationship between our risk assessment of extinction to the delimitation of the BH. For this evaluation, we created our definition of a hotspot based on our data of endemism and habitat loss. In this definition, an ecoregion is considered a hotspot when their number of endemic vertebrates is above the median of the ecoregions, and their current accumulated habitat loss has surpassed 50% (criteria further discussed in Appendix A). On the other hand, we considered ecoregions as a BH those that have half or more of their area inside the boundaries of at least one BH. We then confronted the two approaches of identification of hotspots using a chi-squared test, comparing the proportion of ecoregions classified as a hotspot by our criteria with the observed proportions based on the delimitation of the BH (see Appendix A, Table A3).

2.7. Statistical analyses

For general analyses, we used Pearson's correlation coefficient as the correlation statistics and Wilcoxon-Mann-Whitney, Kruskal–Wallis, and Dunn's Test for the analyses of variance. We performed all statistical analyses in the software R (R Core Team, 2017).

3. Results

3.1. Quantification of habitat loss

Presently, the terrestrial ecoregions have, on average, 63.2% (sd = 29.7%) of their habitat remaining, ranging from virtually none (e.g., Cape Verde Islands Dry Forests, Cape Verde) to 100% of natural
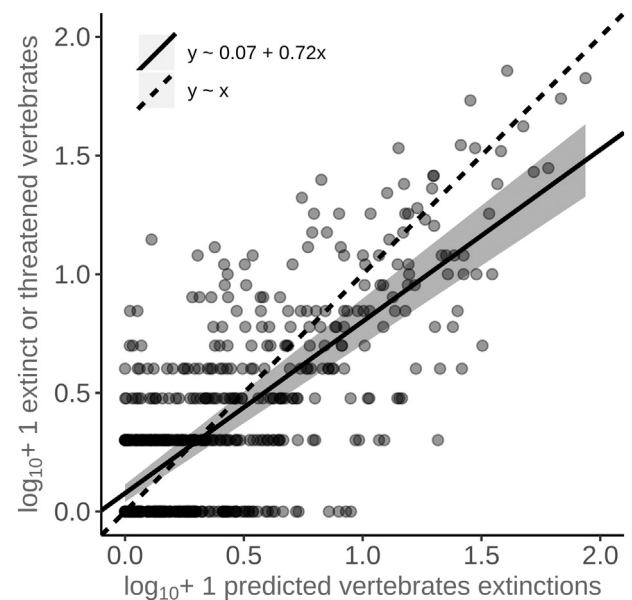

Fig. 1. Comparison between the number of vertebrates expected to be extinct due to the accumulated habitat loss until 2015 and the number of endemic vertebrates listed as extinct or threatened by IUCN. The dashed line indicates the expected relationship. The solid line and the gray band indicate the observed relationship and its confidence interval, respectively (based on the logarithm relationship).

cover (e.g., Northwestern Hawaii Scrub, United States). An additional 47,232,806 km² of natural area loss is expected as a result of the change of land use projected for 2040, lowering the global average to 34% (sd = 30.9%) (Appendix A, Fig. A2).

3.2. Current threat and model validation

We identified 6075 endemic species distributed in 513 ecoregions, with a mean of 7.6 endemics (sd = 16.8) per ecoregion. These endemics includes 2629 amphibians (43.3% of the total of endemics), 1308 birds (21.5%), 874 mammals (14.4%) and 1264 reptiles (20.8%). Considering the accumulated habitat loss until the year 2015, our EAR model predicted approximately 2134 endemic vertebrates (35.1% of the total of endemics) to be threatened with extinction, being ≈ 922 amphibians (43.2% of the total of predictions), 444 birds (20.8%), 294 mammals (13.8%) and 473 reptiles (22.2%).

The backward EAR successfully represented the threat of extinction to endemics of the ecoregions, but with a tendency to overestimation, as indicated by the slope of the linear regression of our predictions against the number of threatened species according to IUCN Red List (β = 0.7, 95% CI [0.65, 0.74]; Fig. 1). Also, by absolute numbers, we predict more risk to the endemic vertebrates from our analyses than the IUCN Red List since 1817 (29.9%) of the endemics are considered as threatened or already extinct by the list. For the four groups of terrestrial vertebrates separately, we found that the slope of the linear regression between our predictions against the IUCN Red List ranged from β = 0.47 95% CI [0.4, 0.54] to 0.83 95% CI [0.75, 0.9] being the birds the group with the weakest correlation and amphibians with the strongest one.

