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► **To cite this version:**

Victor Cazalis, Megan D. Barnes, Alison Johnston, James E.M. Watson, Cagan H. Sekercioglu, et al..
Mismatch between bird species sensitivity and the protection of intact habitats across the Americas.
Ecology Letters, In press, 10.1111/ele.13859 . hal-03321017

HAL Id: hal-03321017

<https://hal.science/hal-03321017>

Submitted on 16 Aug 2021

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Mismatch between bird species sensitivity and the protection of intact habitats across the Americas

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Abstract:

Protected areas are highly heterogeneous in their effectiveness at buffering human pressure, which may hamper their ability to conserve species highly sensitive to human activities. Here, we use 60 million bird observations from eBird to estimate the sensitivity to human pressure of each bird species breeding in the Americas. Concerningly, we find that ecoregions hosting large proportions of high-sensitivity species, concentrated in tropical biomes, do not have more intact protected habitat. Moreover, 266 high-sensitivity species have little or no intact protected habitat within their distributions. Finally, we show that protected area intactness is decreasing faster where high-sensitivity species concentrate. Our results highlight a major mismatch between species conservation needs and the coverage of intact protected habitats, which likely hampers the long-term effectiveness of protected areas at retaining species. We highlight ecoregions where protection and management of intact habitats, complemented by restoration, is urgently needed.

Data availability statement:

All spatial data analysed are open access and free to use for research. Bird abundance data were taken from eBird, version of October 2019 (accessed on the 30th of November 2019) and are available on request at <http://www.ebird.org>. Species distribution maps came from BirdLife International and HBW version 2019.1 and are available on request at <http://datazone.birdlife.org/species/requestdis>. Protected areas polygons are from the World Database on Protected Areas by UNEP-WCMC and IUCN, version of January 2020, and are available on request at www.protectedplanet.net. All scripts used to run data selection, processing and analyses, together with tables used in taxonomic alignment,

are available at: <http://doi.org/10.5281/zenodo.5004010>.

Keywords: Conservation; Wilderness; Protected areas; Human footprint; Threatened species

Authorship statement:

VC and ASLR designed the study with discussion and inputs from all authors. VC conducted the analyses. VC and ASLR wrote the first draft and all authors commented on several versions.

Acknowledgements:

We thank the numerous observers who contributed records to eBird, and to the eBird team at Cornell Lab of Ornithology for creating and managing this database. We also thank Thomas Brooks and Karine Princé for early comments on the study.

Running title: Bird sensitivity and PA intactness

Type of article: Letter

Number of words in the abstract: 144

Number of words in the main text: 5122

Number of references: 67

Number of figures: 3

Number of tables: 0

Introduction

Protected areas are clearly defined geographical spaces, recognised, dedicated and managed to achieve the long-term conservation of nature (UNEP-WCMC, IUCN and NGS, 2020). Acknowledged as a major biodiversity conservation tools (Watson et al., 2014; Maxwell et al., 2020), there has been a marked expansion in their extent over the past few decades and known coverage currently reaches 15.4% of global land surface (UNEP-WCMC, IUCN and NGS, 2021). Ongoing renegotiation of global policy targets are expected to result in a more ambitious 30% areal target (SCBD, 2020), which is likely to drive further expansion.

However, protected areas vary substantially in both their intended management (i.e., the level of protection as legally defined) and in the practical effectiveness of their implementation (Geldmann et al., 2018; Barnes et al., 2016). As a result, many protected areas are currently under intense and increasing human pressure (Jones et al., 2018; Venter et al., 2016a). For this reason, the percentage of area protected is on its own insufficient to evaluate protected area effectiveness (Rodrigues and Cazalis, 2020; Cazalis et al., 2019). A pure focus on protected area expansion, without guarantee of concomitant quality, has been criticised as encouraging fast expansion into areas of little value to biodiversity, or with little on-the-ground implementation effort (Barnes et al., 2018; Visconti et al., 2019).

This high level of degradation of some protected habitats may be a concern in some cases because degradation is known to impact many species (Di Marco et al., 2019; Watson et al., 2018; Gibson et al., 2011). However, it does not necessarily follow that all protected areas need to be in perfectly intact condition. Indeed, while many species are highly sensitive to human pressure (Barlow et al., 2016; Gibson et al., 2011), many others can tolerate some levels of, or even benefit from, anthropogenic land use change (Guetté et al., 2017; McKinney, 2006; Şekercioğlu et al., 2019). Given the need to reconcile biodiversity conservation and human development, two broad strategies have been proposed: land sparing, focused on setting aside intact habitats while concentrating human pressure elsewhere; and land sharing, integrating conservation and development by spreading human pressure across larger areas, including multiple use protected areas (Green et al., 2005; Phalan et al., 2011; Williams et al., 2017). In practice, the best strategy for each species depends on how it responds to human pressure (Green et al., 2005). Species that respond negatively to even low levels of pressure require strict management of sufficient expanses of intact habitats (with a concomitant concentration of human activities elsewhere; i.e., land sparing), whereas species that can tolerate moderate to high human pressure may be adequately protected in multi-use protected areas, or not need protected areas at all (i.e., land sharing).

The few studies quantifying species responses to increasing human pressure (based on gradients of agriculture yield or urban intensification) in the context of the land sparing/land sharing debate found that many species are strongly impacted by even low levels of human pressure, providing support for the need to set aside intact areas for their conservation (Phalan et al., 2011; Williams et al., 2017; Collas et al., 2017; Şekercioğlu et al., 2019). Understanding how these sensitive species are

distributed across the world may in turn shed light on the extent to which different regions are more or less dependent on the protection of intact habitat for the conservation of their biodiversity.

Here, we investigate the large-scale spatial variation in sensitivity to human pressure for 4,362 bird species, contrasting this with the distribution of intact protected habitat to highlight priorities for expanding or reinforcing intact protected habitat coverage. Taking advantage of the millions of field records collated through the eBird citizen science platform, we focus on the Americas as a study region. We first measure the sensitivity of 2,550 breeding species by modelling the relationship between abundance and human pressure as measured by the human footprint index (Williams et al. 2020). We then impute the sensitivity of the remaining 1,812 breeding species based on their traits, as abundance data were too scarce to measure sensitivity directly. Using ecoregions as spatial unit, we contrast spatial patterns in species sensitivity with the coverage of intact protected habitat of ecoregions, in order to identify the regions with a critical mismatch between the two. In addition, we identify that are highly sensitive to human pressure but whose distributions have minor or no coverage by intact protected habitats. Finally, we analyse these results in light of the recent trends in human footprint to understand if the adequacy of protected areas to the conservation of high-sensitivity species is improving or worsening.

Methods

Study area

We focused on the Americas (i.e., the Nearctic and Neotropical realms) given the large concentration of bird observations and wide ecological variation (from tropical to boreal biomes). We analysed data within the corresponding 325 terrestrial ecoregions (Olson et al., 2001) for which there is human footprint data (Figs. 2-3).

Species data

Bird distribution and abundance data

We used data from eBird (Sullivan et al., 2014), a unique online platform gathering hundreds of millions of bird observations across the globe. Observers report observations in checklists and provide information on sampling effort, allowing eBird data to be transformed into a dataset of relative abundance (Sullivan et al., 2009) while controlling for the most common observation biases (Johnston et al., 2021), as described below. We used the eBird dataset released in October 2019 (eBird, 2019).

In addition, we used species distribution data (coarse polygons delimiting the species' ranges) as mapped by BirdLife International and HBW (2019), having aligned the taxonomies between these two datasets by following the latter (Supplementary Methods 1).

Building a standard abundance dataset

We filtered the dataset following guidelines provided by the eBird team (Sullivan et al., 2009; Strimas-Mackey et al., 2020; Johnston et al., 2021), similarly to the data filtering process described in Cazalis et al., (2020); see details in Supplementary Methods 2.

To enable comparability of checklists, we restricted our dataset to recent observations (2010-2019), for which observers certified having reported all species identified, emerging from stationary counts or transects (with distance travelled <5km and duration between 0.5-10 hours; duration is then controlled for in analyses), and only kept checklists made by experienced observers (Supplementary Methods 3). To avoid pseudo replication, we removed observation duplicates (i.e., checklists made on the same place and date). We removed “not approved” observations, as well as marine and coastal species and we restricted observations to the species breeding range and season (Supplementary Methods 2).

The final dataset in our main analyses consisted of 59,583,879 observations and 404,086,397 inferred absences, structured into 3,449,486 checklists made by 44,013 observers and representing 4,362 species (all species whose breeding distribution intersects with the ecoregions considered in this study).

Accounting for observer differences

Even when the sampling protocol is similar, eBird checklists may greatly differ because of the important heterogeneity in observers' experience, skills, behaviour, and equipment. As mentioned

above, observations were filtered to include only those made by observers with a minimum level of experience. In addition, we calculated an individual observer calibration index, which we included as control variable in all subsequent analyses of eBird data. This index, is calculated from a mixed model with random effect of observer, then used to estimate the log-scaled number of species each observer is expected to report in an average sampling event (see details in Supplementary Methods 3; Johnston et al., 2018; Kelling et al., 2015).

Bird species traits

For each of the 4,362 species considered, we obtained data on eight species-level variables (that we call “traits” for simplicity; see Supplementary Methods 4). We extracted from BirdBase (Şekercioğlu et al., 2004, 2019) species primary habitat, primary diet, migratory status, specialisation index, body mass and taxonomic Order. We extracted from BirdLife International (2019) Red List status that we used as a quantitative variable, and calculated species’ breeding range size.

Landscape data

Protected areas

We used spatial protected area data from the World Database on Protected Areas (UNEP-WCMC & IUCN, 2020), following the standard filtering procedure (UNEP-WCMC and IUCN, 2019) that excludes ‘Man and Biosphere’ reserves, protected areas with no associated polygons and those that are not yet implemented (i.e., we kept only those ‘designated’, ‘inscribed’, or ‘established’).

Human footprint

We used maps of human footprint in 2000 and in 2013, in raster format at a resolution of ~1km (Williams et al., 2020). These maps are an updated and more complete version of the 1993-2009 index derived by Venter et al. (2016b), generated from the combination of eight human pressure variables (built environments, population density, night-time lights, crop lands, pasture lands, accessibility via roads, railways and navigable waterways) and ranging from 0 (perfect intactness) to 50 (extremely high pressure). Human footprint data have previously been used to analyse species’ responses to human pressures (Di Marco et al., 2018; Barnagaud et al., 2019; Cazalis et al., 2020).

We assigned to each checklist a value of human footprint in 2013 by calculating the mean value of human footprint in pixels intersecting by at least 1% a buffer around the checklist coordinates. We used a buffer of 2.5 km radius to ensure it covers the large majority of the area sampled by the selected travelling protocols.

Altitude

The altitude of each checklist was calculated as the mean altitude of all pixels from the Global Land One-kilometer Base Elevation raster (National Geophysical Data Center, 1999) intersecting by at least 1% the 2.5 km buffer around the checklist coordinates.

Net Primary Productivity

We calculated a Net Primary Productivity (NPP) value for each checklist, using NASA's Earth Observatory Team (2020) maps. We first created a raster layer by calculating for each cell the mean of NPP values from January 2014 to November 2016 (December 2016 data were not available). We then extracted for each checklist, the mean value of each pixel in this raster that intersected by at least 1% the 2.5 km buffer around the checklist coordinates.

Analyses

We analysed the data to answer four questions: (1) How sensitive are bird species to human footprint? (2) Where across the study area are species the most sensitive? (3) Is current protection of intact habitats matched to species' needs? (4) Are protected areas retaining intact habitats over time?

How sensitive are species to human footprint?

Direct measure of sensitivity (data-rich species)

We quantified directly the sensitivity to human footprint for a subset of 2,550 data-rich species, selected according to three conditions: ≥ 200 records with abundance; $\geq 80\%$ of all records with abundance (as 'X' often concerns observations with too many individuals to be counted, which could introduce a bias for gregarious species); and with distributions across a wide range of human footprint values. The latter were selected by first calculating the 1% and the 99% quantiles of human footprint from all checklists within each species' breeding distribution, and then keeping only those species for which quantiles differed by ≥ 25 (an arbitrary threshold corresponding to half of the human footprint range, chosen based on data exploration to be wide without excluding too many species).

For each of these 2,550 data-rich species, we ran a General Additive Model (GAM) modelling the relationship between species' abundance and human footprint of the checklists' location (assuming a negative binomial distribution of abundance and using the *bam* function; (Wood, 2011)). In order to enable a diversity of relationships, from linear to non-monotonous relations, we used a smoothed term on human footprint, but we constrained the degree of the smoothing function to 6 to avoid very complex functions (broadly speaking avoiding overfitting with multimodal relationships, see examples of relations in Fig. 1). In these models, we controlled for some of the most common sampling biases such as differences in sampling effort (logarithm of sampling duration; logarithm of number of observers; observer calibration index, using the maximum if there were multiple observers), differences in ecological conditions (altitude and NPP, both assuming parabolic responses; we could not use smoothed-terms here because of computing limitations), and large-scale patterns of spatial trends (interacting smooth-term with longitude and latitude), with the following structure:

$$\text{Abundance_species} \sim \text{s}(\text{human_footprint}, k=6) + \log(\text{duration}) + \log(\text{N_observers}) + \text{observer_calibration_index} + \text{altitude} + \text{altitude}^2 + \text{productivity} + \text{productivity}^2 + \text{te}(\text{longitude}, \text{latitude})$$

We then predicted the relative abundance of the species across a gradient of human footprint ranging from 0 to the maximum value of human footprint observed within the species' distribution, with a step of 0.05 (fixing all other variables to their median values) and extracted the average human footprint of this distribution weighted by predicted abundance (Fig. 1). Finally, we measured each species' sensitivity as the difference between 50 (i.e., maximum human footprint) and this weighted average (Fig. 1).

Imputed sensitivity (data-poor species)

We used information on species' traits to impute the sensitivity of the remaining (data-poor) 1,812 species, from the 2,550 data-rich species. To do so, we first linked the values of sensitivity measured for data-rich species to their traits using a linear model. We included in the model the species' primary habitat, primary diet, specialisation (log-scaled), body mass (log-scaled), Red List status, range size (log-scaled), migratory status, and taxonomic Order, with the following structure:

Sensitivity ~ Primary_Habitat + Primary_Diet + specialisation + log(Mass) + RedList + log(Range) + migration + Order

We then used this model to impute the sensitivity of the data-poor species (see details in Supplementary Methods 5).

We use species' sensitivity as a relative measure, to compare among species and regions (Supplementary Methods 6). We defined high-sensitivity species as the 25% most sensitive species (Fig. 1).

Where are bird assemblages the most sensitive?

As a measure of the sensitivity of bird assemblages to human footprint, we calculated for each ecoregion the proportion of all breeding species classified as high-sensitivity. The list of breeding species per ecoregion was obtained by overlapping species' breeding distributions with the ecoregion's boundaries.

We analysed whether our results were driven by methodological choices through two additional analyses. In the first one, using all species (N=4,362 species), we mapped two alternative measures of the sensitivity of bird assemblages to human footprint: median sensitivity across all species that breed in the ecoregion; and absolute number of high-sensitivity species per ecoregion (Fig. S5). In the second one, we investigated the effects of extreme imputation errors on the spatial pattern of the proportion of high-sensitivity species per ecoregion (Fig. S6).

Is intact habitat protection matched to species' needs?

We created a 0/1 raster layer of intact protected habitat across the study area as a transformation of the 2013 human footprint raster, by assigning the value 1 only to those pixels with intact habitat (human footprint value <4, Williams et al., 2020) whose centre was located within a protected area. We then used this layer to investigate if intact habitat protection is matched to species' conservation

needs (i.e., their sensitivity), both across space (ecoregions) and across species.

