


# Biogeographical, environmental and anthropogenic determinants of global patterns in bird taxonomic and trait turnover

Jean-Yves Barnagaud<sup>1,2</sup>  | W. Daniel Kissling<sup>3</sup> | Constantinos Tsirogiannis<sup>4</sup> |  
Vissarion Fisikopoulos<sup>5</sup> | Sébastien Villéger<sup>6</sup> | Cagan H. Sekercioglu<sup>7,8</sup> |  
Jens-Christian Svenning<sup>2</sup>

<sup>1</sup>Biogéographie et Ecologie des Vertébrés – UMR 5175 CEFE – CNRS - Université de Montpellier - EPHE - SupAgro - IND - INRA - PSL Research University, Montpellier, France

<sup>2</sup>Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, Aarhus, Denmark

<sup>3</sup>Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, The Netherlands

<sup>4</sup>Center for Massive Data Algorithmics (MADALGO), Department of Computer Science, Aarhus University, Aarhus, Denmark

<sup>5</sup>Département de Mathématique, Boulevard du Triomphe, Université libre de Bruxelles, Brussels, Belgium

<sup>6</sup>Laboratoire Biodiversité Marine et ses Usages (MARBEC), UMR 9190 CNRS-IRD-UM-IFREMER, Université de Montpellier, Montpellier Cedex 5, France

<sup>7</sup>Department of Biology, University of Utah, Salt Lake City, Utah

<sup>8</sup>College of Sciences, Koç University, Rumelifeneri, Istanbul, Sariyer, Turkey

## Correspondence

Jean-Yves Barnagaud, Biogéographie et Ecologie des Vertébrés – CNRS, PSL Research University, EPHE, UM, SupAgro, IND, INRA, UMR 5175 CEFE, 1919 route de Mende, F34293 Montpellier 5, France. Email: jean-yves.barnagaud@cefe.cnrs.fr

## Funding information

Aarhus University Research Foundation; VILLUM FONDEN

Editor: Ana Santos

## Abstract

**Aim:** To assess contemporary and historical determinants of taxonomic and ecological trait turnover in birds worldwide. We tested whether taxonomic and trait turnover (1) are structured by regional bioclimatic conditions, (2) increase in relationship with topographic heterogeneity and environmental turnover and change according to current and historical environmental conditions, and (3) decrease with human impact.

**Major Taxa:** Birds.

**Location:** Global.

**Methods:** We used computationally efficient algorithms to map the taxonomic and trait turnover of 8,040 terrestrial bird assemblages worldwide, based on a grid with 110 km × 110 km resolution overlaid on the extent-of-occurrence maps of 7,964 bird species, and nine ecological traits reflecting six key aspects of bird ecology (diet, habitat use, thermal preference, migration, dispersal and body size). We used quantile regression and model selection to quantify the influence of biomes, environment (temperature, precipitation, altitudinal range, net primary productivity, Quaternary temperature and precipitation change) and human impact (human influence index) on bird turnover.

**Results:** Bird taxonomic and trait turnover were highest in the north African deserts and boreal biomes. In the tropics, taxonomic turnover tended to be higher, but trait turnover was lower than in other biomes. Taxonomic and trait turnover exhibited markedly different or even opposing relationships with climatic and topographic gradients, but at their upper quantiles both types of turnover decreased with increasing human influence.

**Main conclusions:** The influence of regional, environmental and anthropogenic factors differ between bird taxonomic and trait turnover, consistent with an imprint of niche conservatism, environmental filtering and topographic barriers on bird regional assemblages. Human influence on these patterns is pervasive and demonstrates global biotic homogenization at a macroecological scale.

## KEYWORDS

Anthropocene, beta diversity, biogeographical legacies, biotic homogenization, functional diversity, life-history traits, regional assemblages

## 1 | INTRODUCTION

Global biodiversity gradients are shaped from regional to local scales by the concurrent effects of biogeographical and orographic barriers, climate and habitat (Caley & Schluter, 1997; Ficetola, Mazel, & Thuiller, 2017; Ricklefs, 2004). However, the accelerating pace of human-driven global change over the last centuries has deeply modified environmental filters and species interactions, has created or removed barriers or broken down old biogeographical boundaries that could affect these patterns (Capinha, Essl, Seebens, Moser, & Pereira, 2015; Ellis, 2015; Ficetola et al., 2017). Whether anthropogenic imprint on global biodiversity gradients has become comparable to that of ecological and evolutionary processes has therefore become a central question of macroecology (Ellis, 2015).

