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► **To cite this version:**

Victor Cazalis. Species richness response to human pressure hides important assemblage transformations. *Proceedings of the National Academy of Sciences of the United States of America*, 2022, 119 (19), pp.e2107361119. 10.1073/pnas.2107361119 . hal-04889508

**HAL Id: hal-04889508**

**<https://hal.science/hal-04889508v1>**

Submitted on 22 Jan 2025

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## **Title:** Species richness response to human pressure hides important assemblage transformations

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### **Abstract:**

Human activities' negative impact on biodiversity is undisputed, but debate remains vivid on their effect on species richness, a key index in ecology and conservation. While some studies suggest species richness declines with human pressure, others show that it can be insensitive or even respond positively to some human pressure, because some species ("losers") are replaced by others ("winners"). However, many "winners" are favoured by intermediate pressure but decline when pressure becomes too high, and we can thus expect species richness to decline above a certain human pressure. Analysing eBird data in tropical forests, I find that, under a certain threshold, increasing human footprint causes important composition changes with "losers" (habitat specialist, endemic, sensitive and threatened species) being replaced by "winners" (habitat non-specialist, large-range, human-tolerant, anthropophilic and non-native species), resulting in a slight increase in species richness. Above this threshold though, richness in "winners" drops (except for anthropophilic and non-native species), leading to a steep decline in overall species richness. I find that the shape of species richness response to human footprint varies between regions (comparing results from the North America Breeding Bird Survey, PREDICTS database, and eBird data across eight biodiversity hotspots) and identify five different trajectories in species richness response to human pressure. I suggest they can be classified depending on their slope and monotony in the "Replace then remove framework", unifying contradictory effects of human pressure on species richness.

### **Significance statement:**

Human activities are causing biodiversity loss but there is still strong debate on their effect on species richness. Here I propose a unification of five trajectories of species richness response to increasing human pressure under the "Replace then remove framework". It consists in a first phase of assemblage transformation (with the replacement of "loser" by "winner" species), often followed by a second phase of steep decline in species richness (with the decline of many "winner" species) when human pressure exceeds a certain threshold. The empirical results presented in this study provide an outstanding illustration of assemblage transformations that may cause biotic homogenisation, demonstrating how habitat specialist, endemic, sensitive and threatened species are replaced by others with increasing human pressure.

## Introduction

The overall negative impact of human activities on wildlife species is widely recognised<sup>1</sup>. However, not all species are negatively impacted by human pressure<sup>2-4</sup>, and their response strongly depends on their traits and characteristics. For instance, many studies report that increasing human pressure causes the decline of most habitat specialist species, while many generalists can benefit from this pressure, resulting in biotic homogenisation<sup>5-7</sup>. Similarly, species that have a small geographic range tend to decrease with human pressure while species with a large range tend to respond more positively<sup>8</sup>, thus replacing small-range species across time<sup>9,10</sup>. As a result, some species are threatened with extinction because they are particularly impacted by such activities, while other species are currently expanding, sometimes helped by human introduction as non-native species<sup>1</sup>. Overall, this highlights that some species are negatively affected by human pressure (hereafter “losers”), while some can benefit from it (“winners”).

Because of this heterogeneity in individual species response to human activities, there is uncertainty regarding the effect that human pressure has on the local number of species present in an assemblage – the species richness – which remains the most used biodiversity index in ecology and conservation. It is often expected that local extinctions of losers exceed colonisation by winners, and thus that species richness decreases with human pressure, as evidenced by several empirical studies<sup>11,12</sup>. Contrastingly, numerous studies found that, although assemblage composition is strongly affected by human pressure, species richness often remains stable through time<sup>13-16</sup>. These studies showed that winners are replacing losers as they go locally extinct, suggesting that local species richness may be insensitive to human pressure<sup>14,17</sup>. Some studies even reported that assemblage transformation leads to an increase in species richness through time<sup>9</sup>, or that species richness can be higher in degraded than in intact habitats<sup>18</sup>, suggesting cases where colonisation by winners may be stronger than local extinction of losers.

These three possible trajectories – where species richness either systematically decreases, remains stable, or increases with human pressure – all assume that individual species responses to human pressure are monotonous. However, this response can take very different shapes<sup>3</sup>, with many species being favoured by an intermediate level of human pressure but negatively affected when human pressure becomes too high (e.g., bird species associated with agricultural habitats that are negatively impacted by agriculture intensification<sup>19</sup>). As a result, we could expect that some winner species will go locally extinct (or at least stop colonising) above a certain human pressure, resulting in a threshold in species richness response to human pressure<sup>20</sup>. The above-mentioned insensitivity of species richness to human pressure would thus not hold when human pressure becomes too high, as suggested by some local studies<sup>21-23</sup>. Similarly, in cases of systematic increases of species richness with human pressure, we could expect species richness to reach a peak at intermediate pressure, before declining. This somewhat echoes the intermediate disturbance hypothesis, which suggests that species coexistence may be maximal at disturbance with intermediate frequency or intensity<sup>24,25</sup>. As species richness is a key index in ecology and conservation, we need to increase and unify our understandings on the exact impact of human pressure on biodiversity.