Across ecoregions

For each ecoregion, we measured the level of intact habitat protection as the proportion of its pixels (those included by >50% within the ecoregion) classified as intact protected habitat. We then analysed how this index relates to the proportion of high-sensitivity species per ecoregion, both quantitatively (using the Pearson correlation coefficient) and visually (mapping the correspondence between these variables using a bivariate colour scale).

For comparison, we also analysed two alternative measures of the investment in habitat protection per ecoregion: protected area extent (the fraction of the ecoregion covered by protected areas); and protected area intactness (the mean intactness of protected pixels, where intactness is the opposite of human footprint).

Across species

For each high-sensitivity species, we quantified their coverage by intact protected habitat. Given that a pixel measures $\sim 1 \text{ km}^2$, we calculated the area of intact protected habitat per species by summing the values in the 0/1 raster layer of intact protected habitat for pixels included (by >50%) within the species' breeding distribution.

We then assessed whether high-sensitivity species were adequately covered by intact protected habitat, by comparing their coverage by intact protected habitat against a predefined representation target. For each species, this target was calculated based on a widely-used approach (e.g., Rodrigues et al., (2004), Maxwell et al., (2020), Butchart et al., (2015)) whereby species with very small ranges ($< 1000 \text{ km}^2$) have a 100% target, those with very widespread ranges ($>250,000 \text{ km}^2$) have a 10% target, with the target for species with ranges of intermediate size being interpolated between these two extremes. A high-sensitivity species was considered inadequately covered if its coverage by intact protected habitat falls below this representation target. Among these, we highlight a subset we designate having no or minor coverage ($\leq 10\%$ of their target met; i.e., less than 10% of the range for highly-restricted species, less than 1% for species with very large range).

Are protected areas retaining intact habitats over time?

We created a raster layer that maps the trends in human footprint between 2000 and 2013, from the difference between human footprint values in 2013 and in 2000. We then calculated, for each ecoregion, the trend in protected area intactness as the mean decrease in human footprint in all pixels intersecting (by 50%) protected areas (i.e., a positive value means an increase in protected area intactness) and calculated its Pearson correlation coefficient with the proportion of high-sensitivity species.

Results

How sensitive are species to human footprint?

Across the 4,362 bird species that breed in the Americas, values of sensitivity to human footprint range from 2.9 to 50.0, following a Gaussian distribution with a median value of 33 (Fig. 1). Sensitivity is higher in data-poor species than in data-rich ones. The threshold for high-sensitivity species is 37.7. Among the 1,091 high-sensitivity species, 24.2% are threatened with extinction (compared with 7.8% for species not categorised as high-sensitivity).

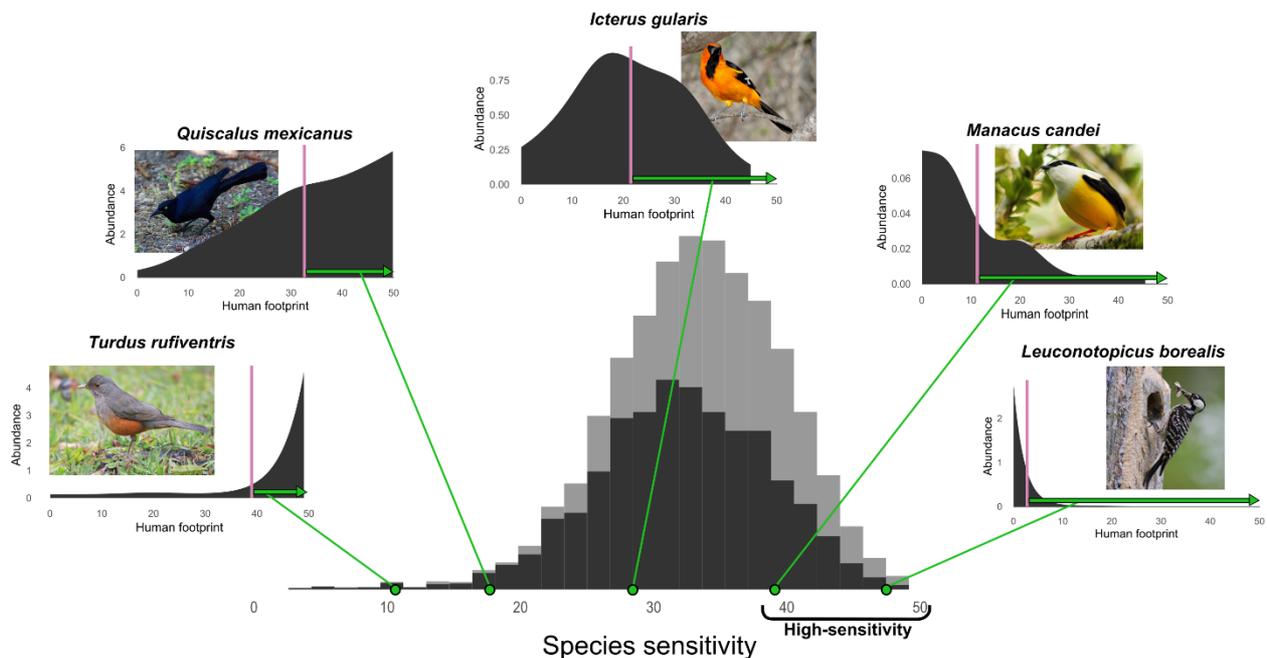


Fig. 1: Stacked frequency distribution of sensitivity values across all 4,362 bird species that breed in the Americas, including data-rich species for which sensitivity was measured directly (dark grey, N=2,550), and data-poor species for which it was imputed from trait information (light grey, N=1,812). Insets correspond to five examples of data-rich species across a gradient of sensitivity, showing for each: the modelled response of abundance to human footprint; the measure of sensitivity (green horizontal arrow) obtained from the difference between 50 (i.e., the maximum value of human footprint) and the weighted mean value of predicted abundance (pink vertical line). High-sensitivity species were defined as the 25% most sensitive. High-sensitivity species have an abundance strongly biased towards sites with low human footprint (e.g., *Leuconotopicus borealis*), medium-sensitivity species have an abundance unrelated to human footprint or biased towards medium human footprint (e.g., *Icterus gularis*), and low-sensitivity species have an abundance biased towards sites with high human footprint (e.g., *Turdus rufiventris*).

Photo credits: *T.r.* (Luiz Carlos Rocha, <https://www.flickr.com/photos/luizmrocha/>), *Q.m.* (BarbeeAnne, <https://pixabay.com/photos/cuba-black-bird-great-tailed-grackle-2555949/>), *I.g.* (Skeeze, <https://www.needpix.com/photo/729995/>), *M.c.* (David Rodriguez Arias, <https://www.flickr.com/photos/82969027@N04/>), *L.b.* (Sam D. Hamilton, https://upload.wikimedia.org/wikipedia/commons/6/61/Picoides_borealis_-_Mississippi%2C_USA_-_feeding-8.jpg).

Where are bird assemblages the most sensitive?

Assemblages most sensitive to human footprint (i.e., with highest proportion of local species being high-sensitivity) are concentrated in tropical ecoregions, especially along the Andean mountain range and its eastern slopes towards the Amazonian basin, as well as in Central America (Fig. 2A).

We found that this pattern is robust to extreme errors in imputing sensitivity to data-poor species (Fig. S6). Furthermore, a very similar pattern was found when assemblage sensitivity was measured as the number of high-sensitivity species or the median sensitivity of species per ecoregion (Fig. S5). We thus focus henceforth on the proportion of high-sensitivity species measured across all species (Fig. 2A).

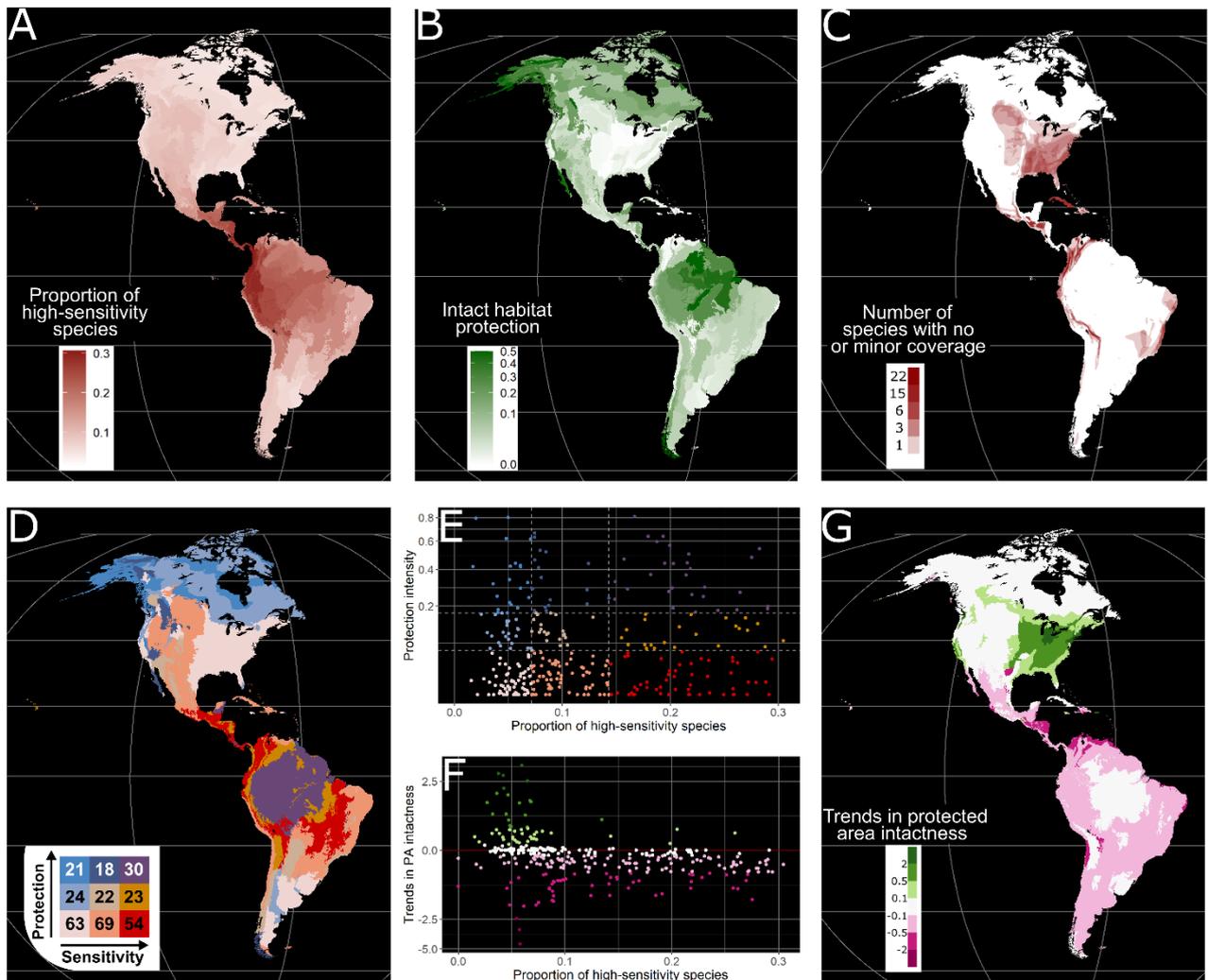


Fig. 2: Spatial patterns in bird assemblage sensitivity and intact habitat protection. (A) Assemblage sensitivity measured as the proportion of species per ecoregion that are high-sensitivity species. (B) Intact habitat protection per ecoregion (i.e., proportion of ecoregion area simultaneously protected and with human footprint <4). (C) Spatial distribution of the 266 high-sensitivity species with no or minor coverage by intact protected habitat. (D) Spatial pattern and (E) Scatterplot of the relationship between assemblage sensitivity and intact habitat protection, across ecoregions. The bivariate colour scale in D and E is built by cutting proportion of high-sensitivity species into terciles ($[0; 0.070[$, $[0.070; 0.143[$, $[0.143; 1]$) and intact habitat protection into $[0; 0.05[$, $[0.05; 0.17[$, $[0.17; 1]$ (dashed lines in E). (G) Trends in protected area intactness per ecoregion (i.e., decrease in human footprint within protected areas between 2000 and 2013); and (F) in relation to the proportion of high-sensitivity species per ecoregion. Green shades show improvement, rose shades degradation.

Is intact habitat protection matched to species sensitivity?

Across ecoregions

Intact habitat protection is highest in the Amazonian basin, Boreal region, western North America, and Patagonia (Fig. 2B, Table S2), where ecoregions combine relatively high protected area extent and high protected area intactness (Fig. S7). Conversely, intact habitat protection is lowest in Eastern North America, and in much of South America outside the Amazonian basin (Fig. 2B). The proportion of high-sensitivity species per ecoregion is not correlated with intact habitat protection (coef = 0.055, $P=0.327$; Fig. 2D-E), neither with protected area extent, nor with protected area intactness (Fig. S7), and we only found a small correlation for median sensitivity (Fig. S5).

Areas with highly sensitive bird assemblages but low intact habitat protection are concentrated in tropical ecoregions, especially in the tropical Andes and their western slopes towards the Pacific coast, Colombia's Choco region and Magdalena Valley, Venezuela Coastal Range, Central America, and the Cerrado savannahs of Brazil (red in Fig. 2D, Fig. 3). These ecoregions mainly correspond to tropical and subtropical forest biomes, mostly moist broadleaf (21 ecoregions), but also dry broadleaf (15), mangroves (7) and coniferous forests (3). They also include grasslands and shrublands, including montane (4), deserts and xeric (2), tropical (1), and flooded (1) (Fig. 3).

Additionally, 23 ecoregions have high proportions of high-sensitivity species, but intermediate levels of intact habitat protection (caramel in Fig. 2D-E; Fig. 3), also mainly concentrated in tropical ecoregions. Finally, 69 ecoregions have intermediate proportions of high-sensitivity species but low intact habitat protection, found not only in tropical eastern South America but also in North American temperate grasslands and West (salmon in Fig. 2D-E; Fig. 3).

Conversely, 30 ecoregions, mainly in the Amazonian basin (including the eastern slope of the Andes) have a high proportion of high-sensitivity species while being relatively well covered by intact protected habitat (purple in Fig. 2D-E), mainly corresponding to tropical and subtropical moist broadleaf forests and mangroves (Fig. 3).