Beta diversity, or the compositional difference between two or more species assemblages, is the most direct and informative measure of changes in species composition along biodiversity gradients (Koleff, Gaston, & Lennon, 2003). Depending on the spatial scale, variations in beta diversity convey signals of habitat composition and biotic interactions, species' rarity and commonness, metacommunity dynamics or legacies of speciation/extinction dynamics (Kraft et al., 2011). Beta diversity can be defined as the additive outcome of two simultaneous processes: changes in species richness (nestedness-resultant component) and changes in species composition (turnover component) (Baselga, 2010; Legendre, 2014; Leprieur et al., 2011). These two components are independent, as an assemblage may be a strict subset of another (full nestedness) or exhibit the same richness with completely different species composition (full turnover). They can thus be analysed separately in the prospect of separating processes that trigger species richness and compositional variations between assemblages. While nestedness informs on how species are sorted along environmental or historical gradients from a regional species pool (Svenning, Normand, & Skov, 2008; Ulrich, Almeida-Neto, & Gotelli, 2009), turnover is especially helpful at broad spatial scales to understand how multiple regional species pools are separated by biogeographical barriers, environmental gradients and human impact (Antonelli, Nylander, Persson, & Sanmartín, 2009; Caley & Schluter, 1997; Gaston et al., 2007).

Taxonomic turnover is an incomplete measurement of the multifaceted structure of biodiversity because it does not reflect variations in the ecological and evolutionary characteristics of species assemblages (Pavoine & Bonsall, 2011). Trait turnover, or the turnover in species' ecological characteristics or life-history traits, is more appropriate to investigate non-neutral gradients in assemblage composition, as it accounts for the ecological non-equivalence of coexisting species (De Bello et al., 2009). High taxonomic and trait turnovers are expected to be associated with changes in both resource availability and composition, such as along altitudinal gradients or other sources of steep environmental variation (Swenson, Anglada-Cordero, & Barone, 2010). However, high taxonomic turnover can be associated with low trait turnover under the effects of niche-based filtering or as a legacy of historical processes, such as postglacial recolonization events (Villéger, Grenouillet, & Brosse, 2013). Moreover, patterns of trait turnover can

depend on trait selection and resolution. A comparative analysis of turnover measures computed with different traits that reflect species' responses to environmental conditions, resource use, dispersal abilities and biotic interactions is therefore essential to gain a deeper understanding of trait turnover (Ackerly & Cornwell, 2007; Lavorel & Garnier, 2002).

Species assemblages are shaped by broad-scale environmental gradients and by historical legacies related to diversification (speciation and extinction) and colonization (Ricklefs, 2004; Svenning et al., 2008). For instance, long-term climatic stability might promote high species richness and pronounced levels of endemism, especially in the tropics (Buckley & Jetz, 2007; Kissling, Baker, et al., 2012; Svenning et al., 2008). Taxonomic turnover can thus be expected to be higher in tropical than temperate and boreal biomes. In addition, patterns of taxonomic and trait turnover should bear the imprint of glacial refugia and post-glacial recolonization dynamics as well as of physical barriers (Antonelli et al., 2009; Baselga, 2010; Buckley & Jetz, 2007). Both types of turnover are therefore expected to increase along mountain chains, but also in extremely poor environments, such as deserts, where low resource availability selects for rarity and small range sizes (Gaston et al., 2007; Ulrich et al., 2014). Furthermore, niche replacement associated with environmental heterogeneity should translate into a positive relationship between the steepness of environmental gradients (i.e., environmental turnover) and taxonomic or trait turnover, as observed in amphibians and birds (Buckley & Jetz, 2007; Gaston et al., 2007).

Well-established global diversity patterns, such as Bergmann's rule (Blanchet et al., 2010), the diversity-productivity relationship (Pautasso et al., 2011) or evidence from the fossil record, show a strong human imprint on biodiversity of our planet (Ellis, 2015; Faurby & Svenning, 2015; Šizling et al., 2016). Anthropogenic land use decreases net primary productivity and modifies habitat gradients, favouring common and widespread species with traits associated with ecological generalism (Eskildsen et al., 2015; Haberl et al., 2007). This triggers biotic homogenization that should, at global and regional scales, result in a decrease in both taxonomic and trait turnover along gradients of human impact (Baiser & Lockwood, 2011). However, few studies have quantitatively compared the influence of biogeographical, environmental and anthropogenic factors on regional species assemblages (Capinha et al., 2015).