Here I take advantage of three large-scale occurrence biodiversity datasets to study the effect of human pressure on local assemblages by comparing the richness and composition of assemblages in

sites with different level of human pressure. First, I apply a modelling method that enables discriminating between all the above-mentioned possible trajectories of species richness with increasing human pressure, with subsets from eBird in eight tropical forest biodiversity hotspots<sup>26</sup>, from the North America Breeding Bird Survey<sup>27</sup> and from the PREDICTS database<sup>28</sup> (Fig. 1). Second, I explore how assemblage composition in the eBird data is impacted by human activities and how this explains trends in species richness (Fig. 2). Specifically, I characterise assemblage composition based on its specialisation to forest habitats (measuring richness in species with high/medium dependence, *vs* species with low or no dependence on forest habitats), its endemism (measuring richness in endemic species, *vs* large-range species), its sensitivity to human activities (measuring richness in high-sensitivity species, *vs* tolerant and anthropophilic species), and its global dynamic (measuring richness in threatened and Near Threatened species, *vs* non-native species). Combining these results on overall species richness and composition, I propose a unifying framework on species richness response to human pressure (Fig. 3).

All analyses consisted in two successive models. First, the “ecological model” controlled for variation in diversity indices that is not due to human pressure, controlling for sampling heterogeneity (e.g., duration of sampling events, number of observers) and ecological heterogeneity (altitude, latitude, and Net Primary Productivity) between samples. Then, the “footprint model” used the residuals from the “ecological model” to measure the specific effect of human footprint on diversity indices (see details in Methods).

## Results

### Human footprint impact on overall species richness

The relationship between human footprint and local overall species richness of eBird checklists showed a significant threshold. It consisted in a first phase where overall species richness slightly increased with human footprint, followed by a second phase of steep decline, when human footprint exceeded 33.8 (Fig. 1A; Table S1). This threshold broadly corresponds to urbanised and highly intensive agricultural habitats (note that the model could not estimate a threshold >33.9 which corresponds to the ninth decile of the response variable; see details in Methods). Compared with a linear model, this threshold model enabled reducing the AIC by 368 (Table S2) and the pattern was supported by General Additive Models with smoothed response curves (i.e., with fewer *a priori* assumptions; Supplementary Figures S4-5).

When hotspots were considered separately, the above-mentioned two-phase relationship emerged very clearly from the hotspots with the highest statistical power (Mesoamerica and Tropical Andes, representing respectively 50% and 27% of sampling events) as well as Indo-Burma and Sundaland (Fig. 1B; Table S1). A threshold was also significant in the Atlantic Forest with a first phase with no significant trend followed by a steep decline. Finally, I fitted linear models in three hotspots, because thresholds were not significant, and found that species richness was increasing with human footprint in the Eastern Afrotropical (coef=0.013, P=0.019) and Western Ghats and Sri Lanka (coef=0.009, P<10<sup>-4</sup>), and did not change significantly in Tumbes-Chocó-Magdalena (coef=0.003, P=0.37; Fig. 1B, Table S1).

Species richness in the PREDICTS database did not show a significant threshold. A linear model was thus fitted and presented a significant decline with human footprint (coef=-0.004,  $P < 10^{-4}$ ; Fig. 1C, Table S1), and a lower AIC than the threshold model (Table S2). When considering taxa separately, the threshold was significant for none of them (respectively  $P=0.36$ ,  $P=0.53$ ,  $P=0.15$  for vertebrates, invertebrates and plants) and species richness decreased linearly for invertebrates (coef=-0.0071,  $P < 10^{-4}$ ), tended to decrease for plants (coef=-0.0034,  $P=0.088$ ) and was stable for vertebrates (coef=-0.0016,  $P=0.32$ ). I observed the same pattern when looking only at birds (N=1644, threshold P-value=0.76, linear model P-value=0.38) and birds in tropical regions (N=892, threshold P-value=0.19, linear model P-value=0.88). Species richness in BBS data showed a similar pattern as the one observed in eBird Atlantic Forest checklists, with a first phase with no significant trend until a threshold estimated at 25.45 and followed by a steep decline (Fig. 1D; Table S1).