3.3. Prediction of future extinctions

Based on accumulated habitat loss expected until 2040, our model predicted 4209 extinctions of endemic terrestrial vertebrates, being ≈ 1895 amphibians (45% of the total of predictions), 855 birds (20.3%), 595 mammals (14.1%) and 865 reptiles (20.6%).

The top fifteen most affected ecoregions sum 1114 species

Table 1

Ecoregions with the highest number of predictions of terrestrial vertebrates' extinction due to expected habitat loss accumulated until 2040, the countries and biomes they belong, the percentage of their areas formally protected, and their percentage of remaining habitat in 2040.

| Ecoregion	Country	Biome	Area protected (%)	Remaining habitat 2040 (%)	Predictions of extinction 2040
Madagascar Lowland Forests	Madagascar	Tropical and Subtropical Moist Broadleaf Forests	19.2	6.1	140.9
Northwestern Andean Montane Forests	Colombia and Ecuador	Tropical and Subtropical Moist Broadleaf Forests	14.1	24.3	112.8
Solomon Islands Rain Forests	Solomon Islands	Tropical and Subtropical Moist Broadleaf Forests	1	45.6	98
Eastern Cordillera Real Montane Forests	Ecuador, Colombia, and Peru	Tropical and Subtropical Moist Broadleaf Forests	18.1	24.9	96.1
Peruvian Yungas	Peru	Tropical and Subtropical Moist Broadleaf Forests	14.5	23	89.3
Madagascar Dry Deciduous Forests	Madagascar	Tropical and Subtropical Dry Broadleaf Forests	6.4	0.8	84.3
Greater Negros-Panay Rain Forests	Philippines	Tropical and Subtropical Moist Broadleaf Forests	11.2	2.4	65.4
Madagascar Subhumid Forests	Madagascar	Tropical and Subtropical Moist Broadleaf Forests	8.3	1.6	63
Serra Do Mar Coastal Forests	Brazil	Tropical and Subtropical Moist Broadleaf Forests	33.4	21.8	58.6
Magdalena Valley Montane Forests	Colombia	Tropical and Subtropical Moist Broadleaf Forests	12.9	28.6	55
Mascarene Forests	France and Mauritius	Tropical and Subtropical Moist Broadleaf Forests	38.9	6.3	51.5
Northern Indochina Subtropical Forests	China, Laos, Myanmar, Thailand, and Vietnam	Tropical and Subtropical Moist Broadleaf Forests	4.7	3.4	51.2
Eastern Arc Forests	Tanzania and Kenya	Tropical and Subtropical Moist Broadleaf Forests	19.5	2.1	50.9
Albertine Rift Montane Forests	Democratic Republic of the Congo, Uganda, Rwanda, Burundi, and Tanzania	Tropical and Subtropical Moist Broadleaf Forests	18.2	5	50.4
Sierra Madre Del Sur Pine-Oak Forests	Mexico	Tropical and Subtropical Coniferous Forests	2.7	1.9	47.1

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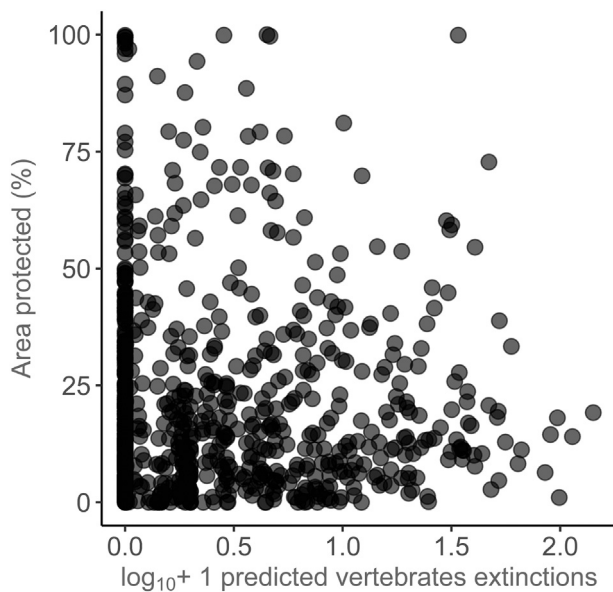
Fig. 2. Scatterplot of the relationship between the predictions of extinctions of terrestrial vertebrates based on the projected accumulated habitat loss for 2040 with the percentage of the ecoregion's area formally protected.

threatened with extinction due to 2040 accumulated habitat loss (Table 1). This amount represents more than one-quarter of the total of species predicted to go extinct and in 1.2% of the total area of all ecoregions (Table 1).