Here, we quantified global bird taxonomic and trait turnover among adjacent species assemblages using a moving window approach ('neighbourhood turnover'). In doing so, we focused on taxonomic or trait differences among assemblages that are directly neighbouring each other, with the aim being to produce a continuous map of compositional change (as did, e.g., McKnight et al., 2007). We studied the variation in turnover among biomes and along gradients of environmental conditions, environmental turnover and anthropogenic influence. We grounded our study on a global dataset of > 8,000 regional bird assemblages at 110 km × 110 km grid cell resolution and on trait data reflecting habitat use, diet and mobility for > 7,900 species. At this spatial extent and resolution, we expected bioclimatic and historical

processes to be of key importance for structuring regional bird assemblages (Ricklefs, 2004). We therefore hypothesized that taxonomic and trait turnover in bird assemblages are structured by biomes, environmental gradients and topography. We tested the following three complementary predictions.

1. The 'biome hypothesis': Legacies of biogeographical processes have triggered biome-level differences in turnover, with high taxonomic and trait turnover in deserts and high taxonomic but low trait turnover in tropical biomes.
2. The 'environmental hypothesis': Taxonomic and trait turnover increase near topographic barriers and in association with high environmental turnover. Taxonomic turnover increases and trait turnover decreases with increasing primary productivity.
3. The 'biotic homogenization hypothesis': Taxonomic and trait turnover decrease with increasing human impact.

## 2 | METHODS

### 2.1 | Data collection

#### 2.1.1 | Bird assemblages

We retrieved global extent-of-occurrence maps for 9,886 bird species (Birdlife International & Nature Serve, 2012). These data have been compiled from multiple sources, including specimens, distribution atlases, survey reports, published literature and expert opinion, and currently represent the most comprehensive assessment of global bird species occurrences. We overlaid these maps onto a grid in cylindrical equal area projection with 110 km × 110 km resolution, corresponding to 40,680 grid cells (10,599 terrestrial cells), which we used to define bird assemblages (Kissling, Sekercioglu, & Jetz, 2012). We excluded Antarctica, cells covering > 50% of water, and cells for which at least one of the eight neighbours did not have any bird record. We concentrated on terrestrial bird assemblages and therefore excluded all pelagic birds and species related to wetlands that never occur in other terrestrial habitats. Out of 8,255 terrestrial species, we excluded a further 291 species because of missing trait data (see section 2.1.2), considering that this additional filter would induce less uncertainty than gap filling in the trait matrix. This selection resulted in a final matrix of 8,040 cells × 7,964 species, with an average species richness of 177.8 ± 129.6 (mean ± SD).

#### 2.1.2 | Ecological traits

We recorded the following nine traits that reflect major axes of bird ecological niches: dietary preference (scores of use summing up to 10 among eight diet categories: invertebrates, fruits, nectar, seeds, vegetation, fishes, vertebrates and scavenging); Levin's index of dietary specialization (Belmaker, Sekercioglu, & Jetz, 2011); habitat use (binary) among 11 habitat classes arranged along a gradient from forested to open habitats, derived from the International Union for Conservation of Nature (IUCN) habitat classification version 3 (Supporting Information Appendix S1); preferential vegetation layers (among eight levels

ranging from ground to canopy species); propensity to latitudinal or altitudinal migrations (three levels: migratory, sedentary or partial migrant); propensity to irregular dispersal events (three levels: disperser, partial disperser or non-disperser); body mass (in grams); and thermal preference (average temperature over a species' range; Barnagaud et al., 2014). We acquired these traits from a comprehensive literature survey covering 8,255 terrestrial bird species (Şekercioglu, Daily, & Ehrlich, 2004), corrected and updated with the most recently published literature on bird traits (Belmaker et al., 2011; Del Hoyo, Elliott, & Sargatal, 2013). Most of the data retrieved are averages over multiple individuals with no information on intraspecific variability, which is beyond the scope and resolution of this study. Among the 291 species excluded because of missing trait values, 65 species lacked dietary scores, and five, 18 and two species lacked data for latitudinal migration, altitudinal migration and irregular movements, respectively. The remaining 201 missing species were lacking body mass information. Furthermore, we chose not to include traits related to sociality and reproductive productivity because of the lack of data for too many species. We therefore built our analyses on a complete trait matrix without relying on gap filling.

#### 2.1.3 | Biogeographical regions

We assigned every grid cell to one of 13 biomes as defined by combinations of coherent climatic and habitat features (World Wide Fund for Nature, <https://www.worldwildlife.org/biomes>, updated from Olson et al., 2001).