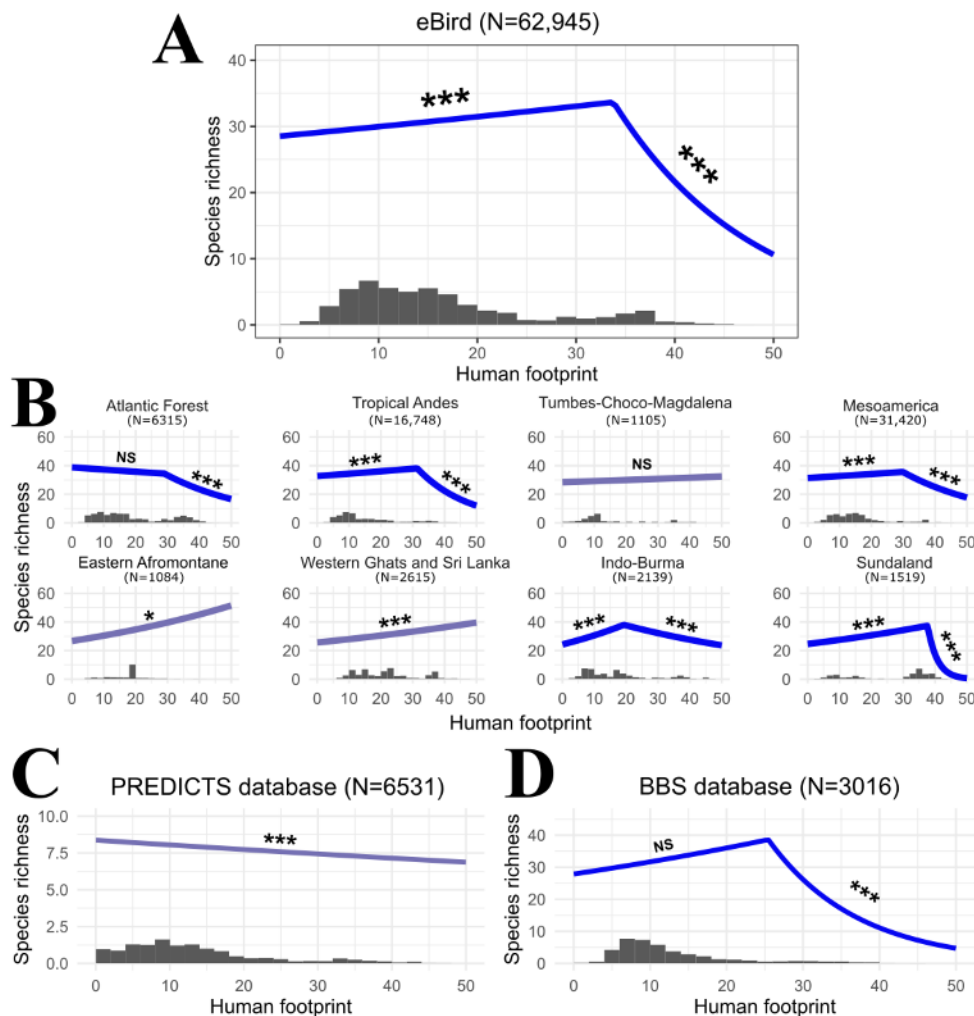


Figure 1: Effect of human footprint on overall species richness for each region and dataset. A: eBird data across the eight tropical forest biodiversity hotspots. B: eBird data modelled independently for each hotspot. C: PREDICTS data across the globe. D: BBS data across the US and Canada. Each curve represents the selected model: threshold model if significant (blue; two p-values are provided: the first one corresponds to the test of the first slope compared to 0, the second corresponds to the test of the difference of the second slope compared to the first slope), a linear model otherwise (purple; a single p-value, corresponding to the slope compared to 0). Detailed statistics in Tables S1-2 and fit in Fig. S3. To facilitate interpretation, the y-axis does not present residuals of ‘ecological models’ but rather the predicted species richness for a standard sampling event (see details in Methods). Histograms (grey bars) represent the distribution of human footprint values of sampling sites for each region (distribution of species richness values is given in Supplementary Figure 2). P-values: NS>0.05>\*>0.01>\*>0.001>\*\*\*.

Results were consistent when using the human footprint maps of 2009<sup>29</sup> and 2013<sup>30</sup>, showing similar patterns but with some variations in the value where thresholds occurred (Supplementary Figures S6-7, Supplementary Tables S3-4).

#### Changes in assemblage composition in eBird data

Forest specialists, endemic species, threatened and Near Threatened species and high-sensitivity species are overall negatively affected by human footprint: they are “losers” of the ongoing global increase in human footprint (Fig. 2, Table S1). Conversely, species with low and null dependence to forest habitats, species with large ranges, non-native species and tolerant or anthropophilic species are mainly positively affected by human footprint: they are “winners” (Fig. 2, Table S1). More specifically, in terms of forest-specialisation (Fig. 2A, Table S1), I found that species with high dependence on forest habitats present the steepest decline (linear decline; coef=-0.042,  $P < 10^{-10}$ ), followed by species with medium dependence that show a low decline, accelerating when human footprint exceeds 32.3. Conversely, both non-forest species and species with low dependence on forest habitats see their richness increase up to a human footprint of ca. 24 before reaching a plateau. In terms of endemism (Fig. 2B, Table S1), richness in endemic species declines with human footprint, especially above a threshold of 30.7, while richness in species with a large range increases up to a threshold of 33.7 before declining. Richness in threatened and Near Threatened species declines with human footprint, especially when human footprint exceeds 7.5. Conversely, richness in non-native species increases with human footprint, especially when it exceeds 31.1 (Fig. 2C, Table S1). Finally, in terms of sensitivity to human activities (Fig. 2D, Table S1), I found that richness in high-sensitivity species declines linearly with human footprint (coef=-0.049,  $P < 10^{-10}$ ). Conversely, richness in tolerant species increases with human footprint, up to a limit of 31.6 and then decreases while richness in anthropophilic species increases continuously, especially when human footprint is below 6.8.

Results were consistent when using the human footprint maps from Venter et al.<sup>29</sup> and Williams et al.<sup>30</sup> (Supplementary Figures S8-9, Supplementary Tables S3-4).