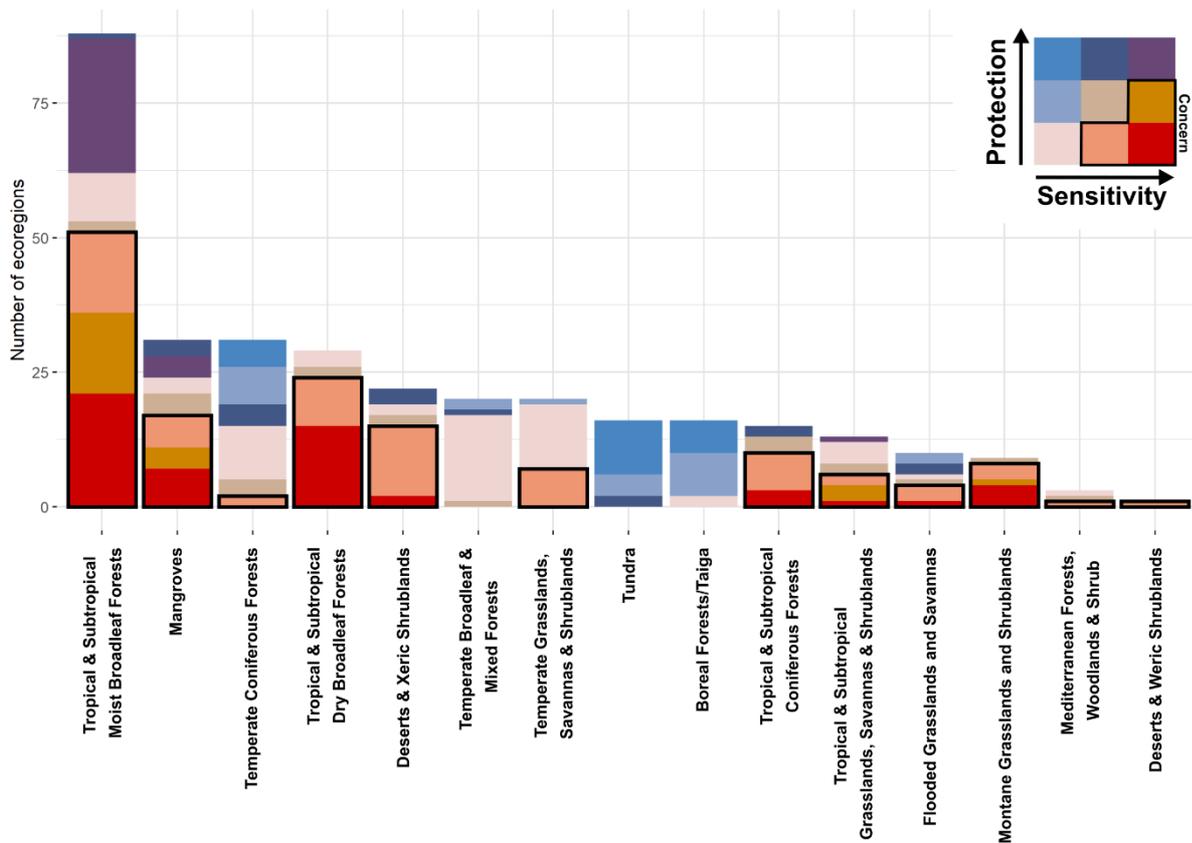


Fig. 3: Distribution of ecoregions per biome (following Olson et al. 2001), colour-coded according to the relationship between the proportion of high-sensitivity species and intact habitat protection (colours as in Fig. 2D-E). The three categories of particular concern are outlined in black.

Across species

Among the 519 data-rich high-sensitivity species, 353 (68%) are inadequately covered by intact protected habitat, including 53 (10%; Table S3) with no or only minor coverage. When considering all 1,091 species that we predicted as high-sensitivity (i.e., also including 572 data-poor species), these values increase to 820 (75%) and 266 (24%, including 141 threatened species), respectively (Fig. 2C; Fig. S8). Species with no or minor coverage are mainly concentrated in the East part of North America, Caribbean, Tropical Andes, Venezuela Coastal Range, and Atlantic Forest of Brazil (Fig. 2C, Fig. S8). On average an additional 31% of these species' ranges would need to be covered by intact protected habitats to reach their respective representation targets (Fig. S9).

When compared with all breeding species, they are disproportionately sedentary (95% vs. 83%), found in forest habitats (88% vs. 61%), specialised (average of 3.8 vs. 3.3), and have disproportionately small breeding ranges (average of 7.9×10^4 vs. 1.8×10^6 km²).

Our analysis overestimates real intact habitat coverage, because we consider all intact habitat within a species' range as suitable, which may be inaccurate (e.g., intact forest patches in a grassland species' range). Accordingly, the numbers of inadequately covered species we obtained are conservative (i.e., underestimated).

Are protected areas retaining intact habitats over time?

Between 2000 and 2013, protected area intactness: decreased in 161 ecoregions, concentrated in South and Central America; was stable (i.e., $|\text{change}| < 0.1$) in 114 ecoregions, mostly in western North America and the Amazonian basin; and increased in 50 ecoregions, mainly in eastern North America (Fig. 2G). Trends in protected area intactness are negatively correlated with the proportion of high-sensitivity species per ecoregion (coef = -0.23 , $P=3.9 \times 10^{-5}$; Fig. 2F), with most ecoregions with $>10\%$ of local species being high-sensitivity (104 of 148; 70%) having experienced a decline in intactness (Fig. 2F).

Discussion

We introduce here a new index of species' sensitivity to anthropogenic land use changes (as measured through the human footprint), derived from field data on the variation of species' abundance over their distributions. We focused on the breeding grounds, but the same methods can be applied to estimate sensitivity during other parts of the species' annual cycle (which may also present important conservation challenges; e.g., Runge et al., 2015; Gaget et al., 2020) as species sensitivity probably varies with season. Even though adequate field data are not available for the vast majority of species in most regions, citizen science is rendering possible to estimate sensitivity for a growing number of species across the globe. The importance of measuring sensitivity directly from field records is stressed by the relatively poor link between sensitivity and traits that we found ($R^2=0.18$), suggesting that traits are a poor proxy for sensitivity (our results are robust to errors in data-poor species imputation; Fig. S6).

Breeding bird species in the Americas vary widely in their sensitivity to human pressure, as evidenced by the diversity of relationships between abundance and human footprint (Fig. 1), as previously shown (Rosenberg et al., 2019; Clavel et al., 2011; Guetté et al., 2017; Phalan et al., 2011; Williams et al., 2017). There is substantial overlap between threatened and high-sensitivity species, but the two measures are not the same. Indeed, whereas sensitivity to human footprint can be seen as an intrinsic ecological trait, threat levels result from the interaction between sensitivity and exposure to human pressure. We found that sensitivity is highly structured in space, being particularly dominant among species within tropical forest ecoregions, especially in the Andes, Central America and Amazonian basin, while being lower in temperate and boreal ecoregions (Fig. 2A). Even though we focused only on birds in the Americas, previous studies reported a high sensitivity of tropical forest assemblages to even low levels of human pressure (Gibson et al., 2011; Barlow et al., 2016; Newbold et al., 2020), suggesting that our results may reflect a broader pattern applicable to other taxa and regions.

These results confirm our prediction that the need for highly intact protected habitat is not the same everywhere, at least when it comes to the conservation of bird species. Placed in the context of the land sparing/land sharing debate (Green et al., 2005; Phalan et al., 2011; Williams et al., 2017), our

results suggest that the best way for reconciling conservation and socio-economic targets varies across regions. A land sparing strategy is particularly crucial in the tropics, where bird assemblages include many species whose conservation depends on the maintenance of intact habitats, and that may thus require the establishment of strict protected areas. In contrast, land sharing may prove a more suitable strategy in temperate and boreal ecosystems, where fewer species now depend on intact habitats. This said, we found high-sensitivity species in each one of the 325 ecoregions analysed but two (Table S2), which means that the protection of at least some intact habitat is crucial across all latitudes and biomes.

Intact habitat protection is also widely variable (0% to 81%) and highly structured in space (Fig. 2B), being stronger in the Amazonian basin and some high latitude ecoregions that combine both low human footprint and large coverage by protected area. Worryingly, it does not correlate with the distribution of high-sensitivity species, which need the protection of intact habitats the most. This is consistent with previous work that also found no correlation between the location of protected areas and species' conservation needs, as measured by the presence of threatened species (Venter et al., 2018). Of particular concern are the 54 ecoregions that have very low levels (<5%) of intact habitat protection despite hosting bird assemblages with a large proportion (>14%) of high-sensitivity species (Fig. 2D). These overlap extensively with Biodiversity Hotspots (i.e. biogeographic regions of exceptional plant endemism that have already lost >70% of their natural habitat, Mittermeier et al., 2004; Myers et al., 2000), particularly with the Tropical Andes, Tumbes-Chocó-Magdalena, Mesoamerica, and Cerrado hotspots (47 of the 54 ecoregions overlap one of these hotspots by >90%). Furthermore, many of these ecoregions (particularly in the Tropical Andes and Central America) cover areas identified as urgent priorities for the expansion of the global network of protected areas (Rodrigues et al., 2004; Butchart et al., 2015).

A complementary perspective is obtained by analysing mismatches between sensitivity and protected area coverage at the species level. This is particularly important as some narrow-range species, while living in ecoregions with low intact habitat protection, could be adequately covered if the distribution of intact protected habitats within an ecoregion matches species' distribution. We identified (conservatively) 266 high-sensitivity species whose distributions have no or only minor coverage by intact protected habitat. The latter include species that are not protected at all (Maxwell et al., 2020) as well as others whose distributions are apparently well covered by protected areas but these are dominated by transformed habitats. For instance, the Critically Endangered Santa Marta wren, *Troglodytes monticola* (sensitivity = 41), is protected across 99.7% of its range, and would thus be considered as adequately covered based on protected area coverage alone (Butchart et al., 2015), yet we found no intact protected habitat within its range. This corresponds to its Red List assessment, which highlights a long history of severe deforestation and degradation across the species range, which continues apace despite protection (IUCN, 2018). This example illustrates the importance of taking species' sensitivity into account when evaluating the effectiveness of existing networks of protected areas as well as when identifying new priority areas for protection.

The persistence of many high-sensitivity species requires the establishment and effective

management of strict protected areas, or other adequate mechanisms that guarantee the long-term maintenance of sufficient extents of intact habitats. This is all the most urgent for the 141 species we highlighted as being of major concern because they are simultaneously high-sensitivity, have no or only minor coverage by intact protected habitats, and are already at risk of extinction (Fig. 2C, Table S3). With nearly all (136; 96%) threatened by habitat loss (i.e., “Residential and commercial development” or “agriculture and aquaculture”; BirdLife International (2019)), the mismatch between their high-sensitivity and the poor coverage of their range by intact protected habitats may prove dramatic in the near future in the absence of active measures to protect any remaining intact patches. The distributions of these species highlight ecoregions overlapping the same Biodiversity Hotspots as above, as well as the Atlantic Forest hotspot, all of which have already suffered major loss and transformation of their habitats (Williams et al., 2020). Restoration of currently degraded habitat is likely to play a key role in the long-term conservation of these species (Bull et al., 2020; Benayas et al., 2009), and indeed the regions where they occur are recognised global priorities for ecosystem restoration (Strassburg et al., 2020).

The importance of effective protected areas in these ecoregions will increase over time as pressures outside mount. Indeed, previous studies have shown that protected areas are becoming the last bastions for some species (Pacifci et al., 2020; Boakes et al., 2018). Unfortunately, though, we found that ecoregions with higher proportions of high-sensitivity species have experienced a faster degradation in the intactness of their protected areas, indicative of a growing mismatch between species needs and the availability of intact protected habitat (Fig. 2F-G). Previous studies had already raised stern warnings regarding the mounting human pressure within protected areas (Jones et al., 2018; Geldmann et al., 2014, 2019), through ongoing habitat loss and degradation (Spracklen et al., 2015; Cuenca et al., 2016; Bruner et al., 2001; Moore et al., 2017). Here we show that these trends have been faster (between 2000 and 2013) precisely where species need intact habitats the most. Moreover, it is likely that the situation has worsened for many species since, given ongoing habitat destruction in some parts of the continent, as shown by the 2020 update of the Global Forest Change (Hansen et al., 2013).

Overall, our results show that the Americas’ protected area network is distributed such that it is not strategically located to conserve those bird species that need it the most, undermining its effectiveness in achieving the long-term conservation of nature (Rodrigues and Cazalis, 2020; SCBD, 2010), and highlight the importance of considering the habitat quality of protected areas (Barnes et al., 2018; Visconti et al., 2019). We highlight ecoregions and species where it is particularly urgent to ensure that remaining intact habitat is preserved, through protected areas and other relevant mechanisms, potentially complemented by the restoration of degraded habitat. With these ecoregions and species mostly concentrated in countries with limited economic resources, international cooperation is key to meeting this goal.

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Supplementary methods

1) Alignment with BirdLife International taxonomy

The taxonomy followed by eBird (source of bird observation records) is different from the one followed by BirdLife International (source of species' ranges, and Red List status). We aligned the former with the latter by: (1) replacing the species name used in eBird by the one in BirdLife International in simple cases of different names (but no taxonomic mismatch); (2) merging different eBird species (and summing their local abundance, if applicable) whenever they are lumped into a single species in the BirdLife International taxonomy; and (3) splitting single eBird species that correspond to multiple species in the BirdLife International taxonomy, using species distribution maps to separate the corresponding records (see Cazalis et al., (2020) for more details and Supplementary Spreadsheet 1 for list of species concerned by these changes).

2) Building a standard abundance dataset

We restricted our dataset to recent (2010-2019) observations, to increase synchronisation between bird records and landscape data. We kept only checklists for which observers certified having reported all species identified, thus obtaining a count dataset that included non-detections. Further, we filtered checklists based on sampling effort and protocol to create a set of checklists with relatively consistent effort. Specifically, we kept only checklists that reported a duration of sampling between 0.5-10 hours and less than 5 km distance travelled arising from: the 'Stationary Points' protocol (i.e., the observer did not move during sampling); the 'Travelling' protocol (i.e., the observer moved during sampling); or 'Historical counts' (if they included information on duration and distance travelled). This protocol selection excludes sampling events targeting particular taxonomic groups (e.g. wader surveys, nocturnal protocols) or using specific methods (e.g. banding). Each checklist is associated with a point, with coordinates provided by observers (often the middle of the route for 'Traveling' checklists).

Pseudo-replication in the database may occur when several observers record birds at the same place at the same time. To eliminate these records, we first used the *auk_unique* function from the '*auk*' package (Strimas-Mackey et al., 2017), specifically designed to process eBird data. This function combines checklists from multiple observers reported to be birding together, in order to obtain a single checklist for each sampling event (the number of observers associated with each checklist alters the detection probability, and will be subsequently controlled for). Second, because even observers who are not birding together can create pseudo-replication if they overlap in space and time, whenever several checklists were less than 5 km apart on the same day we randomly and sequentially selected one checklist (i.e., iteratively until no two checklists were less than 5 km apart). All the checklists we selected were 'complete' with each observer recording all the species they could detect and identify. However, more experienced

observers will be able to detect and identify more species and therefore non-detections will be more likely to equate to real species absences. Therefore, we only considered observations made by observers with a minimum level of experience, i.e. those who submitted ≥ 50 checklists, including ≥ 100 species during the study period (2010-2019; see Supplementary Methods 3).

We excluded from the dataset “not approved” observations (corresponding to exotic, escaped or feral individuals), as well as domestic species, but kept established invasive species. Using the *auk_rollup* function from the '*auk*' package, we removed subspecies, moving all observations to the species level. We also excluded marine species, defined as species with ‘sea’ or ‘coastal’ as primary habitat (cf. bird species traits section below).

In many species, individuals are the most territorial and selective in terms of habitat requirements when breeding (Zuckerberg et al., 2016). We thus focused our analyses on potentially breeding individuals, by narrowing each species’ observations records to the respective breeding season and breeding grounds. For each 10° latitudinal band, we derived the broad breeding season (all species considered together) based on the temporal distribution of records coded as ‘breeding’ in the eBird database (e.g., 6 April to 9 August for latitudes 50°N to 60°N; all year round for latitudes 10°S to 10°N; see Supplementary Methods 3). Within these dates, we then focused on the observations made in the breeding grounds of each species (as mapped by BirdLife International and HBW (2019)).

We have restricted our dataset of bird records to observations made within each species’ broad breeding season and breeding grounds. Bird breeding season is known to vary with latitude (Baker, 1939). Although not all species within a given latitude necessarily breed at the same time (Baker, 1939), we did not have sufficiently detailed information to take these differences into account, and have instead assumed that within a given latitudinal band all species breed within the same broad season. To delimit the breeding season within each 10° latitudinal band, we studied the temporal distribution of the breeding codes that are sometimes associated with eBird observations (available for 1.2% of the observations in our dataset). First, we restricted the breeding codes to those that either correspond to probable breeding or confirmed breeding (i.e., by removing codes: “Flyover”, which does not correspond to a breeding behaviour; and “In appropriate habitat” and “Singing male”, which correspond to possible breeding only). We then plotted the temporal distribution of these breeding records (all species combined) per 10° latitudinal bands (Fig. S1). Based on these distributions, we considered that breeding occurs all year round between latitudes -10° and 10°. For other latitudinal bands, we defined the limits of the breeding season (Table S1) as the period containing 95% of the observations with breeding codes, bounded by circular quantiles at 2.5 and 97.5% of observations (black lines on Fig. S1) using the *circular* package (Agostinelli and Lund, 2017). For each species, in each latitudinal band, we included only records inside the boundaries of the breeding season.