#### 2.1.4 | Environmental gradients

We compiled data on current climate (mean annual temperature and precipitations 1950–2000, from Worldclim, <http://www.worldclim.org/>), topography (altitudinal range, Global Land Cover Characterization Data Base, <https://lta.cr.usgs.gov/GLCC>), net primary productivity (NPP, from Moderate-Resolution Imaging Spectroradiometer (MODIS), Zhao, Heinsch, Nemani, & Running, 2005) and Quaternary climate change [represented as anomalies, i.e., absolute differences of temperature and precipitations, between the Last Glacial Maximum (LGM) and the present; Araújo et al., 2008; Kissling, Baker, et al., 2012]. The two Quaternary climate change variables were calculated across two palaeoclimatic simulations, the Community Climate System Model version 3 and the Model for Interdisciplinary Research on Climate version 3.2 (PMIP2; <http://pmip2.lsce.ipsl.fr/>; Braconnot et al., 2007). We averaged each environmental variable across all eight surrounding cells of a focal cell and the focal cell itself, so that the resolution of environmental assessment matched that of bird turnover.

#### 2.1.5 | Human impact

To estimate human impact, we used the human influence index (HII), which measures the total amount of anthropogenic footprint accumulated in 1 km<sup>2</sup> pixels [Wildlife Conservation Society (WCS), 2005; updated from Sanderson et al., 2002]. Its computation is extensively justified elsewhere (Sanderson et al., 2002). In brief, influence scores from zero (lowest) to 10 (highest) were assessed for eight items considered to impact wildlife and their habitats directly, based on expert

advice and published literature (11 human population density classes, proximity to railways, roads, navigable rivers and coastlines, four night-time light values, inside or outside urban polygons and four land cover categories). The HII was subsequently computed by summing up these scores at a 1 km<sup>2</sup> grain size. We averaged these HII values to yield a synthetic measure of the amount of anthropogenic footprint for each of our 100 km × 100 km grid cells.

## 2.2 | Turnover computations

### 2.2.1 | Taxonomic turnover

We computed neighbourhood taxonomic turnover from a decomposition of neighbourhood beta diversity measured by Jaccard's dissimilarity index (Baselga, 2012), as follows:

$$\frac{b+c}{a+b+c} = \frac{2 \times \text{minimum}(b,c)}{a+2 \times \text{minimum}(b,c)} + \frac{|b-c|}{a+b+c} \times \frac{a}{a+2 \times \text{minimum}(b,c)} \quad (1)$$

where  $a$  is the number of species shared by two adjacent assemblages which have  $b$  and  $c$  unique species, respectively, such that  $a + b + c$  equals the total species richness among the two communities. In Equation 1, the first component reflects taxonomic turnover (changes in species composition irrespective of species richness, ranging from zero, where one assemblage is a subset of the other, to one, where there are no shared species) and the second is a nestedness-resultant measure that accounts for the species richness gradient across the two cells (beyond the scope of this study). Several alternative frameworks allow a similar decomposition of Jaccard's or Sorensen's dissimilarity indices and are essentially equivalent in the way they compute turnover (Legendre, 2014). However, the independence of turnover from species richness variations is only ensured by the framework of Baselga (2012), which we used in this study (Baselga & Leprieur, 2015). We obtained a unique measure of turnover for each bird assemblage by averaging pairwise turnovers across each given assemblage and its eight nearest neighbours. We did not investigate the variation in turnover for higher-order neighbourhoods. Although considering a range of neighbourhood distances smooths the effects of range limits and grain size (McKnight et al., 2007), meaningful predictions for the relationships between turnover in non-adjacent assemblages and environmental gradients would be hard to formulate, especially because of the confounding effects of historical legacies. Also note that computations of beta diversity indices at multiple neighbourhood orders could become intractable at the scale of our study.

### 2.2.2 | Trait turnover

We computed trait dissimilarity between all pairs of species using an extended version of Gower's distance that allows dealing with mixed trait types with adequate weighing to account for structural non-independencies that typically arise with dietary scores or binary variables (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009). We then summarized this dissimilarity matrix with a principal coordinates analysis (PCoA), from which we retained the three first axes to build a multidimensional trait space that faithfully represents trait-based distance between species (Supporting Information Appendix S2 displays

correlations of traits with PCoA axes and the amount of variance explained by each axis).