Considering the extinctions and extinction debt accumulated until 2015, the additional extinctions after 2040 habitat loss will result in the increase of the debt by 2075 species (34.2% of all endemics). The top fifteen ecoregions sum 29.2% of all extra extinctions. Among these ecoregions, 13 of them are part of tropical biomes (Appendix A, Fig. A3).

3.4. Vulnerability of current protection network

We found that 14.2% of the area of ecoregions harboring endemic vertebrates are formally protected. No significant correlation was found between the percentage of protected areas on the ecoregions and our predictions of future extinctions ($r = 0.07$, $p = .78$) (Figs. 2–3) or with the distribution of endemics vertebrates ($r = 0.01$, $p > .69$; Appendix A, Fig. A5b). However, there is a weak correlation between the protection of ecoregions with the current remaining habitat ($r = 0.26$, $p < .05$; Appendix A, Fig. A5a).

3.5. Comparison with biodiversity hotspots

While 369 of the ecoregions (46.2%) analyzed have at least half of their area inside the delimitation of the BH, we identified only 163 ecoregions (20.4%) as hotspots based on our criteria and data of endemism and habitat loss (Fig. 4). We were able to highlight 44 ecoregions that are not regarded as a BH but have a high number of expected extinctions, such as Dry Chaco, Jian Nan Subtropical Evergreen Forests, and Changjiang Plain Evergreen Forests. On the other hand, 250 of the ecoregions considered as BH were not considered as such by our criteria. These ecoregions have on average, less predictions of extinction when compared with those that are solely categorized as hotspot by our classification or those that share the hotspot status by both criteria (Kruskal-Wallis $\chi 2 = 303.2$, df = 3, $p < .01$; Dunn's Test $p < .05$; Appendix A, Fig. A4a). Moreover, we found a significant difference concerning the distribution in the axis of habitat loss and endemic richness when comparing the ecoregions classified as BH with the ecoregions classified as hotspots by our criteria ($\chi 2 = 1554.5$,

df = 3, $p < .01$; Appendix A, Table A3).

Despite the divergence between the two approaches of hotspots classification, the concordance is apparent when we observe the overlap between the ecoregions classified as BH with the ecoregions with the highest number of expected future extinctions (Appendix A, Fig. A6). When considering the expected habitat loss accumulated until 2040, ecoregions classified solely as BH have on average a higher number of additional expected endemics extinctions when compared with the ecoregions classified as hotspots solely by our data and criteria (Kruskal-Wallis $\chi 2 = 157$, df = 3, $p < .01$; Dunn's Test $p < .05$; Appendix A, Fig. A4b).

4. Discussion

This study presents an assessment of the possible effect of current and future habitat destruction on biodiversity, by applying the EAR on terrestrial vertebrates distributed across global terrestrial ecoregions. Based on the premise that loss of natural areas leads to extinction of species, we pinpointed geographical patterns of expected extinction, presenting ecoregions that most likely have their biodiversity threatened in present times and those that might have their biodiversity threatened in the future. Using the fundamental concepts of irreplaceability and vulnerability, we highlight priority areas for conservation, complementing the well-established biodiversity hotspots approach (Myers et al., 2000). We also assessed how the current distribution of protected areas relates to our predictions of threat of future extinction.

We believe that the use of EAR to predict extinctions should not be considered a substitute to other methods of risk assessments. Rather, we perceive the complementary value of such approach in addressing some of the incompleteness of more nuanced assessments. For instance, the main limitation of species-based estimates of threat is associated with the lack of comprehensive knowledge on species abundance and its dynamics. As a result, many species cannot be assessed regarding their threat of extinction by this methodological approach. In the IUCN Red List, this gap of assessment is represented in the "Data Deficient" category. As the EAR is based only in species richness and habitat loss, by including these data deficient species we were able to estimate threat of extinction in a broader, although more imprecise, manner. We found that almost one fourth (23.5%) of the endemic vertebrates are in this Data Deficient category. This knowledge gap could partially explain the higher number of threatened species on our analysis when compared with the Red List since some species might be threatened but have not been assessed yet. Data deficient species have a higher chance of being threatened with extinction (Jetz and Freckleton, 2015) because they are generally rare, underrepresented in protected areas, and have a large part of their geographic area overlapping with human-modified areas (Nori and Loyola, 2015).