In addition, we restricted the observations of each species to their respective breeding grounds,

based on the BirdLife International's distribution maps (BirdLife International and HBW, 2019), more specifically the polygons with Season codes 1 (resident) or 2 (breeding season only) and Presence codes 1 (extant), 2 (probably extant), 3 (possibly extant), and 4 (possibly extinct).

Within these temporal and spatial constraints, we considered a species absent if undetected in checklists made during the breeding season and located within the breeding range of the species. For species recorded as present, we used the count (i.e., number of individuals observed) provided by observers. In some cases (4% of the observations in our dataset) observers did not provide an abundance and instead reported species presence with an "X". We treated these as *NA* values in our analyses.

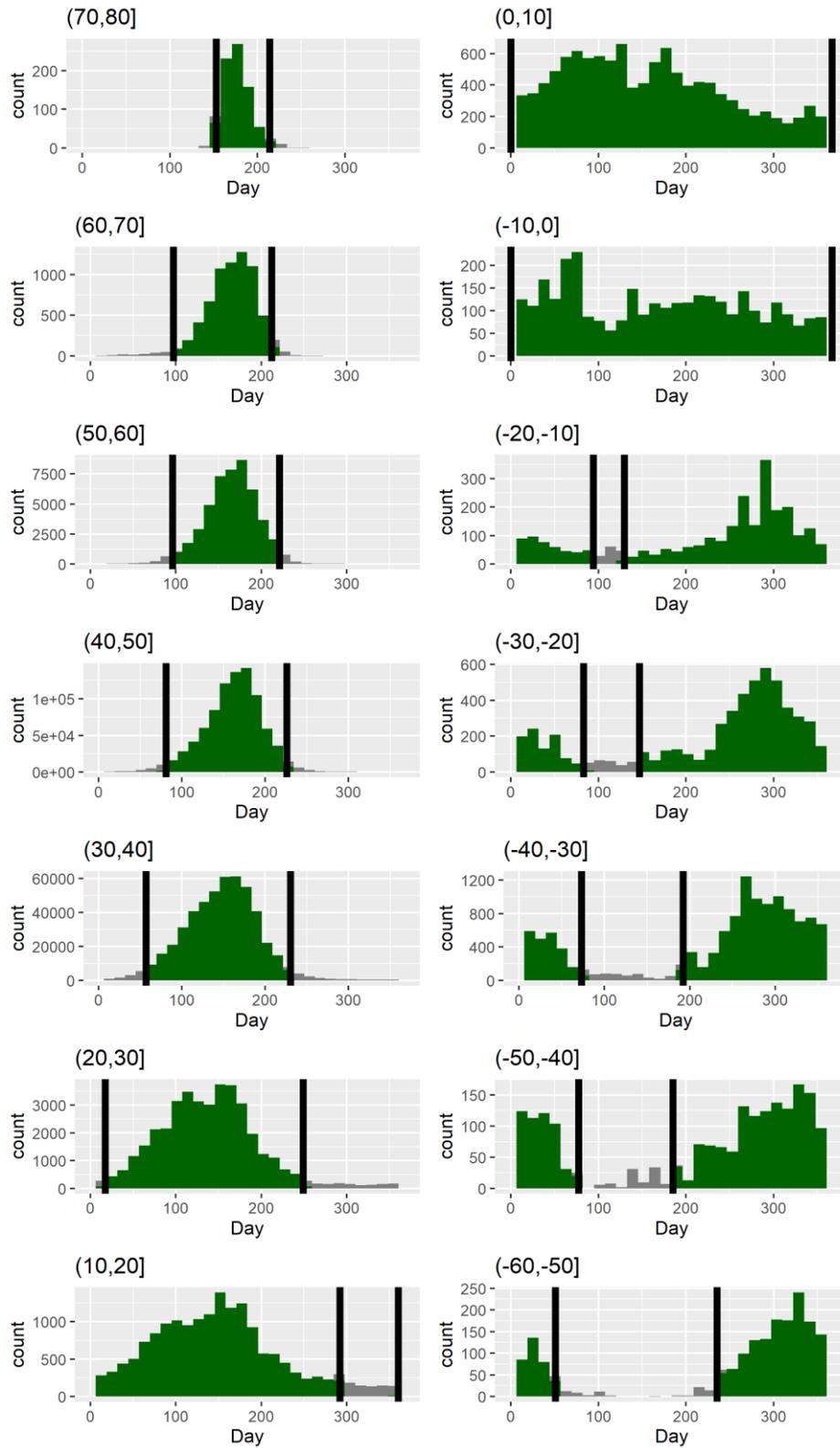


Fig. S1: Temporal distributions of eBird observations with associated breeding codes, per 10° latitudinal band. Vertical lines represent the limits of the breeding season as we defined it (i.e., the 2.5 and 97.5% circular quantiles; see Table S1). Bar colours show whether plotted data fall within (green) or outside (grey) the breeding season.

Table S1: Breeding season per latitudinal band. For two tropical bands (-10° to 0° and 0° to 10°), we considered that breeding occurs all year round. For all other bands, beginning and end dates were derived from the temporal distribution of breeding codes in eBird records (Fig. S1), as the 2.5 and 97.5% circular quantiles of Julian days.

Latitudinal band (degrees)	Breeding season (Julian days)	
	Beginning	End
(70,80]	153	214
(60,70]	97	212
(50,60]	96	221
(40,50]	81	226
(30,40]	57	230
(20,30]	17	249
(10,20]	360	292
(0,10]	0	367
(-10,0]	0	367
(-20,-10]	129	94
(-30,-20]	147	83
(-40,-30]	192	73
(-50,-40]	185	77
(-60,-50]	236	51

3) Calculating observer calibration index

We calculated an individual observer calibration index, closely related to the one calculated in Cazalis et al., (2020) (following Kelling et al., (2015) and Johnston et al., (2018)), for each observer included in the analyses (i.e., with more than a given threshold of experience: ≥ 50 checklists for a total of ≥ 100 species in the Americas during the study period). This index was calculated from a subset of the eBird records, selected through a somewhat different filtering process from the one used in the main analyses. As in the main analyses, we kept only checklists that reported all species detected, observations from 2010-2019, and excluding disapproved observations; in contrast, we did not restrict the dataset based on protocol type or sampling effort.

For any given observer, we calculated the observer calibration index as the log-scaled number of species an observer is expected to report on average during a standard sampling event. Usually this is done by running a mixed-effects model with the richness of each checklist as the response variable, with sampling effort and ecological drivers of species richness as explanatory variables, and with observer as a random effect (Johnston et al., 2018; Kelling et al., 2015; Cazalis et al., 2020). In this study, because of computing limitations, we split this calculation into two models: first we fitted a GAM assuming a negative binomial distribution (using the

function *bam* from the '*mgcv*' package (Wood, 2011)) with the following structure: $\text{species_richness} \sim \text{protocol_type} + \text{number_observers} + \text{s}(\text{duration}) + \text{s}(\text{starting_time}) + \text{te}(\text{longitude}, \text{latitude}, \text{Julian_day})$, with *starting_time* the time at which the sampling event started, *s()* a smoothed term enabling complex relation between variables, and *te()* an interacting smooth term enabling here richness to vary across space and time. We then extracted residuals of this model and used them in a linear mixed-model (using the function *lme* from the '*nlme*' package (Pinheiro et al., 2020)) with no explanatory variable and a random effect on observer. Finally, we simulated a sampling event under the “Stationary Points” protocol, fixing number of observers, duration, starting time, longitude, latitude and Julian day to their median values. We predicted the log-scaled species richness that should be detected in this hypothetical sampling event according to the GAM, and summed it with the random effect of each observer in order to get an observer calibration index per individual observer.

4) Bird species traits

BirdBase is a regularly updated global database of the ecology and life history traits of the world's bird species (Şekercioğlu et al., 2004, 2019). We extracted from it the species' primary habitat, structured into 10 classes (after exclusion of 'coastal' and 'sea' species): Artificial, Deserts, Forests, Grasslands, Riparian, Rocky, Savannahs, Shrublands, Wetlands, Woodlands. Primary diet consisted of eight classes (after combining 'Carnivore', 'Scavenger' and 'Vertebrate' into 'Carnivorous'; combining 'Plant' and 'Herbivore' into 'Herbivorous'; and considering the 42 species with an 'unknown' diet as 'Insectivorous'): Carnivorous, Frugivorous, Granivorous, Herbivorous, Insectivorous, Nectarivorous, Omnivorous, Piscivorous. In addition, we obtained from the same database: migratory status ('strict', 'partial', or 'sedentary'); body mass; and species taxonomic Order (e.g., Accipitriformes, Anseriformes). We calculated a specialisation index for each species based on the number of different habitat (HB) and diet (DB) categories for each species, as in Şekercioğlu (2011): $\log [100/(\text{HB} \times \text{DB})]$. We inferred specialisation and body mass values of species for which it was unknown (respectively N=43 and N=358), by using the mean specialisation and mass of the documented species in the same taxonomic Family.

We extracted Red List status from BirdLife International (2019), and (following Butchart et al., 2007) transformed it into a quantitative variable (from Least Concern as 1, to Critically Endangered as 5). We treated the six species for which the Red List status was Data Deficient as LC. We calculated each species' breeding range size (as defined above) from BirdLife International and HBW (2019), within our study area.

5) Imputing species sensitivity

In order to estimate the sensitivity of the 1,812 data-poor species (i.e. those among the 4,362 that breed in the study area for which we were not able to measure sensitivity directly), we

modelled the link between the sensitivity of the 2,550 data-rich species using the following linear model:

Sensitivity ~ Primary_Habitat + Primary_Diet + specialisation + log(Mass) + RedList + log(Range) + Migration + Order

Even though this model does not have a strong explaining power ($R^2=0.18$), results indicate that major habitat significantly affects species sensitivity ($P<10^{-15}$), with forest, grassland and riparian species being particularly sensitive, while species favouring artificial habitats, deserts, and savannahs being on average less sensitive to human footprint (Fig. S2A). Taxonomic Order also greatly influences species sensitivity ($P=3.10^{-8}$), with Rheiformes, Phoenicopteriformes, and Cariamiformes at highest sensitivity, while Psittaciformes, Podicipediformes, Falconiformes, Columbiformes, Apodiformes, and Accipitriformes showed lower sensitivity (Fig. S2B). Species diet had a slightly significant effect on sensitivity ($P=0.024$) with high sensitivity for nectarivorous and low sensitivity for granivorous (Fig. S2C). Migration status greatly influenced sensitivity, with sedentary species showing higher sensitivity than strict migrating species than partial migrating species ($P=9.10^{-6}$; Fig. S2D). Species sensitivity increased with species specialisation ($P<10^{-15}$, Fig. S2F), decreased with species range size (log-scaled) in the Americas ($P=0.042$, Fig. S2G), increased with species body mass ($P=4.10^{-4}$, Fig. S2H), and increased with species quantitative Red List status ($P=0.049$, Fig. S2E).

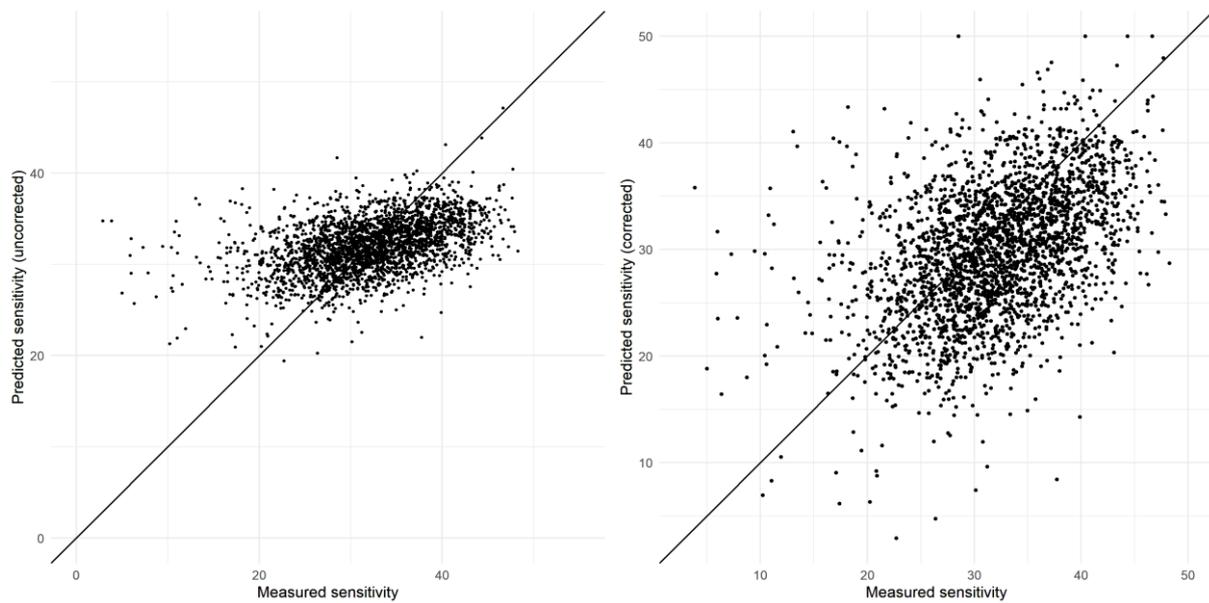


Fig. S3: Imputed sensitivity (left) and corrected imputed sensitivity (right) of the 2,550 species for which sensitivity was directly measured. Correction consisted in scaling the imputed sensitivity, multiplying by the standard deviation of measured sensitivity, adding the mean value of measured sensitivity and finally replacing values below 0 by 0 and values above 50 by 50.

We then used measured sensitivity for the 2,550 data-rich species and corrected imputed sensitivity for the 1,862 data-poor species (see both distributions in Fig. 1).

6) Sampling bias towards sites with high human footprint

There was across the entire study area a strong bias in sampling towards sites with high human footprint and a near-complete absence of sampling in sites with very low human footprint (Fig. S4). For this reason, values of species' sensitivity cannot be interpreted in absolute terms: a sensitivity of 30 does not (necessarily) mean that 30% of the population is found in areas of human footprint lower than 20 ($= 50-30$). Instead, we used values of species' sensitivity in relative terms, to compare sensitivity of species and of regions.