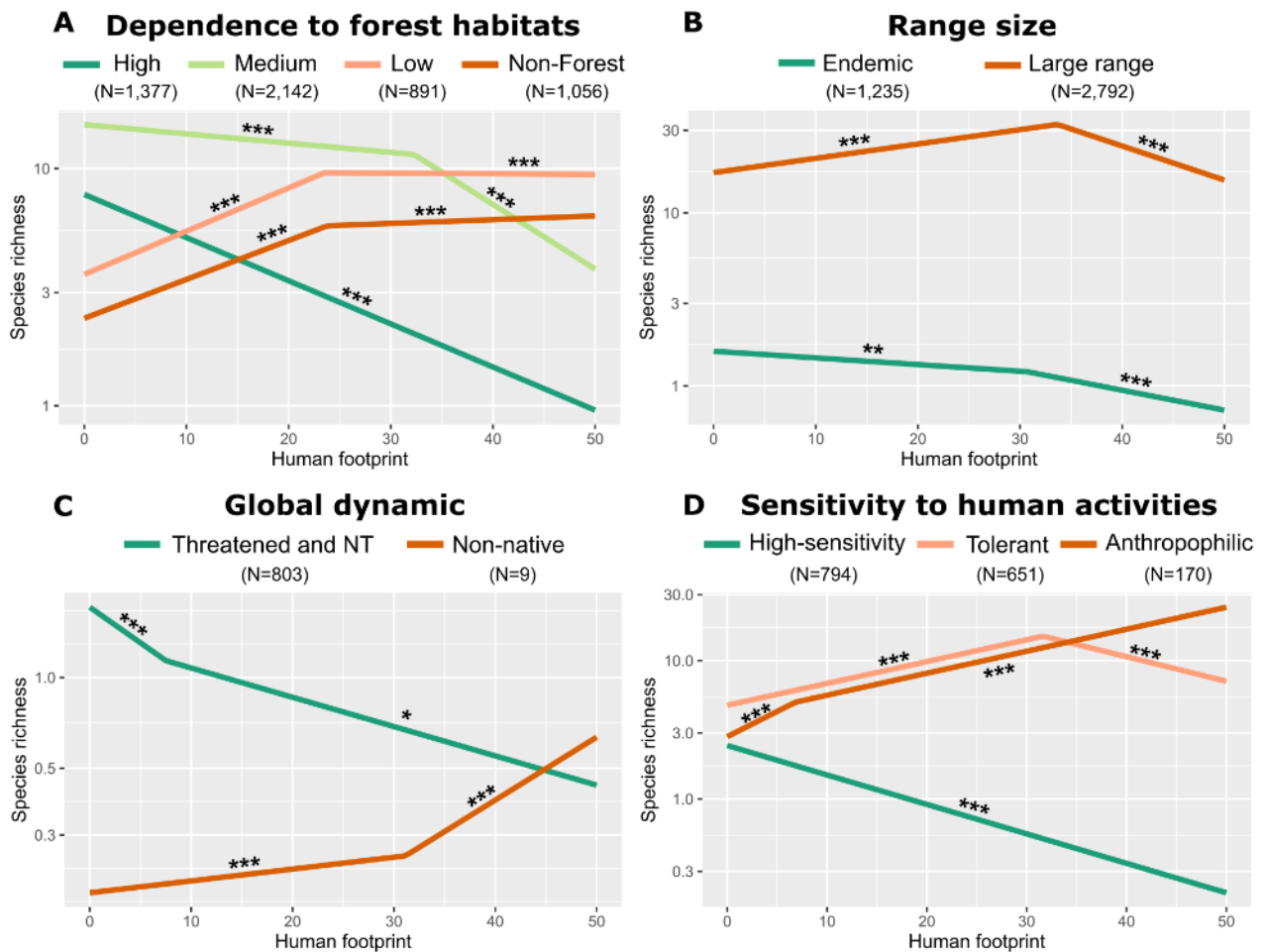


Figure 2: Effect of human footprint on eBird assemblage composition measured by threshold models for 11 indices of assemblage composition. Two p-values are provided when threshold was significant (the first p-value corresponds to the test of the first slope compared with 0, the second p-value corresponds to the test of the second slope compared with the first slope). When threshold was not significant, a linear model was fitted and a single p-value is provided (corresponding to the test of the slope compared with 0). Detailed statistics in Tables S1-2 and fit in Fig. S3. To facilitate interpretation, the y-axis does not present residuals of ‘ecological models’ but rather the predicted species richness for a standard sampling event (see details in Methods). P-values: NS>0.05>\*>0.01>\*\*>0.001>\*\*\*.

## Discussion

In this study, I used a simple methodology to identify a diversity of trajectories in species richness response to human pressure, that I apply to three large-scale empirical datasets. The method aims at isolating human impact on species richness, by controlling for natural drivers of variation in species richness, but this remains imperfect as this only based on correlations. I find that species richness response to human pressure can present important thresholds, with a first phase where species richness is poorly influenced by human pressure although assemblage composition is deeply transformed, followed by a second phase of steep decline in species richness. More importantly, the diversity of trajectories evidenced in this study enables delineating a general unifying framework (the “Replace then remove framework”) which includes five main trajectories that are described and differ by two characteristics: the slope of the first phase and the linearity of species response to human pressure (Fig. 3).

With the eBird data, I find a slight increase in species richness during the first phase (+ 5 species when human footprint increases from 0 to 33.5), typical of the Intermediate peak trajectory (i.e.,

increase in species richness, followed by a decline; Fig. 3). This positive trend hides a strong transformation of assemblage composition due to the replacement of “losers” by “winners”, that I highlight in four comparisons (Fig. 2). First, forest habitat specialists (typical from the studied regions; i.e., tropical forests) decline while species that are associated with other habitat types increase with human footprint, consistently with the biotic homogenisation literature<sup>5,6</sup>. Second, species that are endemic to the studied hotspots decline while species with large range size increase with human footprint<sup>6,8,9</sup>. Third and intuitively, species that are threatened or Near Threatened (i.e., those that have been internationally recognised as negatively affected by human activities) decline with human footprint, while settled non-native species increase with human footprint<sup>31</sup>. Finally, richness in high-sensitivity species declines with human footprint, conversely to tolerant and anthropophilic species. This last result might suffer from partial circularity as the species sensitivity index was elaborated with similar data<sup>3</sup>; but circularity may be weakened by the larger scale considered to create the sensitivity index (most data are not used in the present study) and the difference in response variable (individual species abundances were used to create the index *vs* richness in a certain category of species here). This first phase thus consists in a strong transformation of assemblage composition with a slight positive effect on species richness, highlighting once again that species richness is a poor index to measure human effects on local biodiversity<sup>13,14,17,26</sup>.