Another contribution to risk assessments that the use of EAR to predict extinctions could bring is that it allows the conservation planning to be more up to date to the ongoing destruction of habitat since it does not depend on individual assessment of species, which can be costly and time-consuming (Rondinini et al., 2014). The EAR potentiality can be improved when associated with quantitative scenarios that assess the impact of alternative paths of socioeconomic development on biodiversity (Pereira et al., 2010). With the expected upcoming improvement of high-resolution and real-time satellite data for land use (Pettorelli et al., 2014; Hansen et al., 2013; https://www.globalforestwatch.org/), the EAR comes as a strong ally for a rapid assessment of current and future impacts on ecoregions and the definition of priorities for conservation action. With this long-standing "ecological law", we were able to compare the level of vulnerability of ecoregions, as was done for "Crisis Ecoregions" (Hoekstra et al., 2005), but also including the irreplaceability by considering the expected effect of habitat loss on biodiversity.

A significant result of our study is the comparison with the successful approach for conservation priorities, the Biodiversity Hotspots
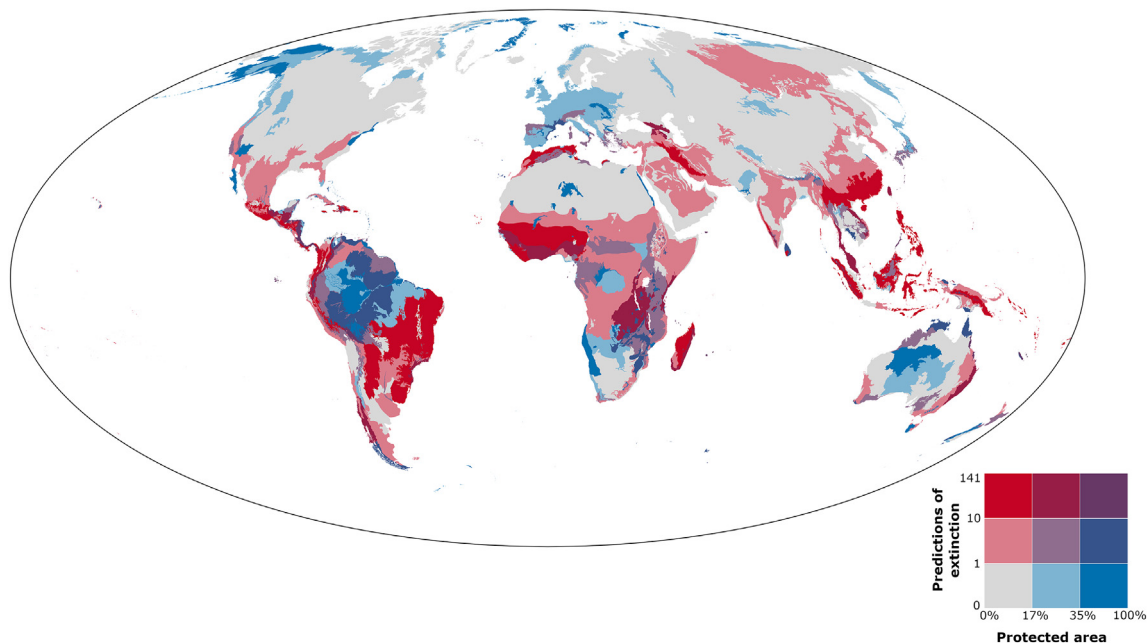
Fig. 3. Bivariate map displaying the relationship between the number of endemics vertebrates predicted to extinction due to the projected accumulated habitat loss until 2040 and the percentage of the ecoregion area formally protected. Darker blue shades indicate more coverage by protected areas. Darker red shades indicate more predictions of extinction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
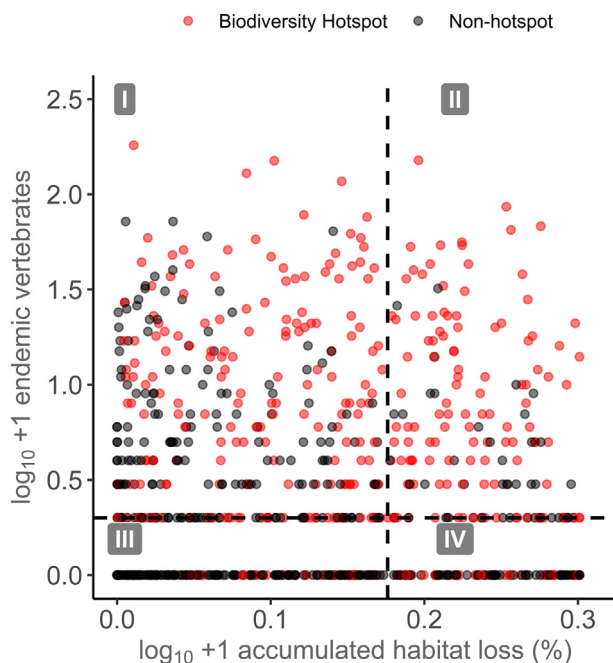