We computed the turnover component of trait neighbourhood beta diversity (hereafter 'neighbourhood trait turnover' or 'trait turnover' in our context) as an adaptation of Equation 1 based on the proportion of the trait space (convex hull) shared and not shared by each bird assemblage and its eight nearest neighbours (Villéger et al., 2013), using species' scores on the three first axes of the PCoA. This computation is challenging because calculating the volume of intersection between convex hulls is disproportionately more difficult than simply calculating the volume of a single convex hull. Hence, we had to use elaborate algorithmic methods together with powerful computational servers. We tested three different convex hull implementations through Polymake (<https://polymake.org>) and ended up using the most efficient for our dataset (Irs: <http://cgm.cs.mcgill.ca/~avis/C/Irs.html>).

To refine the interpretation of trait turnover patterns, we computed turnover based on five alternative three-dimensional PCoA ordinations built with five distinct subsets of traits: dietary scores ('diet turnover'), habitat use ('habitat turnover'), propensity to migration or irregular dispersal events ('mobility turnover'), body mass ('body mass turnover') and thermal preference ('thermal turnover'). Note that these additional turnovers were so highly skewed towards zero (see Results) that we did not subject them to any statistical analysis.

### 2.2.3 | Environmental turnover

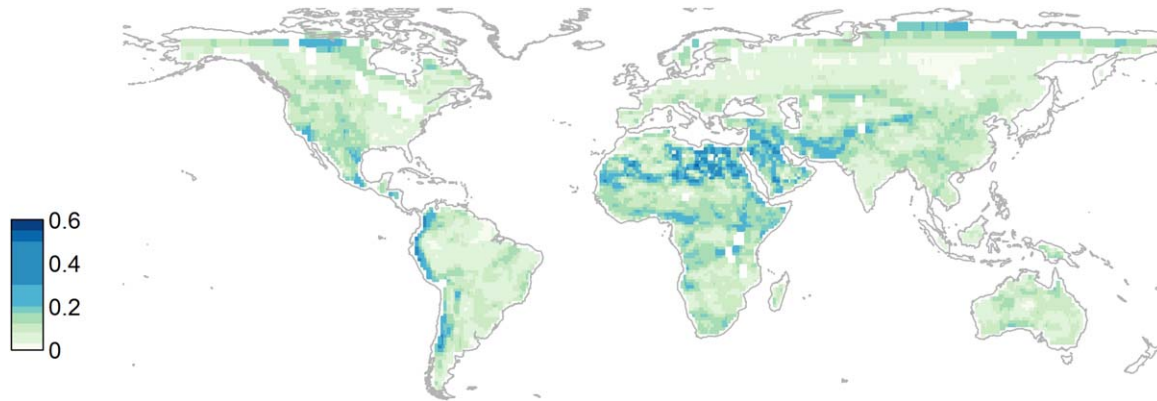
We summarized the six environmental variables into a principal coordinate analysis (PCA), from which we extracted the three first axes, representing 81% of total inertia (see Supporting Information Appendix S3 for variable loadings and maps of the raw variables and the principal components). The first axis (PC1) was dominated by a combination of temperature, precipitations and primary productivity and opposed tropical to temperate and boreal climates. The second axis (PC2) was a temperature axis contrasting cells with warm-wet past climates (negative values) and warm-wet current climates (positive values). The third axis (PC3) was mostly dominated by topographic heterogeneity (highest in negative values). In addition to environmental conditions, we also quantified environmental turnover by calculating the mean Euclidean distance of the coordinates of each grid cell with its eight nearest neighbours on each PC axis (similar to Buckley & Jetz, 2007).

## 2.3 | Statistical analyses

Scatter plots of taxonomic and trait turnover values against environmental covariates revealed highly skewed distributions, high heteroscedasticity and triangular relationships. To overcome these issues, we used quantile regressions with either taxonomic or trait turnover as the response variable, using the .10, .25, .50, .75 and .90 quantiles.

We compared four models aimed at a formal comparison of our biome, environmental and biotic homogenization hypotheses: (a) intercept only (control); (b) biomes only (biome hypothesis); (c) environmental conditions plus human impact plus biomes (environmental and biotic homogenization hypotheses); and (d) environmental turnover plus human impact plus biomes (environmental and biotic homogenization





**FIGURE 1** Taxonomic turnover of birds for 8,040 terrestrial assemblages within cells of 110 km × 110 km resolution. For each cell, turnover is computed as the average difference in its bird species composition with its eight nearest neighbours, including all terrestrial species

hypotheses). We made all regression coefficients comparable within each model by scaling all continuous variables to mean = 0 and  $SD = 1$ . The comparison between model (c) and model (d) allowed us to assess which of environmental turnover, average environmental conditions or human impact most strongly influenced bird turnover. To control for the inherent relationship between species and traits, we added taxonomic turnover as a covariate in models (b), (c) and (d) for trait turnover. We therefore tested an additional control model (e) for trait turnover, with taxonomic turnover as a single covariate.