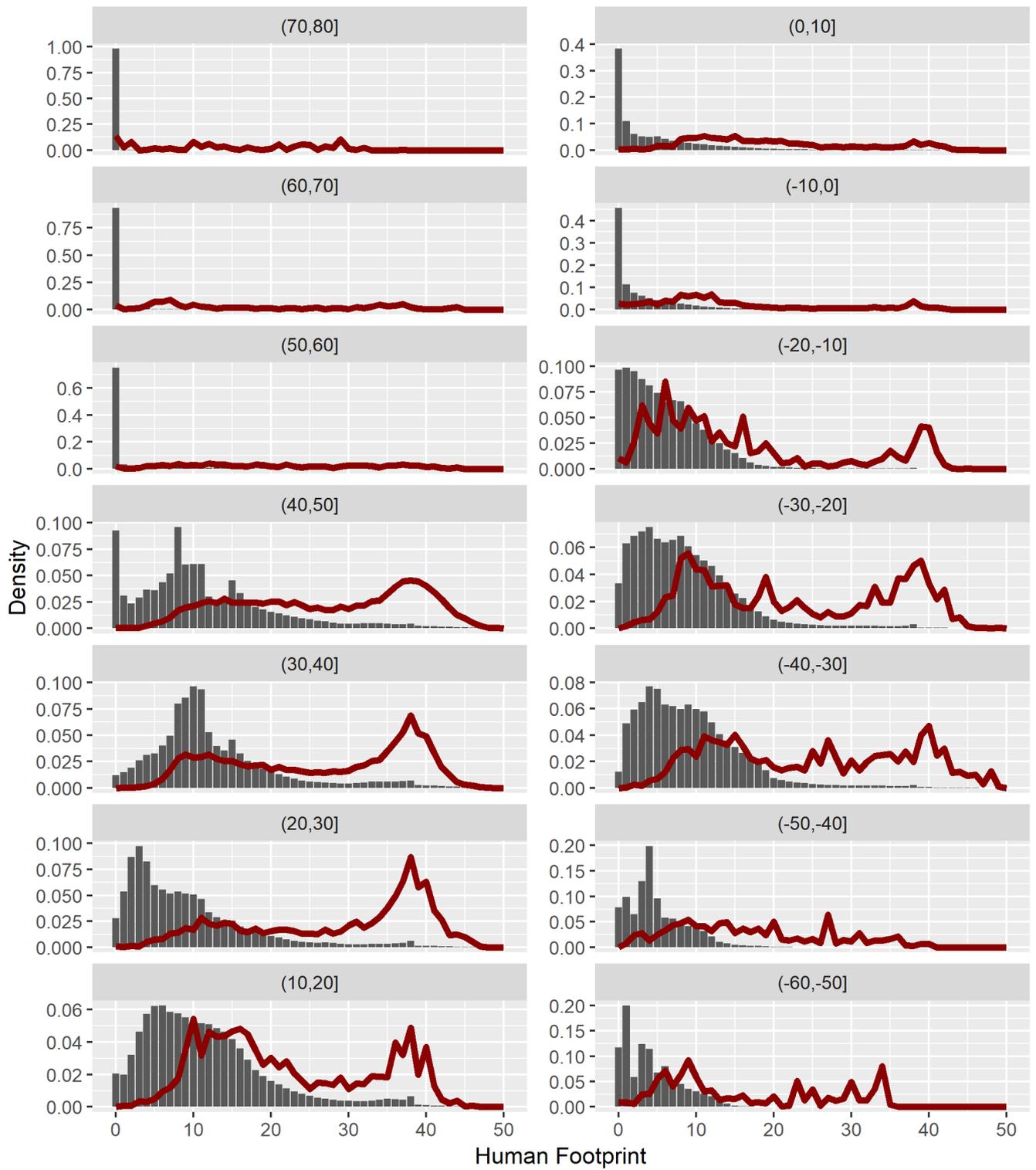


Fig. S4: Distribution of human footprint raster cells (grey bars) compared with distribution of human footprint of checklists (red lines) per 10° latitudinal bands in the study area.

Supplementary results

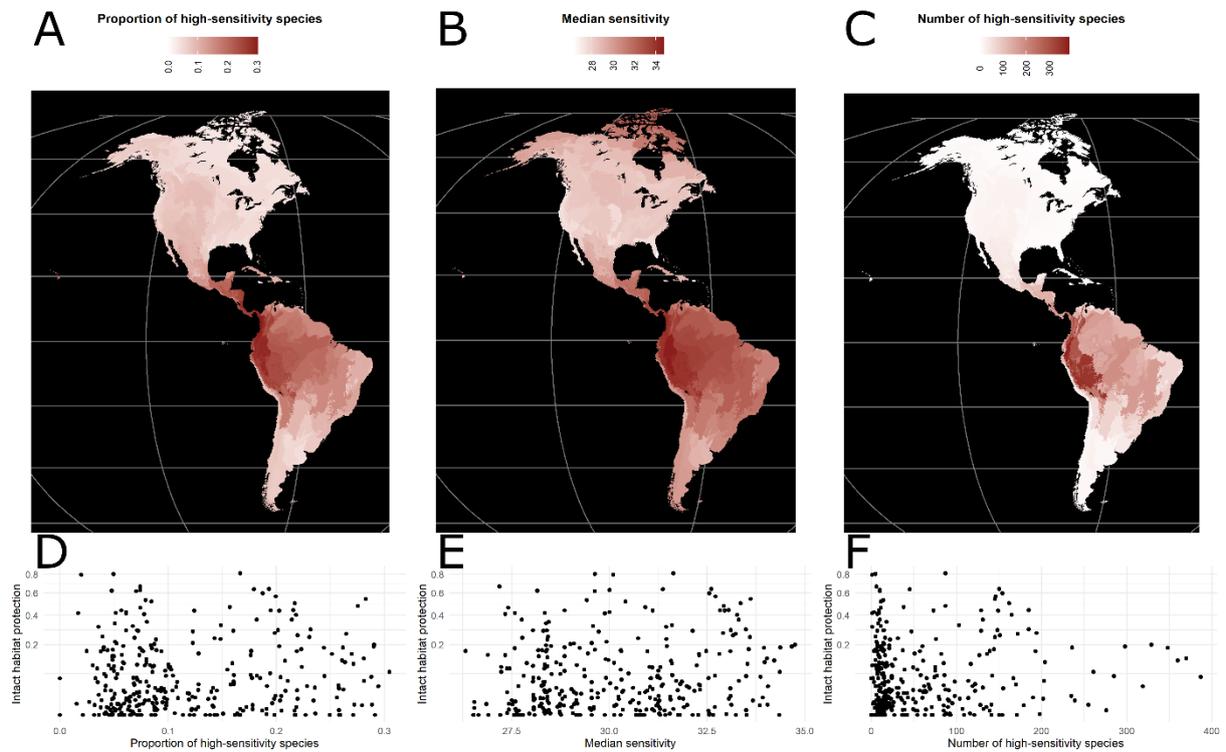


Fig. S5: Spatial patterns in three ecoregion-level metrics of the sensitivity of bird communities to human footprint: (A) proportion of all species breeding in the ecoregion that are high-sensitivity species; (B) median sensitivity across all species that breed in the ecoregion; and (C) number of high-sensitivity species that breed in the ecoregion; and correlation with intact habitat protection (D-F). Intact habitat protection does not correlate with proportion of high-sensitivity species (coef = 0.055, $P=0.327$; D), or with number of high-sensitivity species (coef = 0.058, $P=0.298$; F) but slightly correlates with median sensitivity (coef = 0.125 $P=0.024$; E).

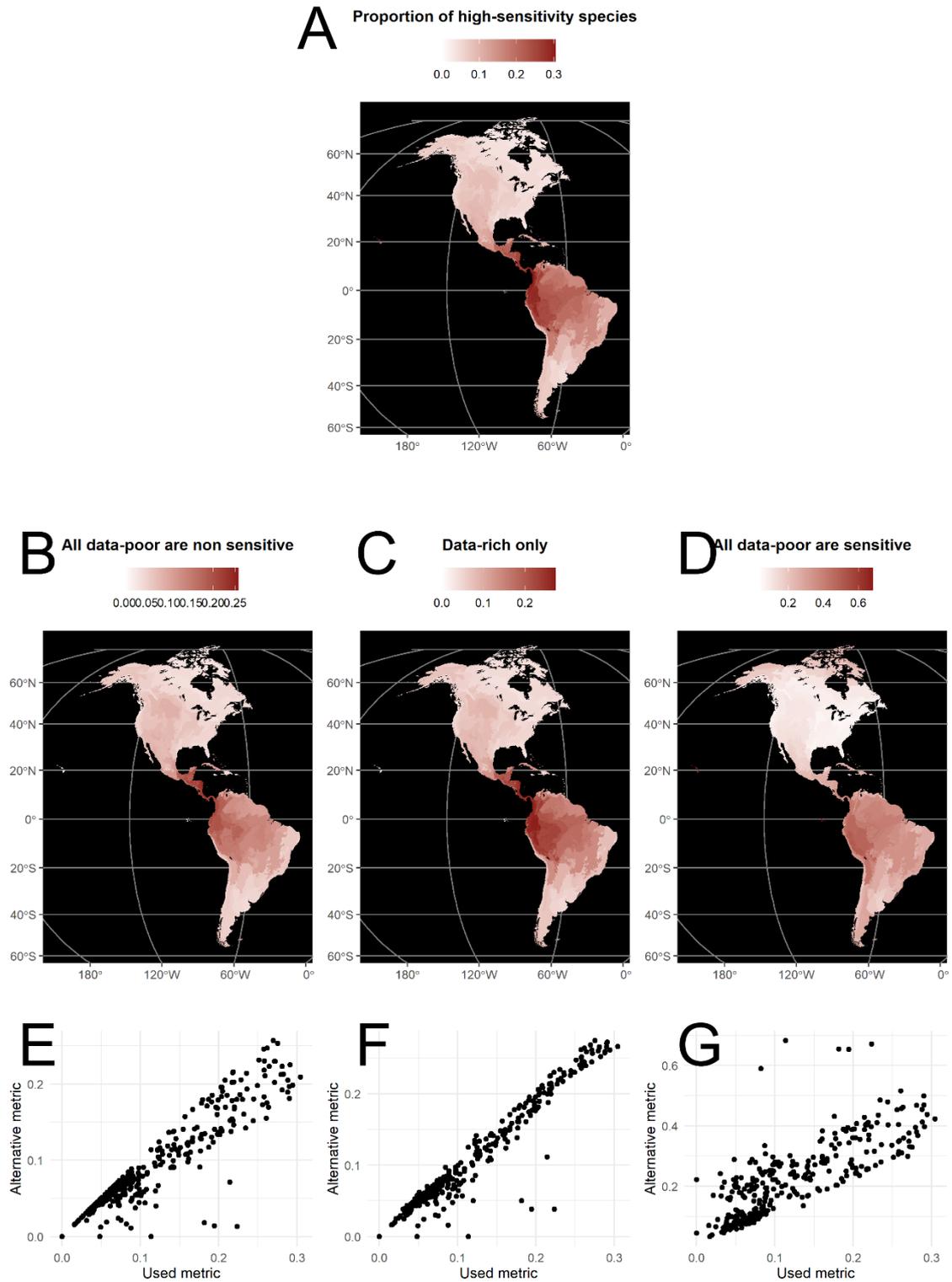


Fig. S6: Variation in the proportion of high-sensitivity species based on errors in the imputed sensitivity for data-poor species. A: proportion of high-sensitivity species as used in the paper (e.g., Fig. 1, Fig. 2A), based on measured sensitivity for data-rich species and imputed sensitivity for data-poor species. B: Proportion of high-sensitivity species if we assume that all imputed species are non-sensitive (and E, scatterplot with the proportion used in the paper). C: Proportion of high-sensitivity species if we only consider data-rich species (and F scatterplot with the proportion used in the paper). D: Proportion of high-sensitivity species if we assume that all imputed species are high-sensitivity species (and G, scatterplot with the proportion used in the paper).

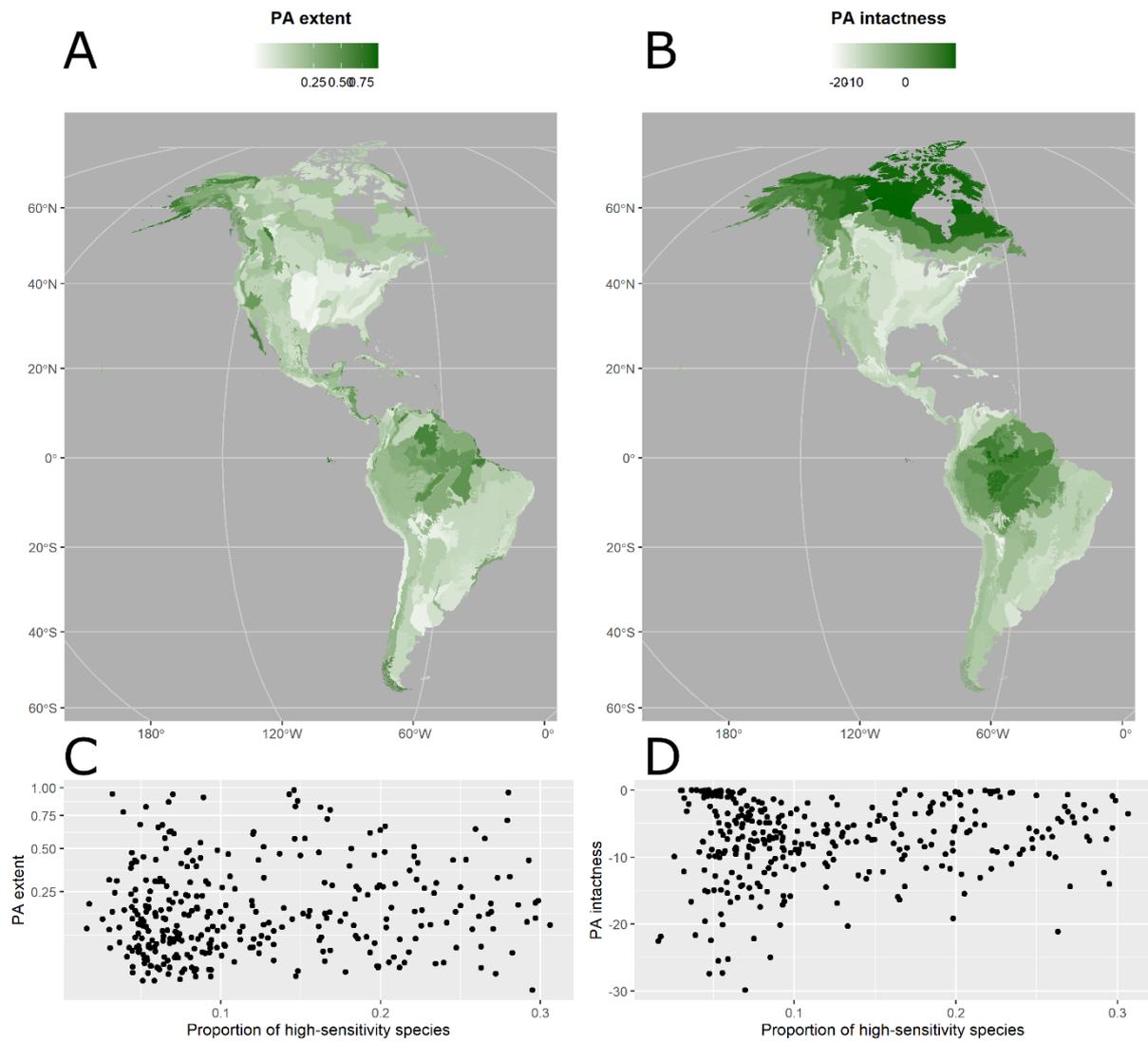


Fig. S7: Spatial patterns of the investment in habitat protection across ecoregions, as measured by: (A) protected area extent (fraction of the ecoregion covered by protected areas), and (B) protected area intactness (mean intactness of pixels within the ecoregion that intersect by >50% with protected areas), and the respective (C, D) correlation with the proportion of high-sensitivity species.