Fig. 4. The relationship of vulnerability (current accumulated habitat loss) and irreplaceability (predictions of extinction) in the ecoregions in the present time. The colors of the dots indicate whether the ecoregion is considered a biodiversity hotspot (red) or not (black). The horizontal dashed line represents the median of endemism, the vertical line represents 50% of accumulated habitat loss, and they delimit four quadrants (I-IV). By our definition, we considered an ecoregion a hotspot when their habitat loss was above 50% and the endemism above the median (II quadrant). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Myers et al., 2000). The BH have received notable attention in terms of the scientific debate and as a tool to attract investments to conservation, highlighting global sensitive areas due to their high plant endemism and severe habitat loss (Brooks et al., 2006). The delimitation of the hotspots encompasses large areas, often harboring multiple ecoregions and countries. Because of that, planning conservation policies for an entire BH can be hindered because of international conflicts and difficulties in resource allocation. As a result of that, efforts to identify critical areas for conservation on finer scales within the hotspots boundaries have been arising in the conservation literature (e.g., Faleiro et al., 2013). By using ecoregions to identify future global priority areas, our results collaterally highlighted smaller areas, inside the hotspots, with different levels of threat. For instance, Madagascar consists of eleven ecoregions and exhibited a higher number of expected extinctions on the coastal region, which comprises of Madagascar Lowland Forests and Madagascar Dry Deciduous Forests ecoregions. Moreover, our analysis complements the hotspots delimitation, pointing to ecoregions that are not considered hotspots but will be at a high biodiversity risk. For example, the Dry Chaco was considered vulnerable by our analysis, following other studies that had already point it out as an ecoregion that is highly representative of Neotropical biodiversity (e.g., Loyola et al., 2009; Villalobos et al., 2013).

Considering that the main effort to hold back biodiversity loss has been the implementation of protected areas, our analyses contributed to its evaluation. By using endemic vertebrates' distribution and focusing on the most degraded habitats, our approach prioritized areas that are vulnerable and harbors irreplaceable biodiversity. Our results suggest that the current distribution of protected areas might not be consonant with the areas that in the future might harbor most of the threatened endemic vertebrates. Previous studies have already pointed to the lack of overlap between loss of habitat and the location of protection sites (Hoekstra et al., 2005; Kehoe et al., 2017a). One explanation for this pattern could be that protected areas are favored to be in more intact areas or in areas with distinct species richness. Our data appears to partially support this scenario, since we found some correlation between protection of the ecoregions and current remaining habitat. However, we found no correlation between the protection coverage and the distribution of endemics vertebrates. It is important to note that such orientation of the protection network is only relevant to conservation when the protected areas are located in intact areas that are representative of biodiversity, but are also under the pressure of human activities, otherwise the protected area presence might not represent a change in the fate of a landscape (see Monteiro et al., 2018).

Considering the scenario of habitat destruction, thousands of vertebrate species might face extinction risk in the future. Being aware of the number of future extinctions and where they are more likely to occur, gives us an opportunity window to take precautionary actions and avoid further biodiversity loss. However, to make these actions possible, we must mitigate the primary driver of habitat loss, the agriculture expansion. A "zero deforestation" policy has been proposed in many fora (e.g., Brown and Zarin, 2013) and should be broadened to incorporate the conservation of nonforested natural environments, which are also threatened and represent habitat for many species. Moreover, it is crucial to recognize that agricultural activity can be combined with biodiversity-friendly practices. It is possible to meet the growing demands for agricultural products and simultaneously improve the conservation of species. Foley et al. (2011) arguments that if we direct our efforts into improve yields of low productive areas, this could result in the actual improvement of environmental conditions without requiring expansion of agriculture to meet the demands for agricultural products. An instance of this is the recent history of the Brazilian Amazon forest. From 2005 to 2013, there was a 70% decrease in the deforestation rates in Brazilian Amazon simultaneously with an increment in soy and beef production (Nepstad et al., 2014). This pattern is a result of governmental, market, and systematic societal policies of sanctions for irregular producers and positive reinforcements to producers that promote productivity and sustainability. This practical situation is a showcase of how future policies must be taken from now on to balance conservation and economic growth (but see the recent increase in deforestation, Dobrovolski et al., 2018).