We selected the most parsimonious model on the basis of the Akaike information criterion (AIC) separately for each quantile. We also computed an approximate measure of goodness of fit for each quantile as the ratio of the objective function at the solution (i.e., optimization) of a given model and the control model (Koenker & Machado, 1999). We performed all analyses with R 3.3.2 (R Core Team, 2016) and the package *quantreg* (Koenker, 2016).

### 3 | RESULTS

#### 3.1 | Geographical structure of bird turnover

Taxonomic turnover was on average  $0.11 \pm 0.06$  (mean  $\pm$   $SD$ ), ranging from zero ( $n = 12$ , in North Africa, Arabia and arctic Canada) to 0.51 ( $n = 1$ , in North Africa), indicating relatively low rates of species replacement among neighbouring assemblages. The highest taxonomic turnover occurred in the Andes, eastern North Africa and the Middle East, whereas Siberia, Europe, North America and Amazonia exhibited comparatively lower values (Figure 1). Trait turnover was expectedly lower (mean =  $0.02 \pm 0.03$ ; minimum = 0 in 209 cells spread worldwide; maximum = 0.6, in two North African cells), indicating that adjacent assemblages tend to have similar trait compositions. Spatial variations in trait turnover were roughly congruent with taxonomic turnover but were lower in sub-Saharan Africa and along mountain chains (Figure 2a). However, the two types of turnover were weakly correlated at the global scale (Pearson's  $r^2 = .26$ ), indicating that changes in the taxonomic composition of bird assemblages do not adequately reflect associated changes in trait composition.

Spatial variation in trait turnover was equally correlated with turnover in habitat (Figure 2b;  $r^2 = .45$ ) and dietary (Figure 2c;  $r^2 = .44$ ) preferences. Turnover in migration, dispersal and body mass were all close to zero except in western and eastern North Africa and the Arabian Peninsula (Figure 2d,e) and therefore contributed little to the global pattern. Turnover in thermal preferences (Figure 2f) was mostly structured by mountains and climatic transition regions, such as that between the Amazonian forest and drier regions of South America (compare with maps in Supporting Information Appendix S3).