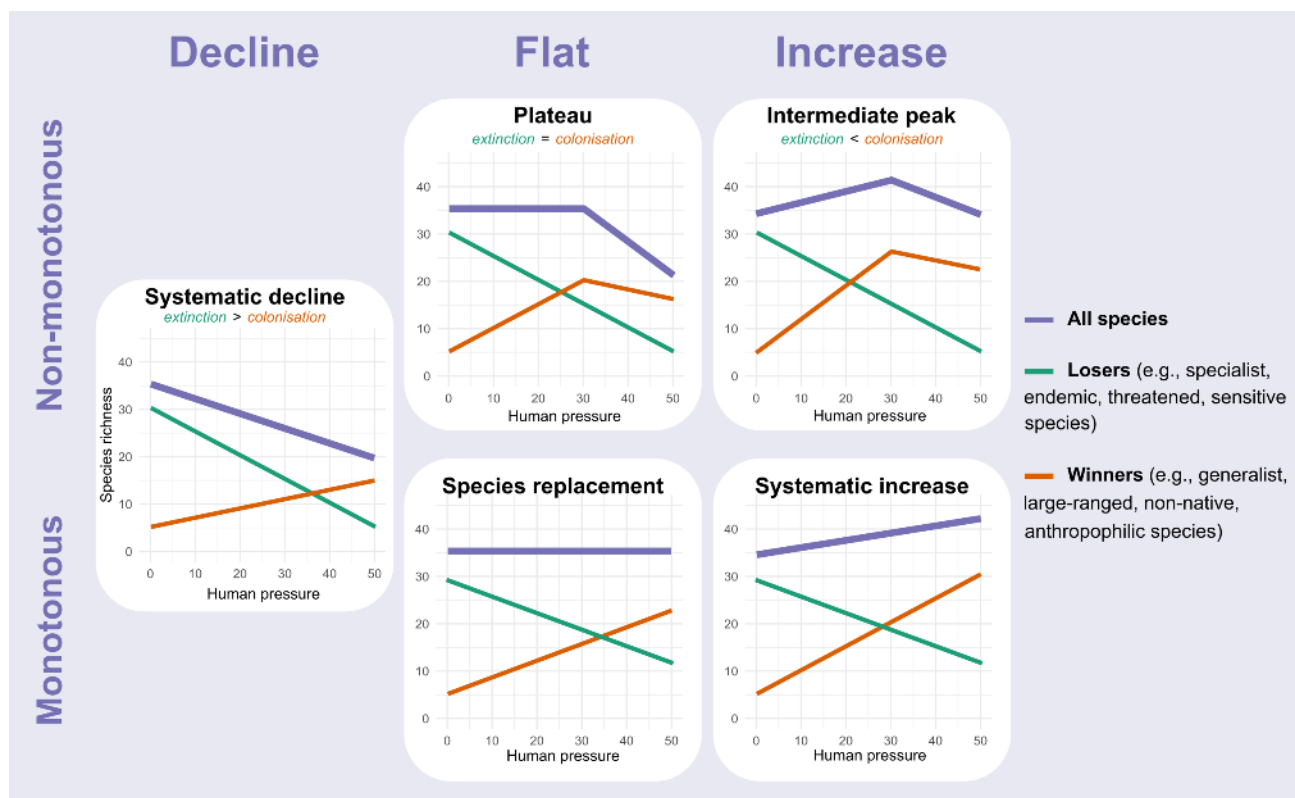


Figure 3: Theoretical plot presenting the “Replace then remove framework” developed in this study and its five trajectories. The two axes present the two characteristics to look at to identify which trajectory applies to a given situation; the slope of the first phase and the strict monotony of the trajectory.

Generalising these findings, I suggest that the first phase of the five trajectories in the Replace then remove framework consists in the replacement of losers by winners, and that the overall slope of species richness depends on the relative rates of colonisation and extinction. If colonisation by



winners is higher than extinction by losers, the Systematic increase (i.e., consistent increase in species richness with human pressure) or the Intermediate peak trajectory can occur. I found the former pattern in Eastern Afrotropical and Western Ghats and Sri Lanka, and the later in the eBird global dataset and four hotspots, echoing the Intermediate Disturbance Hypothesis at a macroecological scale<sup>25</sup>. Conversely, if extinction exceeds colonisation rate in this first phase, a Systematic decline can occur (i.e., monotonous decline in species richness with human pressure; Fig. 3), as I evidenced with the PREDICTS database, and has been reported in previous studies<sup>11,12</sup>. Finally, in some cases, the colonisation of winners perfectly offsets the extinction rate of losers, leading to a flat slope in the first phase in the Plateau trajectory (i.e., flat trend in species richness, followed by a steep decline) and the Species replacement trajectory (i.e., flat trend in species richness across the human footprint gradient; Fig. 3). Such balance is surprisingly common in the literature<sup>13-16</sup>, although methods of these studies have been subject to criticism<sup>32</sup>, and was reported in the present study (with eBird data in Tumbes-Choco-Magdalena and PREDICTS data for vertebrates for the Species replacement trajectory, and in the Atlantic Forest and the BBS analyses for the Plateau trajectory; Fig. 1, Table S1).

In the second phase of the Intermediate Peak trajectory with eBird data, I found that many “winners” are not benefiting anymore from the increase in human pressure above a certain threshold (mainly occurring in built environments and highly intensive agriculture). As a result, richness in “winners” declines or plateaus, leading to a drop in local overall species richness (Figs. 1-2). This was evidenced for species with low or null dependence on forest habitats, with large range, or with tolerance to human activities. Only richness in anthropophilic and non-native species increases continuously with human footprint, consistently with the fact that they are largely associated with urban ecosystems<sup>4,33</sup>. Several previous case studies evidenced similar threshold patterns in species richness response to habitat loss or habitat fragmentation<sup>21-23,34</sup>. Different and complex ecological processes can explain the existence of such thresholds, for instance if species are resilient to habitat fragmentation until suitable patches become too isolated for dispersion or if low-intensity habitat loss does not lead to immediate extinction but creates an extinction debt<sup>20</sup>. By investigating assemblage composition changes across the human pressure gradient (Fig. 2), the present study highlights the importance of understanding the diversity of individual species response to pressure in order to better understand the emergence of species-richness patterns.