Here, we present the possible consequences that the reduction of natural areas can have on biodiversity. However, our results should be seen with cautious. Our model tended to overestimate the threat of extinction, and we acknowledge that this is probably related to the uncertainty about the exact shape and slope of the EAR, that can affect the accuracy of estimates based on this method (Guilhaumon et al., 2008; Keil et al., 2015). There are also inherent problems with the more simplistic equation of EAR we utilized here that assumes that all species respond equally to the loss of habitat, being this habitat loss permanent, instantaneous, and resulting in a single contiguous fragment of habitat surrounded by an inhospitable matrix. In the real world, habitat loss is a historical process, that in some situations, leaves a fragmented landscape with varying degrees of a tolerable matrix. The EAR is a neutral model, that is, a model that assumes that the identity of the species or individuals is not relevant to explain a pattern (Hubbell, 2001). Although neutral models have pertinent criticisms, this kind of model remains relevant to address specific types of questions, especially for macroecological ones. While our approach might not be the best to predict extinction in a fragment of a landscape, a neutral model like EAR can function as null hypothesis and as a start point for understanding the general pattern of extinction at a global scale (Maurer & McGill, 2004), which was the main purpose of our study. In our model, we did not consider that some species could respond to the loss of habitat with migration to more suitable areas or even adapt to the new conditions. By not considering this, we may have estimated the extinction due to habitat loss to a higher number than what we will observe. Also, although the area is a strong predictor of species richness, numerous threats can have an impact on the species survivorship that we did not address. In this study, we presented a method to evaluate threats to biodiversity and conservation efforts using bare minimum data. Other studies have also projected scenarios of extinction, using multiples variables, since the stressors of biodiversity extent beyond habitat area (Kehoe et al., 2017b; Chaudhary et al., 2015; Newbold et al., 2015). Furthermore, habitat loss combined with other threats could lead to more extinctions than would be expected with the simple sum of threats if we consider the synergetic effects (Romero-Muñoz et al., 2019).

In sum, our study quantified the possible the magnitude of terrestrial vertebrates' extinction worldwide in relation to the habitat destruction. Because of its importance, the information on projected habitat destruction and its effect on biodiversity must be included in conservation prioritization (Dobrovolski et al., 2013; Pouzols et al., 2014) if we expect to shift the ongoing trend of an even more severe biodiversity loss. Moreover, our analysis contributes to the refinement of global conservation priorities, such as the BH framework, by displaying the gradient of threat inside their delimitations and by proposing the addition of new areas relevant for conservation. We also suggest that the global protected area network, our fundamental conservation effort, might not be aligned with probable upcoming vertebrates' extinction in the terrestrial ecoregions. Mitigate the biodiversity loss figures as one of the main challenges for humanity in this century. Using global data and projections of socioeconomic change allied with fundamental theoretical ecological tools can help to quantify and overcome the upcoming challenges.

CRediT authorship contribution statement

Daniel Gonçalves-Souza: Conceptualization, Methodology, Data curation, Formal analysis, Validation, Writing - original draft, Writing - review & editing, Funding acquisition. **Peter H. Verburg**: Methodology, Data curation, Formal analysis, Software, Writing - review & editing. **Ricardo Dobrovolski**: Conceptualization, Formal analysis, Data curation, Funding acquisition, Methodology, Supervision, Validation, Writing - original draft, Writing - review & editing.

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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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108579.

References

Arrhenius, O., 1921. Species and area. J. Ecol. 9, 95–99. https://doi.org/10.2307/2255763.

Asselen, S., Verburg, P.H., 2013. Land cover change or land-use intensification: simulating land system change with a global-scale land change model. Glob. Chang. Biol. 19, 3648–3667. https://doi.org/10.1111/gcb.12331.

Balmford, A., Green, R.E., Jenkins, M., 2003. Measuring the changing state of nature. Trends Ecol. Evol. 18, 326–330. https://doi.org/10.1016/S0169-5347(03)00067-3.

Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., Courchamp, F., 2014. Vulnerability of biodiversity hotspots to global change. Glob. Ecol. Biogeogr. 23, 1376–1386. https://doi.org/10.1111/geb.12228.

BirdLife International and NatureServe, 2016. Bird Species Distribution Maps of the World. vol. Version 6.0 BirdLife International, Cambridge,UK and NatureServe, Arlington, USA.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Rylands, A.B., Konstant, W.R., Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. Conserv. Biol. 16, 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Rodrigues, A.S., 2006. Global biodiversity conservation priorities. Science 313, 58–61. https://doi.org/10.1126/science.1127609.