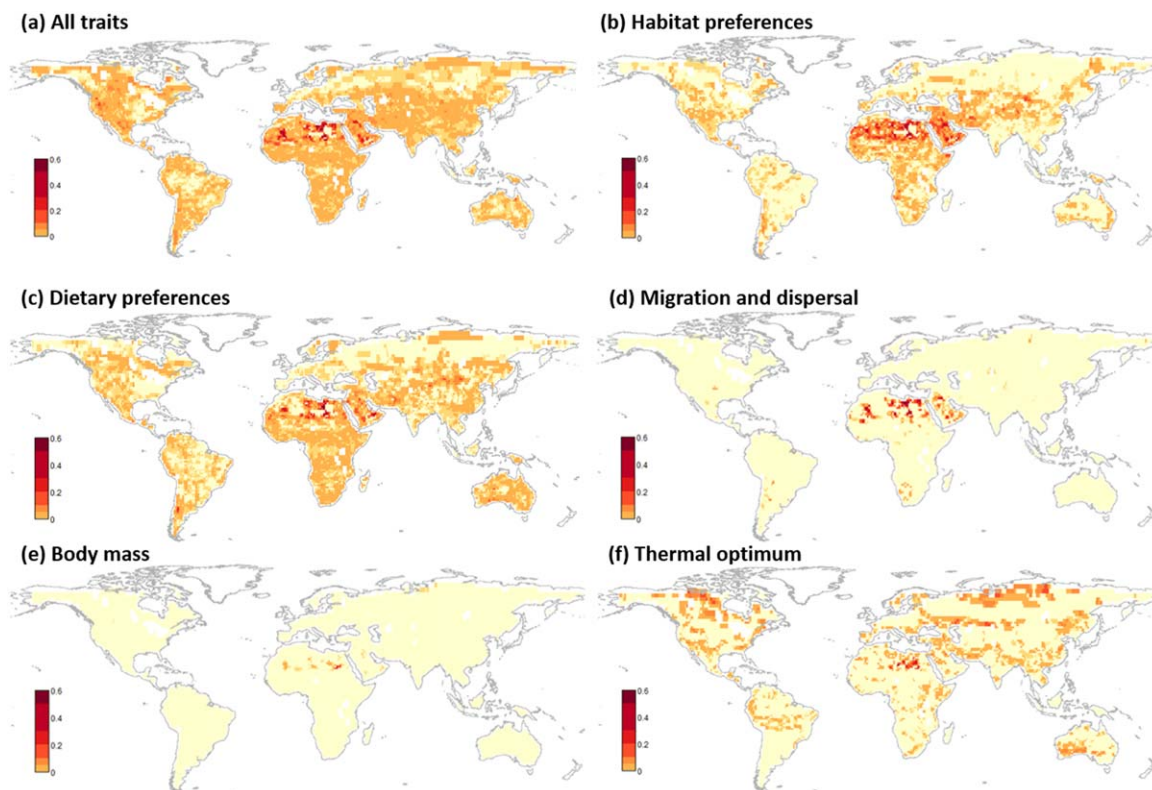
#### 3.2 | Model selection

Models for taxonomic and trait turnover (using all traits) had low fits, especially at the lowest quantiles, where data tend to be more dispersed (adjusted  $R^2$  between .03 and .17). Nevertheless, biomes, environmental variables and human influence explained substantial variation in turnover (Table 1, left side, all AIC differences between the best model and an intercept-only model above 1,600 units). For all quantiles, the biome effect accounted for approximately one-quarter of the AIC difference between the intercept-only model and the most-supported model. Therefore, environmental variation among adjacent assemblages seemed to have a stronger impact on taxonomic turnover than coarse bioclimatic differences.

The influence of environmental variables and human influence on trait turnover increased towards higher quantiles from an AIC difference of 44.62 (.10 quantile) to 1,604.30 (.90 quantile), in comparison to a model including biome and taxonomic turnover only (Table 1, right side). Interestingly, bioclimatic control was strongest for assemblages with high trait turnover (Table 1; increase in the difference between models with and without environmental variables of 33.60 to 1,023.30 AIC units from the .10 to the .90 quantiles).

#### 3.3 | Biome hypothesis

Consistent with the biome hypothesis, deserts and xeric shrublands had the lowest taxonomic and trait turnover of all biomes (Figure 3). However, while tundra had, as expected, the second highest taxonomic



**FIGURE 2** Trait turnover of birds for 8,040 terrestrial assemblages within cells of  $110 \text{ km} \times 110 \text{ km}$  resolution. For each cell, trait turnover is computed as the average difference in its bird trait composition with its eight nearest neighbours, including all terrestrial species and (a) all traits or (b–f) one of five trait subsamples. Trait turnover decreases when fewer traits are considered, demonstrating that functional differences among adjacent assemblages are attributable to changes in trait combinations rather than to variations in individual trait pools

turnover (Figure 3a), it was associated with the lowest trait turnover (Figure 3b). Bird assemblages in the high Arctic therefore differ because of species that share most of their ecological traits, consistent with large-scale environmental filtering. Interestingly, boreal forests, which are geographically adjacent to arctic tundra, had the inverse pattern: low taxonomic turnover (Figure 3a) paired with comparatively high trait turnover (Figure 3b). All four tropical biomes were spread across the distribution of taxonomic turnover values (Figure 3a), but for functional turnover they were in the lower half of the ranking (Figure 3b), in line with our prediction.

### 3.4 | Environmental hypothesis

Environmental turnover was positively correlated with all quantiles of taxonomic turnover (Figure 4a), but it was retained by AIC for the .10, .25 and .50 quantiles only (Table 1). This result supported the prediction that the steepness of environmental gradients imposes a lower bound to bird turnover. However, this was not as clear for the lower quantiles of trait turnover, which either decreased (PC1), increased (PC2) or did not vary (PC3) with increasing environmental turnover (Figure 4b). Also consistent with our predictions, environmental conditions imposed an upper limit to taxonomic and trait turnover (Table 1 and Figure 4c,d). Both turnover values decreased from the tropics to boreal areas (PC1), but whereas taxonomic turnover increased towards

warm and wet areas (PC2) and from high to low topographic heterogeneity (PC3), trait turnover decreased along these two gradients.

### 3.5 | Biotic homogenization hypothesis

Human influence increased both turnover values at lower quantiles but, consistent with our prediction, decreased them at the .75 and .90 quantiles (Figure 4e,f). Hence, while human impact appeared to trigger heterogeneity among adjacent bird assemblages that are otherwise rather homogeneous, it imposed a strong biotic homogenization on areas with higher taxonomic and trait heterogeneity. Interestingly, human influence on bird turnover was of the same order of magnitude ( $10^{-3}$ ) as those of other environmental gradients.