Thresholds are however not systematic and their existence depends on landscape characteristics (e.g., habitat variance or habitat fragmentation) and species characteristics (e.g., dispersal ability, sensitivity to habitat edges, local pool of anthropophilic species that can colonise)<sup>20</sup>. In the Replace then remove framework, I describe two trajectories without thresholds (Species replacement and Systematic increase; Fig. 3), while Systematic decrease can occur with or without a significant threshold. In addition, thresholds are likely undetected in some cases because they are not tested for<sup>20</sup> or due to a low statistical ability to detect them. Indeed, the value of the threshold may vary depending on studied regions, habitats and taxa (e.g., 33.7 for eBird data in tropical forest hotspots and 25.5 with BBS data in North-America) and can be difficult to detect if too high. It can also happen that the threshold is not particularly high, but sampling effort does not include sites with high human footprint (i.e., if only the first phase of the trajectory is correctly sampled). When using temporal datasets, not only do sampling sites need to be located in areas with high pressure, but

they need to cover severe degradation of habitat in the study period (e.g., conversion from semi-natural to urban landscapes) to detect such effect on species richness, which may currently be possible only with a handful of datasets.

In all trajectories, assemblages may be strongly transformed, even at low levels of human pressure. Thus, regardless of the impact of human pressure on species richness, it is important to note that the composition and functioning of assemblages may be affected, possibly resulting in biotic homogenisation (e.g., with the extinction of endemic, specialist, threatened species, replaced by generalist, large-ranged, non-native species). This may result in increased functional homogeneity<sup>5</sup>, with the possible eviction of species with key role in the assemblage such as predators, or specific pollinators. These effects may worsen in the second phase, where assemblages lose species. In addition to these compositional changes, the decline of species richness in the second phase may translate in a decline in overall abundance of assemblages, or defaunation<sup>35-37</sup>, suggesting that species resources are too limited in these degraded habitats and that carrying capacity is thus declining.

## Conclusion

In this study, I propose a framework unifying five different trajectories of species richness response to human pressure – the Replace then remove framework – that describes five trajectories articulated around two characteristics of trajectories. This framework highlights the importance of considering assemblage composition in studies aiming at measuring the impact of human activities or conservation actions, as species richness can hide strong assemblage transformations<sup>14,38</sup>. It also highlights the importance of considering non-linear and non-monotonous assumptions when investigating the effects of human activities on biodiversity in order to detect existing thresholds. Overall, these results provide strong evidence that human pressure deeply transforms assemblages, probably resulting in biotic homogenisation, but that we still have a lot more to lose if human footprint keeps increasing globally.

## Methods

### eBird data

#### Bird counts

eBird is an online platform gathering >700 million bird observations across the globe<sup>39,40</sup>. Observations are made opportunistically but are gathered in checklists and are accompanied with information on sampling effort, allowing for the transformation of data into a standard dataset and the study of assemblage composition across large spatial scales<sup>41,42</sup>. In a previous study, Cazalis et al.<sup>26</sup> created a standard subset of the eBird database, keeping only complete checklists (i.e., for which observers certified having reported all species detected) collected between 2005 and 2018 (I here only kept the checklists made between 2010 and 2018 and later control for year in analyses), arising from sampling events that lasted between 0.5-10 hours, either from “stationary points” or “travelling counts” when distance travelled was <5km, and reported by observers with sufficient experience. Finally, they transformed the eBird data to fit the bird taxonomy used by BirdLife International in order to be able to use BirdLife International species characteristics.

The study area used in Cazalis et al.<sup>26</sup> and here, included eight tropical forest biodiversity hotspots<sup>43</sup> that correspond to areas with exceptional biodiversity and high level of habitat loss. They are thus highly relevant places to measure the impact of human activities. The study area was restricted to the part of biodiversity hotspots that were included in the “Tropical and subtropical moist broadleaf forests” biome<sup>44</sup>, to maximise sites comparability. It included the eight biodiversity hotspots that presented sufficient eBird data after filtration, with 4 in the Americas (Atlantic Forest, Tropical Andes, Tumbes-Chocó-Magdalena, Mesoamerica), 1 in Africa (Eastern Afromontane), and 3 in Asia (Western Ghats and Sri Lanka, Indo-Burma, Sundaland). Of the 66,777 sampling events available from the above-mentioned study, I only kept the 62,945 that were done in 2010 or after, and for which I was able to calculate every landscape covariate (see Fig. 1 for the number of sampling events per hotspot).

#### Sampling covariates

Because data collection in eBird is not standardised, I calculated several covariates of sampling effort and quality following Cazalis et al.<sup>26</sup>, later used to control for sampling heterogeneity in all analyses. I used the duration of sampling (in minutes) and the number of observers, as the probability to detect species increases with time and with number of observers. I also used an observer calibration index calculated in Cazalis et al.<sup>26</sup> and developed from Kelling et al.<sup>45</sup> and Johnston et al.<sup>46</sup>, that incorporates heterogeneity in observers' ability to detect species because of their difference in expertise, equipment and behaviours. Finally, I used the day of the year of observation to control for variation in species presence and detectability with seasons, and the year of observation to control for temporal trends in bird diversity.