Brown, S., Zarin, D., 2013. What does zero deforestation mean? Science 342, 805–807. https://doi.org/10.1126/science.1241277.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253. https://doi.org/10.1126/sciadv.1400253.

Chaudhary, A., Verones, F., de Baan, L., Hellweg, S., 2015. Quantifying land use impacts on biodiversity: combining species–area models and vulnerability indicators. Environmental science & technology 49, 9987–9995. https://doi.org/10.1021/acs.est.5b02507.

Dobrovolski, R., Loyola, R.D., Guilhaumon, F., Gouveia, S.F., Diniz-Filho, J.A.F., 2013. Global agricultural expansion and carnivore conservation biogeography. Biol. Conserv. 165, 162–170. https://doi.org/10.1016/j.biocon.2013.06.004.

Dobrovolski, R., Loyola, R., Rattis, L., Gouveia, S.F., Cardoso, D., Santos-Silva, R., Diniz-Filho, J.A.F., 2018. Science and democracy must orientate Brazil's path to sustainability. Perspectives in Ecology and Conservation 16, 121–124. https://doi.org/10.1016/j.pecon.2018.06.005.

ESA, 2017. Land cover CCI product user guide version 2.0. Available at. http://maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf> (Access in jul 17. 2018).

Faleiro, F.V., Machado, R.B., Loyola, R.D., 2013. Defining spatial conservation priorities in the face of land-use and climate change. Biol. Conserv. 158, 248–257. https://doi.org/10.1016/j.biocon.2012.09.020.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Helkowski, J.H., 2005. Global consequences of land use. Science 309, 570–574. https://doi.org/10.1126/science.1111772.

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Balzer, C., 2011. Solutions for a cultivated planet. Nature 478, 337–342. https://doi.org/10.1038/nature10452.

Grooten, M., Almond, R.E.A., 2018. Living Planet Report 2018: Aiming Higher. WWF, Gland, Switzerland, pp. 22–100.

Guilhaumon, F., Gimenez, O., Gaston, K.J., Mouillot, D., 2008. Taxonomic and regional uncertainty in species-area relationships and the identification of richness hotspots. Proc. Natl. Acad. Sci. 105, 15458–15463. https://doi.org/10.1073/pnas.0803610105.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A.A., Tyukavina, A., Kommareddy, A., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–853. https://doi.org/10.1126/science.1244693.

Harte, J., Kinzig, A.P., 1997. On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. Oikos 417–427. https://doi.org/10.2307/3546614.

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecol. Lett. 8, 23–29. https://doi.org/10.1111/j.1461-0248.2004.00686.x.

Hubbell, S.P., 2001. The unified neutral theory of biodiversity and biogeography. In: Princeton University Press.

IUCN, 2017. Red List Spatial Data. Available at. http://www.iucnredlist.org/download_spatial_data> Downloaded on mar 25. 2017.

IUCN, 2018. The IUCN red list of threatened species. Version 2018-1. Available at. www.iucnredlist.org Downloaded on feb 02. 2018.

Jenkins, C.N., Joppa, L., 2009. Expansion of the global terrestrial protected area system. Biol. Conserv. 142, 2166–2174. https://doi.org/10.1016/j.biocon.2009.04.016.

Jetz, W., Freckleton, R.P., 2015. Towards a general framework for predicting threat status of data-deficient species from phylogenetic, spatial and environmental information. Philos. Trans. R. Soc. B 370, 20140016. https://doi.org/10.1098/rstb.2014.0016.

Kehoe, L., Romero-Muñoz, A., Polaina, E., Estes, L., Kreft, H., Kuemmerle, T., 2017a. Biodiversity at risk under future cropland expansion and intensification. Nature ecology & evolution 1, 1129–1135. https://doi.org/10.1038/s41559-017-0234-3.

Kehoe, L., Senf, C., Meyer, C., Gerstner, K., Kreft, H., Kuemmerle, T., 2017b. Agriculture rivals biomes in predicting global species richness. Ecography 40, 1118–1128. https://doi.org/10.1111/ecog.02508.

Keil, P., Storch, D., Jetz, W., 2015. On the decline of biodiversity due to area loss. Nat. Commun. 6, 8837. https://doi.org/10.1038/ncomms9837.

Laurance, W.F., Sayer, J., Cassman, K.G., 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol. Evol. 29, 107–116. https://doi.org/10.1016/j.tree.2013.12.001.

Lewis, S.L., Maslin, M.A., 2015. Defining the Anthropocene. Nature 519, 171–180. https://doi.org/10.1038/nature14258.