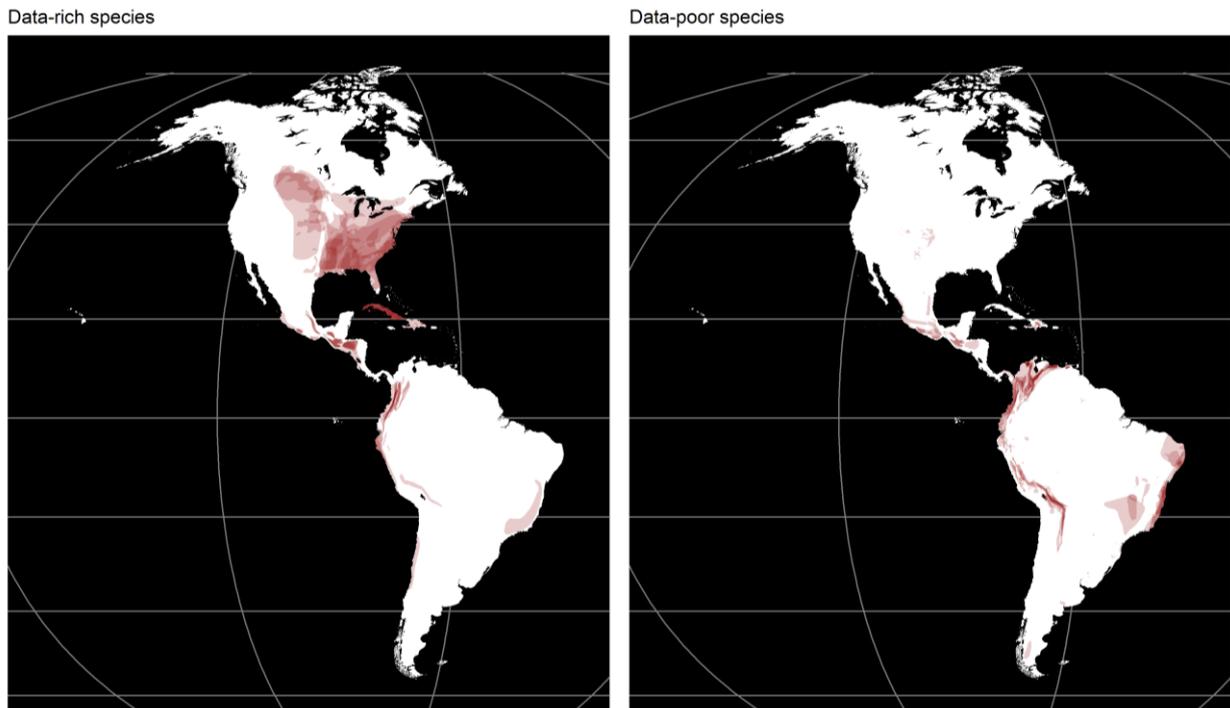


Fig. S8: Spatial distribution of high-sensitivity species with no or minor coverage by intact protected habitats (as in Fig. 2C), with data-rich species (left) and data-poor species (right).

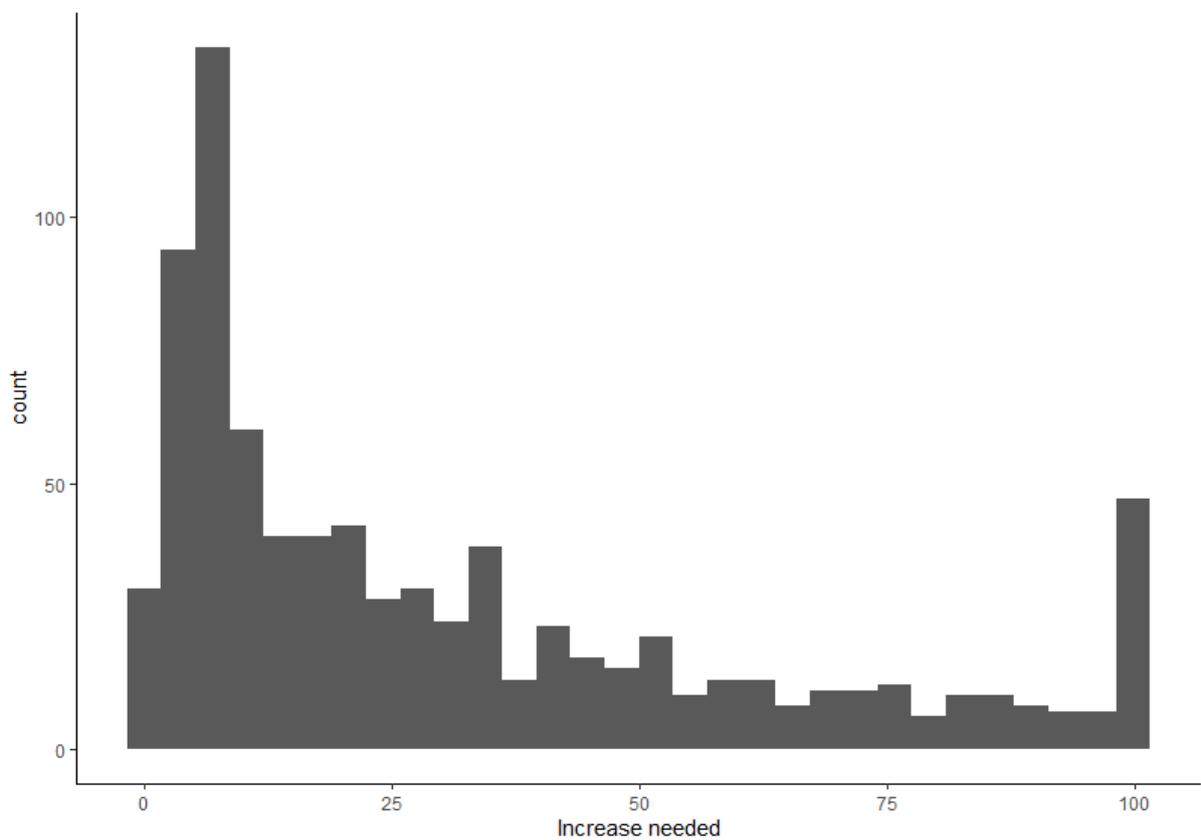


Fig. S9: Increase needed in the proportion of species range covered by intact protected habitats to reach the target from Rodrigues et al. 2004. For instance, if a species has 20% of its range covered by intact protected habitats and a target of 50%, we consider the “Increase needed” as 30.

Table S2: Results at the ecoregion level for the 325 ecoregions used in the study.

Ecoregion name	Eco. code	Extent	PA extent	Intact habitat protection	PA intactness	Trend in PA intactness	Proportion of high-sensitivity species	Number of high-sensitivity species	Median sensitivity of species
Alaska Peninsula montane taiga	7	4.79E+10	0.83	0.8	-0.3	0.04	0.05	5	29.63
Alaska/St. Elias Range tundra	8	1.52E+11	0.45	0.44	-0.3	0	0.06	9	28.85
Alberta Mountain forests	10	3.99E+10	0.68	0.62	-0.8	0.02	0.05	10	28.15
Alberta/British Columbia foothills forests	11	1.21E+11	0.02	0.01	-4.9	0.48	0.07	15	28.42
Aleutian Islands tundra	14	5.48E+09	0.94	0.79	-1.2	0.17	0.02	1	30.1
Allegheny Highlands forests	15	8.41E+10	0.04	0	-9.2	0.93	0.03	6	28.26
Alta Parano Atlantic forests	17	4.85E+11	0.06	0.01	-9.4	-0.31	0.1	80	31.18
Alvarado mangroves	21	4.56E+09	0.28	0.03	-8.2	-0.1	0.19	62	31.33
Amapa mangroves	22	1.57E+09	0.8	0.81	0	0	0.17	87	31.64
Appalachian mixed mesophytic forests	32	1.93E+11	0.03	0	-10.1	0.92	0.04	8	28.29
Appalachian/Blue Ridge forests	33	1.60E+11	0.06	0.01	-7.3	0.54	0.05	9	28.24
Apure-Villavicencio dry forests	35	6.87E+10	0.11	0.01	-9.3	-0.57	0.22	202	33.06
Araucaria moist forests	38	2.17E+11	0.04	0.01	-7.8	-0.37	0.1	60	31.04
Araya and Paria xeric scrub	39	5.29E+09	0.05	0	-15.8	-1.1	0.09	38	30.13
Arctic coastal tundra	40	9.84E+10	0.13	0.12	-0.2	-0.01	0.05	5	29.97
Arctic foothills tundra	42	1.29E+11	0.21	0.22	-0.2	-0.02	0.05	6	29.93
Argentine Espinal	43	1.09E+11	0.02	0	-6.7	-0.27	0.05	17	29.1
Argentine Monte	44	4.10E+11	0.08	0.06	-3.7	-0.15	0.07	24	29.91
Arid Chaco	45	9.91E+10	0.03	0.02	-3.9	-0.07	0.05	16	29.28
Arizona Mountains forests	46	1.09E+11	0.1	0.06	-3.5	0.05	0.1	24	27.81
Aruba-Curacao-Bonaire cactus scrub	48	4.60E+08	0.1	0	-22.5	-0.92	0	0	26.9
Atacama desert	50	1.05E+11	0.02	0.01	-4.8	-0.55	0.08	12	29.15
Atlantic Coast restingas	51	7.89E+09	0.16	0.03	-11.8	-0.74	0.1	69	31.11
Atlantic coastal pine barrens	54	8.98E+09	0.26	0	-15.1	3.03	0.04	6	28.06
Atlantic dry forests	55	1.15E+11	0.07	0.05	-2.8	-0.06	0.07	35	30.31
Baffin coastal tundra	61	9.12E+09	0.05	0.05	-0.2	-0.16	0	0	31.05
Bahamian dry forests	62	4.81E+09	0.01	0	-11.6	-0.36	0.08	6	27.59
Bahamian mangroves	63	6.63E+09	0.02	0	-7.5	-0.01	0.1	7	27.6
Bahia coastal forests	65	1.10E+11	0.08	0.01	-8.3	-0.37	0.12	79	31.56
Bahia interior forests	66	2.30E+11	0.04	0.01	-7.8	-0.35	0.12	90	31.57
Bahia mangroves	67	2.12E+09	0.19	0.09	-8.8	-0.68	0.1	49	31.1
Baja California desert	68	7.79E+10	0.61	0.46	-2.3	-0.11	0.07	11	27.42
Bajio dry forests	69	3.75E+10	0.07	0.02	-10.7	-0.1	0.08	22	29.09
Balsas dry forests	71	6.26E+10	0.11	0.02	-7.7	0.03	0.15	57	30.35

Belizean Coast mangroves	75	2.80E+09	0.11	0	-12.6	-1	0.22	71	32.13
Belizian pine forests	77	2.84E+09	0.03	0	-6.1	-0.77	0.22	71	31.91
Beni savanna	78	1.26E+11	0.01	0	-7.6	-0.07	0.17	135	32.7
Beringia lowland tundra	80	1.51E+11	0.66	0.62	-0.5	-0.02	0.07	10	29.62
Beringia upland tundra	81	9.76E+10	0.43	0.42	-0.1	0	0.06	8	29.88
Blue Mountains forests	84	6.48E+10	0.09	0.04	-4.4	0.01	0.07	16	28.31
Bocas del Toro-San Bastimentos Island-San Blas mangroves	85	5.42E+08	0.23	0	-9.5	-0.49	0.26	109	32.66
Bolivian montane dry forests	88	8.05E+10	0.02	0	-19.2	-1.2	0.19	198	32.99
Bolivian Yungas	87	9.08E+10	0.02	0.01	-3.1	-0.13	0.2	235	33.1
British Columbia mainland coastal forests	94	1.38E+11	0.3	0.29	-0.7	-0.04	0.06	14	28.4
Brooks/British Range tundra	95	1.60E+11	0.63	0.63	0	0	0.07	10	30
Caatinga	97	7.36E+11	0.07	0.03	-5.1	-0.22	0.11	68	31.04
Caatinga Enclaves moist forests	98	4.81E+09	0.28	0.01	-13	-1.76	0.06	20	29.55
California Central Valley grasslands	100	5.52E+10	0.04	0	-12.8	0.23	0.05	11	27.44
California coastal sage and chaparral	101	3.63E+10	0.09	0.02	-8.5	0.24	0.07	15	27.38
California interior chaparral and woodlands	102	6.47E+10	0.07	0.01	-9.6	0.53	0.06	15	27.6
California montane chaparral and woodlands	103	2.05E+10	0.24	0.14	-3.4	0.21	0.07	16	27.33
Campos Rupestres montane savanna	105	2.65E+10	0.26	0.06	-8	-0.26	0.1	77	31.23
Canadian Aspen forests and parklands	106	3.98E+11	0.08	0.01	-11.4	0.38	0.07	20	28.86
Caqueta moist forests	112	1.85E+11	0.27	0.26	-1	-0.24	0.22	151	33.17
Cascade Mountains leeward forests	118	4.64E+10	0.41	0.35	-1.4	0.02	0.08	18	28.45
Catatumbo moist forests	121	2.29E+10	0.28	0	-8.6	-0.27	0.17	107	31.64
Cauca Valley dry forests	122	7.36E+09	0.02	0	-21.1	0.37	0.26	171	33.51
Cauca Valley montane forests	123	3.21E+10	0.13	0	-12.3	-0.3	0.29	255	34.04
Cayman Islands dry forests	125	1.34E+08	0.08	0	-16	0	0.11	5	27.66
Cayos Miskitos-San Andrés & Providencia moist forests	126	9.54E+07	0.38	0	-7.7	-1	0.05	1	27.66
Central American Atlantic moist forests	130	8.97E+10	0.42	0.15	-5.7	-0.57	0.25	136	32.3
Central American dry forests	131	6.82E+10	0.08	0	-11.3	-0.42	0.19	132	31.3
Central American montane forests	132	1.33E+10	0.31	0.03	-9	-0.64	0.23	119	31.98
Central American pine-oak forests	133	1.12E+11	0.12	0.03	-8.5	-0.52	0.24	131	32.04
Central and Southern Cascades forests	161	4.50E+10	0.21	0.11	-3.8	0.06	0.06	13	27.89
Central and Southern mixed grasslands	162	2.83E+11	0.01	0	-8.7	0.17	0.07	14	27.68

Central Andean dry puna	136	3.08E+11	0.11	0.06	-3.4	-0.06	0.18	58	31.61
Central Andean puna	137	1.62E+11	0.14	0.04	-6.6	-0.07	0.16	122	31.81
Central Andean wet puna	138	1.18E+11	0.12	0.01	-8.9	-0.15	0.23	239	33.67
Central British Columbia Mountain forests	142	7.19E+10	0.09	0.09	-0.4	0	0.05	9	28.42
Central Canadian Shield forests	143	4.63E+11	0.13	0.14	-0.5	0	0.05	9	28.19
Central forest/grasslands transition zone	163	4.08E+11	0.02	0	-13.9	1.41	0.07	15	28.35
Central Mexican matorral	150	5.95E+10	0.05	0.01	-15.8	-0.2	0.09	26	29.15
Central Mexican wetlands	151	2.80E+08	0.17	0	-25	0.36	0.09	21	28.68
Central Pacific coastal forests	152	7.38E+10	0.12	0.09	-2.4	0.04	0.03	6	27.38
Central tall grasslands	164	2.49E+11	0.02	0	-14.2	1.36	0.06	11	28.74
Central U.S. hardwood forests	159	2.97E+11	0.03	0	-10	0.89	0.06	10	28.06
Cerrado	165	1.92E+12	0.07	0.04	-5.6	-0.26	0.16	170	32.29
Chaco	166	6.11E+11	0.11	0.08	-2.8	-0.17	0.1	75	31.25
Chiapas Depression dry forests	174	1.41E+10	0.03	0	-15.5	0.46	0.2	85	31.14
Chiapas montane forests	175	5.79E+09	0.04	0.02	-5.2	-0.47	0.22	91	31.75
Chihuahuan desert	176	5.11E+11	0.07	0.03	-5.4	-0.06	0.09	30	28.65
Chilean matorral	177	1.49E+11	0.01	0	-7.6	-0.28	0.07	13	30.18
Chimalapas montane forests	178	2.09E+09	0.14	0.06	-4.4	-0.09	0.2	74	31.23
Chiquitano dry forests	180	2.31E+11	0.01	0.01	-2.6	-0.1	0.14	114	31.79
Choco-Darien moist forests	181	7.38E+10	0.12	0.07	-3.5	-0.29	0.3	261	34.36
Coastal Venezuelan mangroves	184	5.86E+09	0.27	0.01	-8.9	-0.38	0.1	52	30.54
Colorado Plateau shrublands	186	3.27E+11	0.1	0.02	-6.4	0.01	0.09	24	28.34
Colorado Rockies forests	187	1.33E+11	0.15	0.1	-3.2	0.03	0.08	19	28.35
Cook Inlet taiga	189	2.79E+10	0.31	0.25	-2	-0.13	0.04	5	28.43
Copper Plateau taiga	192	1.72E+10	0.21	0.21	-0.9	0.03	0.05	7	29.1
Cordillera Central paramo	193	1.22E+10	0.16	0.11	-3.2	-0.07	0.26	204	33.97
Cordillera de Merida paramo	196	2.82E+09	0.72	0	-10.3	-0.27	0.17	93	31.8
Cordillera La Costa montane forests	194	1.44E+10	0.57	0	-12.2	-0.84	0.14	85	31.2
Cordillera Oriental montane forests	195	6.80E+10	0.27	0.06	-6.2	-0.31	0.24	285	33.5
Cordoba montane savanna	209	5.83E+10	0.06	0.02	-6.4	-0.25	0.05	17	29.54
Costa Rican seasonal moist forests	198	1.07E+10	0.1	0	-14.4	-0.55	0.27	150	33.23
Cuban cactus scrub	203	3.27E+09	0.19	0	-14.5	-0.48	0.12	14	29.54
Cuban dry forests	204	6.59E+10	0.06	0	-10.4	-0.04	0.13	16	29.6
Cuban moist forests	205	2.14E+10	0.21	0	-10.9	-0.09	0.12	15	29.6
Cuban pine forests	206	6.44E+09	0.07	0	-11.4	0.01	0.12	14	29.55
Cuban wetlands	207	5.68E+09	0.62	0.21	-6	-0.04	0.12	14	29.55
Davis Highlands tundra	213	8.81E+10	0.31	0.31	-0.1	-0.01	0.04	1	31.45