#### Landscape covariates

To quantify human pressure, I used the global human footprint index, built from the combination of spatial information on human infrastructures, agricultural land use and population density. Two different datasets of human footprint have been released in the last years with similar methodologies: one mapping the human footprint in 1993 and 2009<sup>29</sup> and the other one mapping the human footprint in 2000, 2005, 2010, and 2013<sup>30</sup>. There are important variations in values between

these two datasets. Indeed, the variation when comparing two different years of a single dataset (the difference between the 2000 and 2013 values from Williams et al.<sup>30</sup> in sampled sites was  $0.7 \pm 1.7$ ) was much lower than the variation when comparing two similar years from the different datasets (the difference in Williams et al.<sup>30</sup> value in 2010 and Venter et al.<sup>29</sup> in 2009 was  $2.7 \pm 4.0$ ). To ensure my results are robust to the measure of human footprint, I therefore used a combined measure in the analyses, and test for the sensitivity of my results to the dataset used (Supplementary Figures S6-9, Supplementary Tables S3-4). As eBird data used in this study were collected between 2010 and 2018, I used the most recent version of both datasets, and calculated the average between the median value of human footprint pixels intersecting with a 1-km buffer around the sampling site in 2009 and in 2013. The remaining temporal mismatch may add some noise in the results and reduce significance (e.g., if human footprint of study sites has greatly increased between human footprint and eBird data collection).

I calculated a value of altitude and Net Primary Productivity for each sampling site. Altitude data were obtained from the GLOBE Digital Elevation Model<sup>47</sup>, which has a 0.008 degree resolution (ca. 930m at latitude 0). I calculated the altitude of each sampling site as the median of the values intersecting a 1-km buffer around the sampling site. Net Primary Productivity was calculated from a raster averaging monthly productivity maps from Jan.2014 to Nov.2016<sup>48</sup> and extracting the median of the values intersecting a 1-km buffer around the sampling site.

### Assemblage indices

For each of the 65,465 checklists I calculated twelve assemblage indices. Overall species richness was the total number of bird species detected in the checklist. I used BirdLife International<sup>49</sup> 4-levels classification of species dependence on forest habitats to characterise the habitat specialisation of assemblages, measuring for each checklist: the richness in species with high dependence on forest habitats, medium-dependence, low-dependence and “Non-Forest species”. I used BirdLife International and HBW<sup>50</sup> distribution maps to characterise species endemism. I measured for each checklist the number of species that were endemic to the hotspot (i.e., >90% of their range in the hotspot; see Cazalis et al.<sup>26</sup>), and the number of large-range species (i.e., that had a global distribution >1,000,000 km<sup>2</sup>). I used BirdLife International<sup>49</sup> Red List status to measure the number of threatened and Near Threatened species of each checklist and BirdLife International and HBW<sup>50</sup> to measure the number of non-native species of each checklist, considering as non-native to a given hotspot every species that only has “Introduced” distribution within the hotspot. Finally, I used an index of bird sensitivity to human footprint developed by Cazalis et al.<sup>3</sup> to measure the sensitivity of assemblages to human (only for hotspots from the Americas). For each checklist from the Americas, I measured the number of species characterised as “High-sensitivity” (i.e., species whose sensitivity index is in the highest quartile of the 4,424 species breeding in the Americas), the number of species characterised as “Anthropophilic” (i.e., species whose sensitivity index is in the 5% lowest values; broadly corresponding to species whose abundance increases continuously with human pressure), and the number of species that are “Tolerant” (i.e., species whose sensitivity index is in the lowest quartile, excluding “Anthropophilic” species).

### Breeding Bird Survey data

I investigated the link between local species richness and human footprint using the North America Breeding Bird Survey (BBS). This scheme consists in yearly sampling by volunteer birders around routes of ca. 25 miles with 50 count points recording every bird detected<sup>51</sup>. Specifically, I used the data processed in a recent study<sup>27</sup> consisting in 3,016 BBS routes, only considering the section including the first 5-stops (to ensure linking local human pressure conditions with local bird assemblages) and combining 5 years of observations randomly selected between 2007 and 2016 (to ensure assemblages are representative of the local diversity). These routes are well distributed in the US and the Southern part of Canada and cover different habitat types (forest, shrubland, cropland, grassland, mosaic, bare area, urban, and others)<sup>27</sup>. I calculated the human footprint (using the average human footprint between the 2009 map from Venter et al.<sup>29</sup> and the 2013 map from Williams et al.<sup>30</sup>, to match with observation dates) within a 500m buffer around the first section of BBS routes, as in Cazalis et al.<sup>27</sup>, and used the value of Net Primary Productivity from the same study.

### PREDICTS data

Finally, I used the PREDICTS – Projecting Responses of Ecological Diversity In Changing Terrestrial Systems – database<sup>52</sup>, from which Newbold et al.<sup>11</sup> found a systematic decline in species richness with human pressure. It gathers data from scientists worldwide in order to produce a global database of terrestrial species' responses to human pressure. It now includes over 3.6 million biodiversity records from > 32,000 sites, covering > 50,000 species of diverse taxa. Specifically, I used the public release of the database developed in Gray et al.<sup>28</sup> consisting in 6,531 sampling sites across most realms (33% in Palearctic, 17% in Neotropical, 15% in Afrotropical, 13% in Indomalayan, 12% in Australasian, and 9% in Nearctic), taxa (40% vertebrates, 37% invertebrates, 23% plants), and land-use (38% of minimal use, 39% of light use, 17% of intense use, and 6% undetermined). After removing the 1.3% of studies that started before 2000, I obtained 6,448 sites, all starting sampling between 2000 and 2012. I used the altitude value from the original dataset and calculated the human footprint (as the average between 2009 map from Venter et al.<sup>29</sup> and the 2005 map from Williams et al.<sup>30</sup>) and Net Primary Productivity (using the same map as with eBird data) from a 1-km buffer around the sites coordinates.