Loyola, R.D., Kubota, U., da Fonseca, G.A., Lewinsohn, T.M., 2009. Key Neotropical ecoregions for conservation of terrestrial vertebrates. Biodivers. Conserv. 18, 2017–2031. https://doi.org/10.1007/s10531-008-9570-6.

Monteiro, L.M., Brum, F.T., Pressey, R.L., Morellato, L.P.C., Soares-Filho, B., Lima-Ribeiro, M.S., Loyola, R., 2018. Evaluating the impact of future actions in minimizing vegetation loss from land conversion in the Brazilian Cerrado under climate change. Biodivers. Conserv. 1–22. https://doi.org/10.1007/s10531-018-1627-6.

Maurer, B.A., McGill, B.J., 2004. Neutral and non-neutral macroecology. Basic and Applied Ecology 5, 413–422. https://doi.org/10.1016/j.baae.2004.08.006.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

Nepstad, D., McGrath, D., Stickler, C., Alencar, A., Azevedo, A., Swette, B., Armijo, E., 2014. Slowing Amazon deforestation through public policy and interventions in beef and soy supply chains. Science 344, 1118–1123. https://doi.org/10.1126/science.1248525.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Day, J., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50. https://doi.org/10.1038/nature14324.

Nori, J., Loyola, R., 2015. On the worrying fate of data deficient amphibians. PLoS One 10, e0125055. https://doi.org/10.1371/journal.pone.0125055.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V., Underwood, E.C., Loucks, C.J., 2001. Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. BioScience 51, 933–938.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P., Fernandez-Manjarrés, J.F., Chini, L., 2010. Scenarios for global biodiversity in the 21st century. Science 330, 1496–1501. https://doi.org/10.1126/science.1196624.

Pettorelli, N., Laurance, W.F., O'Brien, T.G., Wegmann, M., Nagendra, H., Turner, W., 2014. Satellite remote sensing for applied ecologists: opportunities and challenges. J. Appl. Ecol. 51, 839–848. https://doi.org/10.1111/1365-2664.12261.

Pouzols, F.M., Toivonen, T., Di Minin, E., Kukkala, A.S., Kullberg, P., Kuusterä, J., Moilanen, A., 2014. Global protected area expansion is compromised by projected land-use and parochialism. Nature 516, 383–386. https://doi.org/10.1038/nature14032.

. R Core Team. (2017). R: A Language and Environment for Statistical Computing. Vienna, Austria: R Core Team. Available at: http://www.r-project.org/.

Rodrigues, A.S., Pilgrim, J.D., Lamoreux, J.F., Hoffmann, M., Brooks, T.M., 2006. The value of the IUCN Red List for conservation. Trends Ecol. Evol. 21, 71–76. https://doi.org/10.1016/j.tree.2005.10.010.

Romero-Muñoz, A., Torres, R., Noss, A.J., Giordano, A.J., Quiroga, V., Thompson, J.J., Arispe, R., 2019. Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. Diversity and Distributions 25, 176–190.

Rondinini, C., Di Marco, M., Visconti, P., Butchart, S.H., Boitani, L., 2014. Update or outdate: long-term viability of the IUCN Red List. Conserv. Lett. 7, 126–130. https://doi.org/10.1111/conl.12040.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.

Storch, D., Keil, P., Jetz, W., 2012. Universal species-area and endemics–area relationships at continental scales. Nature 488, 78–81. https://doi.org/10.1038/nature11226.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–148. https://doi.org/10.1038/nature02121.

Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. Proc. Natl. Acad. Sci. 108, 20260–20264. https://doi.org/10.1073/pnas.1116437108.

TNC, 2009. Terrestrial Ecoregions. Available at. http://maps.tnc.org/gis_data.html> Downloaded on May 18. 2017.

UNEP-WCMC and IUCN, 2018. Protected Planet: [the World Database on Protected Areas (WDPA)/the Global Database on Protected Areas Management Effectiveness (GD-PAME)]. Online], [may/2018]. UNEP-WCMC and IUCN, Cambridge, UK Available at. www.protectedplanet.net.

Villalobos, F., Dobrovolski, R., Provete, D.B., Gouveia, S.F., 2013. Is rich and rare the common share? Describing biodiversity patterns to inform conservation practices for South American anurans. PLoS One 8, e56073. https://doi.org/10.1371/journal.pone.0056073.

Wolf, S., Schrammeijer, E.A., Schulp, C.J., Verburg, P.H., 2018. Meeting global land restoration and protection targets: what would the world look like in 2050? Glob. Environ. Chang. 52, 259–272. https://doi.org/10.1016/j.gloenvcha.2018.08.002.