East Central Texas forests	223	5.28E+10	0.01	0	-9.8	0.09	0.04	7	27.95
Eastern Canadian forests	235	4.88E+11	0.17	0.16	-0.6	0.03	0.04	7	28.38
Eastern Canadian Shield taiga	234	7.55E+11	0.1	0.1	0	0	0.05	5	29.16
Eastern Cascades forests	236	5.53E+10	0.06	0.01	-7	0.09	0.06	15	28.07
Eastern Cordillera real montane forests	238	1.03E+11	0.19	0.13	-3.1	-0.39	0.28	370	34.03
Eastern forest/boreal transition	252	3.48E+11	0.11	0.09	-3.1	0.12	0.05	10	28.34
Eastern Great Lakes lowland forests	240	1.17E+11	0.02	0	-16.7	1.74	0.05	10	28.45
Eastern Panamanian montane forests	250	3.05E+09	0.71	0.54	-2.2	-0.25	0.28	145	33.62
Ecuadorian dry forests	254	2.13E+10	0.03	0	-9.5	-0.17	0.24	116	32.56
Edwards Plateau savanna	255	6.19E+10	0.01	0	-14.3	-0.65	0.06	9	27.38
Enriquillo wetlands	260	6.32E+08	0.62	0.29	-5.6	-0.1	0.07	7	28.31
Esmeraldes/Choco mangroves	262	6.53E+09	0.32	0.11	-4.9	-0.46	0.27	117	33.53
Everglades	270	2.01E+10	0.25	0.16	-3.2	0.1	0.02	3	26.32
Flint Hills tall grasslands	277	2.97E+10	0.02	0	-9.4	0.26	0.05	7	27.62
Florida sand pine scrub	278	3.89E+09	0.16	0	-12.1	0.28	0.02	2	27.44
Fraser Plateau and Basin complex	279	1.37E+11	0.1	0.1	-0.4	0	0.07	15	28.35
Great Basin montane forests	288	5.80E+09	0.5	0.29	-3.9	0.03	0.07	15	28.05
Great Basin shrub steppe	289	3.37E+11	0.09	0.04	-4.6	0	0.08	20	28.05
Greater Antilles mangroves	293	1.07E+10	0.46	0.1	-8.1	0.01	0.1	24	28.75
Guajira-Barranquilla xeric scrub	295	3.17E+10	0.04	0	-15.9	-0.78	0.16	92	31.27
Guayanan Highlands moist forests	296	3.38E+11	0.61	0.6	-0.5	-0.14	0.19	154	32.56
Guayaquil flooded grasslands	297	2.94E+09	0.02	0	-7.9	0.14	0.2	72	31.43
Guianan Freshwater swamp forests	298	7.74E+09	0.08	0.06	-3.6	-0.27	0.16	86	31.6
Guianan mangroves	299	1.46E+10	0.57	0.32	-3.8	-0.69	0.15	103	31.6
Guianan moist forests	300	5.14E+11	0.29	0.29	-0.6	-0.16	0.16	129	32.13
Gulf of California xeric scrub	304	2.36E+10	0.49	0.41	-1.9	-0.12	0.08	7	27.33
Gulf of Fonseca mangroves	305	1.63E+09	0.67	0	-8.8	-0.36	0.06	12	28.73
Gulf of Guayaquil-Tumbes mangroves	306	3.32E+09	0.16	0	-9.7	-0.74	0.17	54	30.78
Gulf of Panama mangroves	308	2.43E+09	0.05	0	-8.7	-0.39	0.25	121	32.56
Gulf of St. Lawrence lowland forests	309	3.95E+10	0.03	0.02	-4.9	0.45	0.04	6	28.05
Gurupa varzea	310	9.95E+09	0.46	0.44	-1.2	-0.38	0.19	129	32.83
Guyanana savanna	311	1.05E+11	0.22	0.16	-2.5	-0.49	0.18	139	32.48
Hawaii tropical dry forests	314	6.65E+09	0.16	0.07	-4.6	-0.38	0.19	14	30.49
Hawaii tropical high shrublands	315	1.86E+09	0.43	0.37	-1.1	0	0.18	10	27.76
Hawaii tropical low shrublands	316	1.53E+09	0.08	0.03	-5	0	0.08	5	27.67
Hawaii tropical moist forests	317	6.75E+09	0.13	0.09	-3.5	-0.19	0.22	17	31.03

High Arctic tundra	320	4.65E+11	0.1	0.1	0	-0.02	0.03	1	32.24
Hispaniolan dry forests	325	1.55E+10	0.23	0	-10.2	-0.71	0.1	11	28.84
Hispaniolan moist forests	326	4.61E+10	0.11	0	-11.4	-0.17	0.11	12	29.07
Hispaniolan pine forests	327	1.16E+10	0.39	0.02	-7.4	-0.16	0.09	10	28.79
Humid Chaco	333	3.36E+11	0.07	0.02	-6.4	-0.18	0.07	42	30.77
Humid Pampas	334	2.41E+11	0.05	0	-11.9	-0.26	0.04	13	29.03
Ilha Grande mangroves	339	3.21E+09	0.49	0.16	-9.3	-0.06	0.09	57	30.97
Interior Alaska/Yukon lowland taiga	345	4.44E+11	0.32	0.32	-0.3	0	0.07	11	29.58
Interior Yukon/Alaska alpine tundra	346	2.33E+11	0.17	0.18	-0.2	0	0.07	13	29.24
Iquitos varzea	347	1.15E+11	0.2	0.18	-0.7	-0.12	0.26	236	34.37
Isthmian-Atlantic moist forests	352	5.90E+10	0.33	0.05	-7	-0.48	0.28	203	33.31
Isthmian-Pacific moist forests	353	2.94E+10	0.1	0.03	-5.8	-0.29	0.26	155	33.09
Jalisco dry forests	356	2.62E+10	0.09	0.01	-8.4	-0.54	0.11	35	29.55
Jamaican dry forests	357	2.32E+09	0.2	0	-21.8	-0.37	0.02	2	27.79
Jamaican moist forests	358	8.31E+09	0.14	0	-9.9	0.36	0.03	3	28.08
Japura-Solimoes-Negro moist forests	360	2.70E+11	0.41	0.4	-0.2	-0.04	0.22	165	33.27
Jurua-Purus moist forests	366	2.43E+11	0.17	0.17	-0.1	-0.01	0.22	144	33.56
Klamath-Siskiyou forests	387	5.04E+10	0.15	0.09	-3.5	0.01	0.06	12	27.45
La Costa xeric shrublands	395	6.86E+10	0.14	0	-13.2	-1.27	0.14	90	31.28
Lara-Falcon dry forests	398	1.70E+10	0.16	0	-10	-0.78	0.09	39	30.34
Leeward Islands dry forests	399	1.49E+08	0.01	0	-4	0	0.12	6	27.56
Leeward Islands moist forests	400	9.92E+08	0.78	0	-21.6	-0.8	0.05	4	26.55
Leeward Islands xeric scrub	401	1.65E+09	0.25	0	-27.3	0.33	0.07	6	26.65
Lesser Antilles mangroves	402	6.53E+08	0.31	0	-25.5	0.15	0.06	6	27.21
Llanos	404	3.90E+11	0.08	0.05	-3.2	-0.38	0.18	167	32.53
Low Arctic tundra	407	7.98E+11	0.17	0.17	0	0	0.04	5	29.63
Madeira-Tapajos moist forests	422	7.21E+11	0.27	0.27	-0.3	-0.02	0.2	194	32.91
Magdalena-Santa Marta mangroves	425	3.20E+09	0.27	0.01	-9	-0.16	0.2	104	31.89
Magdalena-Uraba moist forests	426	7.69E+10	0.08	0	-11.7	-0.54	0.22	139	32.53
Magdalena Valley dry forests	423	1.97E+10	0.02	0	-11	-0.21	0.23	154	32.28
Magdalena Valley montane forests	424	1.05E+11	0.15	0	-10	-0.24	0.26	276	33.5
Magellanic subpolar forests	427	1.48E+11	0.54	0.52	-1.3	-0.1	0.08	11	30.41
Maracaibo dry forests	437	3.03E+10	0.15	0	-12.2	-0.36	0.15	88	31.55
Marajo Varzea forests	438	8.89E+10	0.66	0.57	-2.2	-0.27	0.2	146	32.72
Maranhao Babacu forests	439	1.43E+11	0.12	0.04	-6.3	-0.27	0.13	67	31.37
Maranhao mangroves	440	1.13E+10	0.88	0.23	-7.4	-0.63	0.15	76	31.46
Maranon dry forests	441	1.14E+10	0.06	0.01	-4.3	-0.35	0.26	190	33.92

Marismas Nacionales-San Blas mangroves	444	2.04E+09	0.91	0.2	-7	-0.22	0.09	15	29
Mato Grosso seasonal forests	448	4.15E+11	0.08	0.06	-1.9	-0.09	0.18	142	32.7
Mayan Corridor mangroves	450	4.10E+09	0.82	0.64	-1.9	-0.1	0.18	45	31.37
Meseta Central matorral	458	1.26E+11	0.05	0.02	-6.1	-0.11	0.12	38	29.7
Mexican South Pacific Coast mangroves	460	1.17E+09	0.08	0	-12.5	-0.25	0.09	18	29.5
Mid-Continental Canadian forests	461	3.69E+11	0.18	0.17	-0.9	0.01	0.05	11	28.4
Middle Arctic tundra	462	1.04E+12	0.05	0.05	0	-0.01	0.03	2	31.29
Middle Atlantic coastal forests	463	1.34E+11	0.07	0.01	-9.1	0.45	0.05	8	28.09
Midwestern Canadian Shield forests	465	5.47E+11	0.14	0.13	-0.4	0.01	0.05	10	28.41
Miskito pine forests	469	1.90E+10	0.16	0.04	-7.3	-0.98	0.26	85	32.32
Mississippi lowland forests	470	1.13E+11	0.07	0.01	-9.7	0.45	0.06	9	28.26
Moist Pacific Coast mangroves	473	1.60E+09	0.26	0.05	-6.2	-1.26	0.19	65	31.07
Mojave desert	474	1.31E+11	0.42	0.18	-4.9	0.04	0.09	21	27.58
Montana Valley and Foothill grasslands	476	8.19E+10	0.05	0.01	-15.1	0.02	0.09	21	28.45
Monte Alegre varzea	478	6.70E+10	0.16	0.16	-0.5	-0.1	0.22	193	33.1
Mosquita-Nicaraguan Caribbean Coast mangroves	479	4.45E+09	0.43	0.03	-7.1	-1	0.26	87	32.32
Motagua Valley thornscrub	480	2.34E+09	0.03	0	-13.1	0	0.22	86	31.76
Muskwa/Slave Lake forests	484	2.63E+11	0.14	0.14	-0.1	0	0.05	9	28.86
Napo moist forests	491	2.52E+11	0.2	0.19	-0.9	-0.18	0.29	298	34.66
Nebraska Sand Hills mixed grasslands	494	6.13E+10	0.02	0	-8	0	0.07	11	27.64
Negro-Branco moist forests	495	2.13E+11	0.29	0.29	-0.2	-0.05	0.2	148	33.11
New England/Acadian forests	502	2.38E+11	0.06	0.02	-5.3	0.26	0.04	9	28.47
Newfoundland Highland forests	504	1.64E+10	0.18	0.17	-0.4	0	0.04	5	28.29
North Central Rockies forests	513	2.46E+11	0.24	0.2	-1.8	0.04	0.08	21	28.38
Northeastern Brazil restingas	523	1.01E+10	0.3	0.12	-6.3	-0.56	0.08	28	29.91
Northeastern coastal forests	527	8.98E+10	0.04	0	-22.4	2.89	0.04	9	28.34
Northern Andean paramo	530	3.00E+10	0.42	0.06	-7.3	-0.21	0.29	387	33.86
Northern California coastal forests	532	1.33E+10	0.16	0	-9.2	0.42	0.05	10	26.85
Northern Canadian Shield taiga	533	6.15E+11	0.07	0.07	0	0	0.04	7	28.75
Northern Cordillera forests	535	2.63E+11	0.19	0.19	-0.2	0	0.06	11	28.51
Northern Dry Pacific Coast mangroves	536	1.06E+09	0.58	0	-16	0	0.07	11	28.77
Northern Honduras mangroves	537	1.06E+09	0.64	0.15	-7	-0.73	0.27	82	32.81
Northern mixed grasslands	549	2.19E+11	0.08	0	-12.3	0.05	0.08	20	28.74

Northern Pacific coastal forests	542	6.06E+10	0.4	0.34	-1.1	-0.07	0.05	8	28.38
Northern short grasslands	550	6.40E+11	0.06	0.01	-8.6	-0.02	0.09	23	28.8
Northern tall grasslands	551	7.62E+10	0.08	0.02	-8.6	0.35	0.06	13	28.4
Northern transitional alpine forests	552	2.57E+10	0.05	0.05	-0.4	0.01	0.05	8	28.2
Northwest Mexican Coast mangroves	555	4.99E+09	0.47	0.17	-4.8	-0.06	0.08	15	28.18
Northwest Territories taiga	557	3.47E+11	0.08	0.08	-0.1	-0.04	0.05	9	28.86
Northwestern Andean montane forests	558	8.14E+10	0.14	0.03	-5.6	-0.49	0.29	319	34.06
Oaxacan montane forests	566	7.62E+09	0.02	0.01	-6.1	0.02	0.2	91	31.28
Ogilvie/MacKenzie alpine tundra	568	2.09E+11	0.11	0.11	-0.1	0	0.06	9	28.65
Okanogan dry forests	569	5.34E+10	0.14	0.04	-8.9	0.24	0.07	15	28.31
Orinoco Delta swamp forests	572	2.82E+10	0.51	0.44	-2.2	-1.27	0.12	73	31.11
Orinoco wetlands	573	6.03E+09	0.3	0.17	-4.1	-0.76	0.09	37	30.29
Ozark Mountain forests	575	6.22E+10	0.14	0.01	-7.3	0.05	0.06	8	28.06
Pacific Coastal Mountain icefields and tundra	576	1.07E+11	0.42	0.42	-0.2	0	0.05	9	28.35
Palouse grasslands	579	4.70E+10	0.03	0.01	-7.4	0.41	0.08	17	28.42
Panamanian dry forests	581	5.12E+09	0.01	0	-4	-0.45	0.27	141	33.12
Pantanal	583	1.71E+11	0.03	0.02	-1.9	-0.04	0.1	63	30.97
Pantanos de Centla	584	1.72E+10	0.28	0.12	-5.5	-0.16	0.21	61	31.58
Para mangroves	585	4.42E+09	0.48	0.11	-7.9	-0.99	0.16	85	31.6
Paraguana xeric scrub	586	1.60E+10	0.12	0	-16.9	-0.9	0.13	64	30.94
Parana flooded savanna	587	3.90E+10	0.24	0.06	-7.8	-0.1	0.04	15	29.37
Patagonian grasslands	589	6.33E+10	0.04	0.03	-4.8	-0.26	0.09	11	30.18
Patagonian steppe	590	4.88E+11	0.07	0.04	-4.3	-0.24	0.07	13	30.02
Patia Valley dry forests	591	2.28E+09	0	0	-14	0	0.29	141	34.34
Pernambuco coastal forests	595	1.76E+10	0.04	0	-17.1	-1.47	0.09	36	30.69
Pernambuco interior forests	596	2.27E+10	0.02	0	-16.6	-1.54	0.09	37	30.69
Peruvian Yungas	598	1.87E+11	0.15	0.12	-2.4	-0.31	0.26	360	34.21
Peten-Veracruz moist forests	600	1.49E+11	0.18	0.05	-6.3	-0.43	0.21	114	31.71
Petenes mangroves	599	1.98E+09	0.94	0.53	-4	-0.1	0.08	14	29.42
Piney Woods forests	603	1.41E+11	0.03	0	-8.7	0.16	0.06	8	28.06
Puerto Rican dry forests	607	1.28E+09	0.08	0	-15	3.66	0.06	6	26.52
Puerto Rican moist forests	608	7.55E+09	0.05	0	-18.5	2.52	0.06	7	26.53
Puget lowland forests	609	2.26E+10	0.06	0	-14.9	0.73	0.05	9	27.52
Purus-Madeira moist forests	611	1.74E+11	0.51	0.5	-0.2	-0.01	0.22	162	33.36
Purus varzea	610	1.78E+11	0.29	0.3	-0.3	0	0.23	185	33.49
Queen Charlotte Islands	618	9.98E+09	0.47	0.42	-0.9	-0.29	0.02	1	27.59
Rio Lagartos mangroves	628	3.47E+09	0.47	0.24	-5.2	0.29	0.14	31	30.74