### Statistical analyses

To measure the effect of human footprint on each diversity index, I first created a model (that I call “ecological model”) for each diversity index, aiming at controlling for ecological effects and sampling heterogeneity. I then created a second model (called “footprint model”), using the residuals of the ecological model as response variable, to study the effects of human footprint. The results from the footprint models cannot be taken as causal evidence as the model is based on correlation, but I expect the ecological model to control for most variation in species richness that is not due to human activities.

#### Controlling for ecological factors

For the three datasets, I used a common model structure, including as predictors: altitude to account for elevational physiological constraints on species and also past patterns of speciation (with a quadratic effect, allowing non-monotonous response of species richness to altitude) and Net

Primary Productivity to account for climatic factors (with a quadratic effect). In addition, I controlled for latitude (assuming a quadratic effect as species richness is likely to peak around latitude 0) for PREDICTS and BBS data, but not for eBird as this information is mostly contained in the control for hotspots (which cover relatively narrow ranges of latitude). In addition, I controlled for several sampling factors, specific to each dataset.

For each eBird diversity index I created an “ecological model” running a GAM<sup>53</sup> with a similar structure to Cazalis et al.<sup>26</sup> and assuming negative binomial distributions. I controlled for 7 continuous variables and 1 factor variable: altitude, Net Primary Productivity, year (linear assumption to account for general temporal trends in response variables, e.g., temporal decline of sensitive species), day of the year (smoothed), duration (smoothed with limited curve complexity), observer calibration index (smoothed with limited curve complexity), number of observers (smoothed with limited curve complexity), and hotspot name (to account for differences in bird diversity indices across regions). The ecological model had the following structure:

```
gam(Index ~ scale(altitude) + scale(altitude)^2 + scale(npp) + scale(npp)^2 + year + s(Day)+ s(Duration, k=4) + s(Observer_Calibration, k=4) + s(N_observers, k=4) + Hotspot_name)
```

For the BBS database, I created an “ecological model” with a GAM model, assuming a negative binomial distribution of the species richness, with the following structure:

```
gam(Richness ~ scale(altitude) + scale(altitude)^2 + scale(npp) + scale(npp)^2 + scale(latitude) + scale(latitude)^2)
```

For the PREDICTS database, following Gray et al.<sup>28</sup>, I created an “ecological model” using a mixed Generalised Linear Model (using the function *glmer* from the *lme4* package<sup>54</sup>), accounting for heterogeneity between studies. It assumed a Poisson distribution and had the following structure, including random effects on the study (SS), study block (SSB), and study sites (SSBS):

```
glmer(Richness ~ scale(altitude) + scale(altitude)^2 + scale(npp) + scale(npp)^2 + scale(latitude) + scale(latitude)^2 + (1|SS)+ (1|SSB) + (1|SSBS)).
```

To investigate the consistency of the results across taxa, I also ran this model independently for studies focusing vertebrates, invertebrates, plants, birds, and tropical birds.

#### Measuring human footprint impact on overall species richness

For each dataset, I built a “footprint model” to link the residuals of the ecological model on overall species richness with human footprint (see distributions in Fig. 1), able to identify the different possible trajectories suggested in the introduction. I used the *chngpptm* function from the R package *chngppt*<sup>55</sup> using a segmented threshold, fitting a function with two join segments. The model tests for the absolute trend of the first segment (i.e., is the trend different from zero), estimates a threshold value (found between the first and ninth deciles of the explanatory variable), and tests for the difference of the second trend (i.e., providing the difference in slope with the first segment and testing whether the change in slope is significant). A significant threshold enables identifying cases of “Intermediate peak trajectory”, where richness peaks at intermediate human footprint (first trend significantly increasing, followed by a significant decline) or Plateau trajectory (first trend not significant, followed by a steep decline). When the threshold was not significant, I instead used a classic linear model, using the *lm* function from the R package *stats*<sup>56</sup>, even if the threshold model

presented a lower AIC (Table S2). Such linear models enable identifying cases of Systematic decline (trend significantly negative), Systematic increase (trend significantly positive) or Species replacement (trend not significant; Fig. 3).

In addition, I tested for the consistency between hotspots in the eBird data by applying the same modelling approach to each hotspot independently.

The plots presented in Figs. 1-2 result from the use of the sum predictions (R function *predict*) of the “ecological model” and the “footprint model”, from a dataset with every quantitative variable fixed to their median value in the dataset. The hotspot name variable in eBird models was fixed to “Atlantic Forest” and the three variables used as random effects with the PREDICTS database fixed to their first value in the dataset.

#### Measuring changes in assemblage composition in eBird data

Using eBird data, I tested the impact of human footprint on assemblage composition by modelling the relationship between human footprint and the residuals of ecological models for the eleven assemblage composition indices. I first fitted a threshold model and, when the second segment was not significant (i.e., there is no significant threshold), I replaced it by a simple linear model.

#### **Acknowledgments:**

I thank Elie Gaget and Ana S.L. Rodrigues for their insightful and constructive comments on previous versions of the manuscript. I am also grateful to the numerous observers who contributed records to eBird, and to the eBird team at Cornell Lab of Ornithology for creating and managing this database, as well as the thousands of U.S. and Canadian participants who annually perform and coordinate the Breeding Bird Survey, and the contributors and managers of the PREDICTS database. Time and effort were supported by sDiv, the Synthesis Centre of iDiv (DFG FZT 118, 202548816).

**Data and materials availability:** Data and code used in this study is available at

<https://doi.org/10.5281/zenodo.6345865>.

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