Rio Negro-Rio San Sun mangroves	630	4.78E+08	0.95	0.48	-4.2	-1.44	0.28	87	32.93
Rio Negro campinarana	629	8.10E+10	0.36	0.37	0	0	0.21	131	33.31
Rio Piranhas mangroves	631	2.12E+09	0.2	0	-22.2	-1.7	0.07	27	30.28
Rio Sao Francisco mangroves	632	2.62E+09	0.14	0.01	-20.1	-1.28	0.09	39	30.76
San Lucan xeric scrub	643	3.89E+09	0.18	0.07	-8.7	-0.99	0.09	7	27.24
Santa Marta montane forests	644	4.80E+09	0.46	0	-7.4	-0.64	0.14	71	30.89
Santa Marta paramo	645	1.25E+09	0.98	0	-7.1	-0.53	0.14	63	30.88
Sechura desert	655	1.85E+11	0.04	0.01	-6.1	-0.35	0.09	31	30.23
Semi-arid Pampas	657	3.28E+11	0.01	0.01	-6.1	-0.16	0.05	13	29.18
Serra do Mar coastal forests	660	1.05E+11	0.33	0.09	-11.1	-0.24	0.1	75	31.3
Sierra de la Laguna dry forests	669	3.99E+09	0.23	0.09	-7	-1.02	0.09	7	27.24
Sierra de la Laguna pine-oak forests	670	1.07E+09	0.87	0.67	-2.9	-0.12	0.07	6	27.19
Sierra de los Tuxtlas	671	3.91E+09	0.39	0	-8.5	-0.19	0.19	52	31.42
Sierra Juarez & San Pedro Martir pine-oak forests	662	4.01E+09	0.17	0.14	-1.3	-0.01	0.06	8	26.89
Sierra Madre de Chiapas moist forest	665	1.13E+10	0.17	0.08	-4.3	-0.22	0.15	54	30.29
Sierra Madre de Oaxaca pine-oak forests	666	1.44E+10	0.06	0.01	-11.7	-0.48	0.2	98	31.26
Sierra Madre del Sur pine-oak forests	667	6.13E+10	0.03	0.01	-5.6	-0.31	0.14	49	30.24
Sierra Madre Occidental pine-oak forests	663	2.23E+11	0.14	0.08	-3.9	-0.12	0.1	39	29.36
Sierra Madre Oriental pine-oak forests	664	6.58E+10	0.32	0.15	-5.1	-0.11	0.13	51	29.46
Sierra Nevada forests	668	5.30E+10	0.3	0.24	-1.9	0.03	0.07	16	27.77
Sinaloan dry forests	673	7.77E+10	0.11	0.04	-6.6	-0.24	0.11	37	29.55
Sinu Valley dry forests	674	2.50E+10	0.03	0	-8.9	-0.52	0.16	92	31.3
Snake/Columbia shrub steppe	675	2.19E+11	0.15	0.02	-7.6	0.03	0.07	18	28.36
Solimoës-Japura moist forest	678	1.68E+11	0.24	0.25	-0.4	-0.11	0.23	145	33.59
Sonoran-Sinaloan transition subtropical dry forest	683	5.11E+10	0.05	0.02	-6.4	-0.2	0.12	31	29.15
Sonoran desert	682	2.24E+11	0.16	0.1	-3.8	0	0.09	25	28.05
South Avalon-Burin oceanic barrens	685	2.03E+09	0.04	0.04	-1	-0.04	0.03	3	28.35
South Central Rockies forests	686	1.60E+11	0.29	0.23	-1.8	0.02	0.09	22	28.42
South Florida rocklands	690	2.08E+09	0.11	0.01	-16.6	1.37	0.03	3	26.55
Southeastern conifer forests	707	2.37E+11	0.05	0.01	-9.9	0.36	0.04	6	27.51
Southeastern mixed forests	708	3.49E+11	0.02	0	-12.3	0.56	0.05	9	28.4
Southern Andean steppe	714	1.79E+11	0.17	0.11	-2.8	-0.16	0.08	18	30.12
Southern Andean Yungas	713	6.13E+10	0.06	0.02	-6.1	-0.2	0.1	61	30.92
Southern Cone Mesopotamian savanna	716	7.78E+10	0.02	0	-6.2	-0.06	0.06	25	30.12

Southern Dry Pacific Coast mangroves	718	9.08E+08	0.16	0	-16.3	-0.38	0.17	54	30.79
Southern Great Lakes forests	719	2.45E+11	0.01	0	-15	2.09	0.04	9	28.49
Southern Hudson Bay taiga	720	3.75E+11	0.18	0.19	-0.1	0	0.04	7	28.85
Southern Pacific dry forests	726	4.25E+10	0.04	0.01	-9.5	-0.06	0.2	95	31.24
Southwest Amazon moist forests	730	7.51E+11	0.19	0.18	-0.8	-0.13	0.24	348	33.95
Talamancan montane forests	763	1.64E+10	0.57	0.27	-4.7	-0.25	0.26	172	33.23
Tamaulipan matorral	764	1.63E+10	0.06	0.03	-7.1	-0.73	0.09	21	29.03
Tamaulipan mezquital	765	1.42E+11	0.11	0.02	-14.6	-0.07	0.07	17	28.73
Tapajos-Xingu moist forests	766	3.37E+11	0.48	0.44	-0.7	-0.05	0.2	149	32.95
Tehuacan Valley matorral	771	9.91E+09	0.16	0.01	-9.5	-0.15	0.12	43	29.7
Tehuantepec-El Manchon mangroves	772	2.70E+09	0.44	0.1	-7.1	-0.28	0.08	17	29.17
Tepuis	774	4.90E+10	0.63	0.64	-0.2	-0.1	0.19	150	32.6
Texas blackland prairies	776	5.04E+10	0.01	0	-13.7	0	0.05	8	27.63
Tocantins/Pindare moist forests	786	1.94E+11	0.11	0.04	-5.1	-0.46	0.16	98	31.86
Tornat Mountain tundra	790	3.24E+10	0.42	0.43	0	0	0.06	3	30
Trans-Mexican Volcanic Belt pine-oak forests	794	9.20E+10	0.18	0.02	-12.7	-0.16	0.14	64	30.33
Trinidad and Tobago dry forests	796	2.72E+08	0.05	0	-20.1	-2.46	0.05	15	29.15
Trinidad and Tobago moist forests	797	4.75E+09	0.3	0	-15.4	-3.23	0.06	16	29.25
Trinidad mangroves	798	1.86E+08	0.15	0	-25.2	-4.45	0.06	15	29.18
Tumbes-Piura dry forests	803	4.14E+10	0.07	0.02	-5.1	-0.16	0.21	122	32.18
Uatuma-Trombetas moist forests	805	4.74E+11	0.45	0.44	-0.2	-0.02	0.22	185	33.05
Ucayali moist forests	806	1.15E+11	0.21	0.2	-1.5	-0.47	0.29	329	34.75
Upper Midwest Forest/Savanna transition zone	808	1.66E+11	0.04	0	-14.4	1.46	0.07	15	28.73
Uruguayan savanna	810	3.56E+11	0.03	0.01	-7.5	-0.07	0.07	36	30.6
Usumacinta mangroves	812	3.14E+09	0.83	0.47	-5.2	-0.27	0.16	38	30.92
Valdivian temperate forests	813	2.49E+11	0.23	0.16	-3.1	-0.3	0.08	14	30.3
Venezuelan Andes montane forests	815	2.95E+10	0.5	0	-11.6	-0.23	0.18	128	31.99
Veracruz dry forests	816	6.65E+09	0.05	0	-14.4	-0.42	0.18	49	31.1
Veracruz moist forests	817	6.93E+10	0.08	0.02	-6.9	-0.08	0.13	49	29.86
Veracruz montane forests	818	4.97E+09	0.06	0	-20.3	0.75	0.13	42	29.88
Wasatch and Uinta montane forests	823	4.16E+10	0.1	0.06	-4.6	0.28	0.07	15	28.05
Western Ecuador moist forests	830	3.42E+10	0.04	0	-7.5	-0.39	0.28	179	33.84
Western Great Lakes forests	832	2.75E+11	0.16	0.07	-5.2	0.21	0.05	12	28.52
Western Gulf coastal grasslands	834	8.08E+10	0.12	0.03	-8.8	0.21	0.04	9	28.26
Western short grasslands	843	4.36E+11	0.01	0	-9	0.04	0.09	24	28.34

Willamette Valley forests	845	1.49E+10	0.02	0	-19.6	1.8	0.04	6	27.21
Windward Islands dry forests	846	4.93E+08	0.15	0	-27.4	-1.7	0.05	4	27.73
Windward Islands moist forests	847	2.02E+09	0.39	0.01	-17.4	-0.85	0.09	8	28.31
Windward Islands xeric scrub	848	1.03E+09	0.2	0	-29.9	-1.58	0.08	7	27.73
Wyoming Basin shrub steppe	850	1.33E+11	0.04	0	-8.4	-0.01	0.07	16	28.22
Xingu-Tocantins-Araguaia moist forests	851	2.67E+11	0.15	0.14	-0.7	-0.09	0.18	127	32.3
Yucatan dry forests	856	4.99E+10	0.1	0.03	-7.8	0.02	0.14	32	30.61
Yucatan moist forests	857	6.99E+10	0.23	0.19	-2.1	-0.11	0.2	60	31.47
Yukon Interior dry forests	858	6.25E+10	0.02	0.02	-0.8	0	0.06	9	28.36
Zacatonal	860	3.03E+08	0.61	0.28	-5.2	-0.38	0.12	47	29.73

Table S3: List of the 53 data-rich high-sensitivity species with no or minor coverage by intact protected habitat. Intact protected habitat corresponds to the area within each species' range that is both protected and with a human footprint <4 (see Methods). The proportion of intact protected habitat is obtained by dividing by the species' range size.

Name	Sensitivity	Area of intact protected habitat (km ²)	Proportion of intact protected habitat (%)	RL status
<i>Abeillia abeillei</i>	38.6	2514	1.73	LC
<i>Agelaius xanthomus</i>	43.6	0	0	EN
<i>Anisognathus igniventris</i>	43	789	0.81	LC
<i>Aphelocoma unicolor</i>	45.6	1275	0.85	LC
<i>Basileuterus trifasciatus</i>	37.7	328	1.11	LC
<i>Boissonneaua jardini</i>	42.4	224	0.72	LC
<i>Calamospiza melanocorys</i>	40.5	11046	0.66	LC
<i>Charadrius melodus</i>	42.1	3898	0.79	NT
<i>Chlorochrysa phoenicotis</i>	44.8	415	1.23	LC
<i>Coeligena wilsoni</i>	38.8	692	2.01	LC
<i>Corvus leucognaphalus</i>	41.7	329	3.95	VU
<i>Corvus nasicus</i>	38.7	1044	3.7	LC
<i>Cyanocorax sanblasianus</i>	39.8	1186	1.75	LC
<i>Cyanolyca pumilo</i>	43.6	1320	1.27	LC
<i>Dendrocygna arborea</i>	47.2	377	0.37	NT
<i>Eriocnemis derbyi</i>	39.9	843	3.41	NT
<i>Glaucidium siju</i>	39.5	2459	2.25	LC
<i>Habia cristata</i>	39.1	155	0.28	LC
<i>Heliodoxa imperatrix</i>	41.4	795	3.58	LC
<i>Helmitheros vermivorum</i>	39.8	4880	0.28	LC
<i>Icterus melanopsis</i>	39	2459	2.24	LC
<i>Lamprolaima rhami</i>	39.6	1580	1.14	LC
<i>Leuconotopicus borealis</i>	47.2	3729	0.62	NT
<i>Limnothlypis swainsonii</i>	40.3	7171	0.63	LC
<i>Melanerpes superciliaris</i>	38.3	2464	2.17	LC
<i>Mellisuga helenae</i>	39.1	2459	2.26	NT
<i>Myioborus chrysops</i>	43.5	295	0.57	LC
<i>Myiotriccus ornatus</i>	43.4	2572	1.71	LC
<i>Nesocittes micromegas</i>	37.8	540	0.72	LC
<i>Odontophorus hypertythrus</i>	39.5	428	0.7	NT
<i>Passerculus bairdii</i>	42.1	7268	0.88	LC
<i>Peucaea aestivalis</i>	46.3	3306	0.44	NT
<i>Piezorina cinerea</i>	40.3	665	1.64	LC
<i>Poospiza hispaniolensis</i>	42.9	2304	2.03	LC
<i>Priotelus temnurus</i>	40.2	2459	2.26	LC
<i>Pseudelaenia leucospodia</i>	40.4	1343	2.67	LC
<i>Pyrilia pulchra</i>	44.3	2279	2.48	LC
<i>Pyrrhulagra nigra</i>	41.4	2459	2.24	NT
<i>Quiscalus nicaraguensis</i>	40.2	0	0	LC

<i>Scelorchilus albicollis</i>	44.6	509	0.49	LC
<i>Semnornis ramphastinus</i>	40.7	1218	2.71	NT
<i>Setophaga cerulea</i>	41.4	4804	0.26	NT
<i>Setophaga chrysoparia</i>	40.4	8	0.02	EN
<i>Setophaga citrina</i>	38.3	7517	0.38	LC
<i>Setophaga kirtlandii</i>	39.9	169	0.45	NT
<i>Setophaga pityophila</i>	39.9	0	0	LC
<i>Tangara labradorides</i>	40.4	1102	1.05	LC
<i>Tangara lunigera</i>	43	247	0.85	LC
<i>Trogon aurantius</i>	38	3005	0.87	LC
<i>Trogon elegans</i>	38.9	1078	0.78	LC
<i>Tympanuchus cupido</i>	48.3	110	0.03	VU
<i>Urochroa bougueri</i>	43.1	1523	3.76	LC
<i>Zentrygon albifacies</i>	42	2725	1.41	LC