## 4 | DISCUSSION

Our study unifies previous work on taxonomic turnover (Buckley & Jetz, 2008), trait turnover (Villéger et al., 2013) and the role of large-scale environmental determinants in shaping regional assemblages (Hortal, Rodríguez, Nieto-Díaz, & Lobo, 2008). Taxonomic and trait turnover values among adjacent assemblages were correlated with dominant bioclimatic gradients and their steepness, consistent with a major role of bioclimatic filters and physical barriers to dispersal in shaping global patterns of bird assemblage composition (Pigot, Owens,

TABLE 1 Akaike information criterion (AIC)-based selection of quantile regressions for bird taxonomic and trait turnover with five quantiles

Model Quantile	Taxonomic turnover					Trait turnover				
	.1	.25	.5	.75	.9	.1	.25	.5	.75	.9
Environmental turnover + HII + region	-25,764.24	-26,143.26	-24,690.24	-21,445.89	-17,653.13	-48,323.28	-46,934.15	-43,561.16	-37,811.49	-31,095.17
Environmental conditions + HII + region	-25,765.62	-26,093.9	-24,596.68	-21,454.97	-17,796.11	-48,322.43	-46,917.31	-43,565.37	-37,891.85	-31,242.22
Environmental turnover + region	-25,718.21	-26,113.38	-24,680.08	-21,447.3	-17,601.18	-48,318.18	-46,935.75	-43,553.01	-37,733.47	-30,831.99
Environmental conditions + region	-25,709.75	-26,052.89	-24,591.46	-21,455.54	-17,728.14	-48,316.4	-46,918.61	-43,559.25	-37,821.09	-31,005.62
HII + region	-25,489.25	-25,765.49	-24,265.04	-21,024.86	-17,146.6	-48,320.26	-46,919.37	-43,520.02	-37,710.75	-30,932.31
Region	-25,418.56	-25,710.13	-24,232.28	-21,023.35	-17,101.81	-48,312.29	-46,920.85	-43,511.54	-37,618.93	-30,661.13
Taxonomic turnover	-	-	-	-	-	-48,278.66	-46,758.3	-43,109.84	-36,989.66	-29,637.88
Intercept only	-23,970.93	-24,344.3	-23,041.47	-19,616.03	-14,903.53	-47,795.06	-45,427.52	-40,844.34	-33,799.11	-24,896.88
Fit (adjusted R <sup>2</sup> , lowest AIC model)	.11	.11	.1	.11	.17	.03	.09	.16	.16	.16

AIC = Akaike information criterion; HII = human influence index. Note. Retained models are indicated in bold, and the adjusted R<sup>2</sup> is reported for the lowest AIC model. Environmental conditions and environmental turnover correspond to the scores of the 8,040 bird assemblages on three principal component axes and their average difference with their eight nearest neighbours.

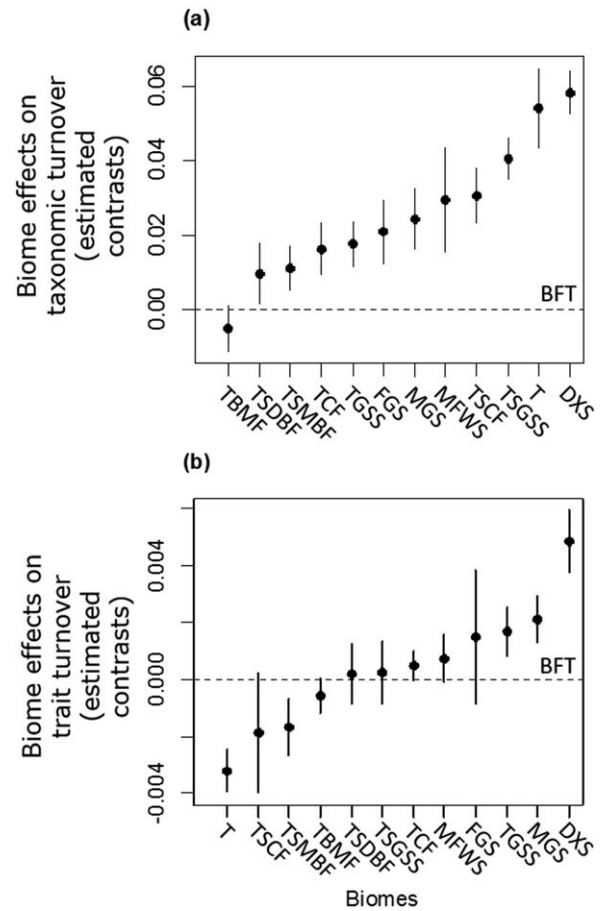
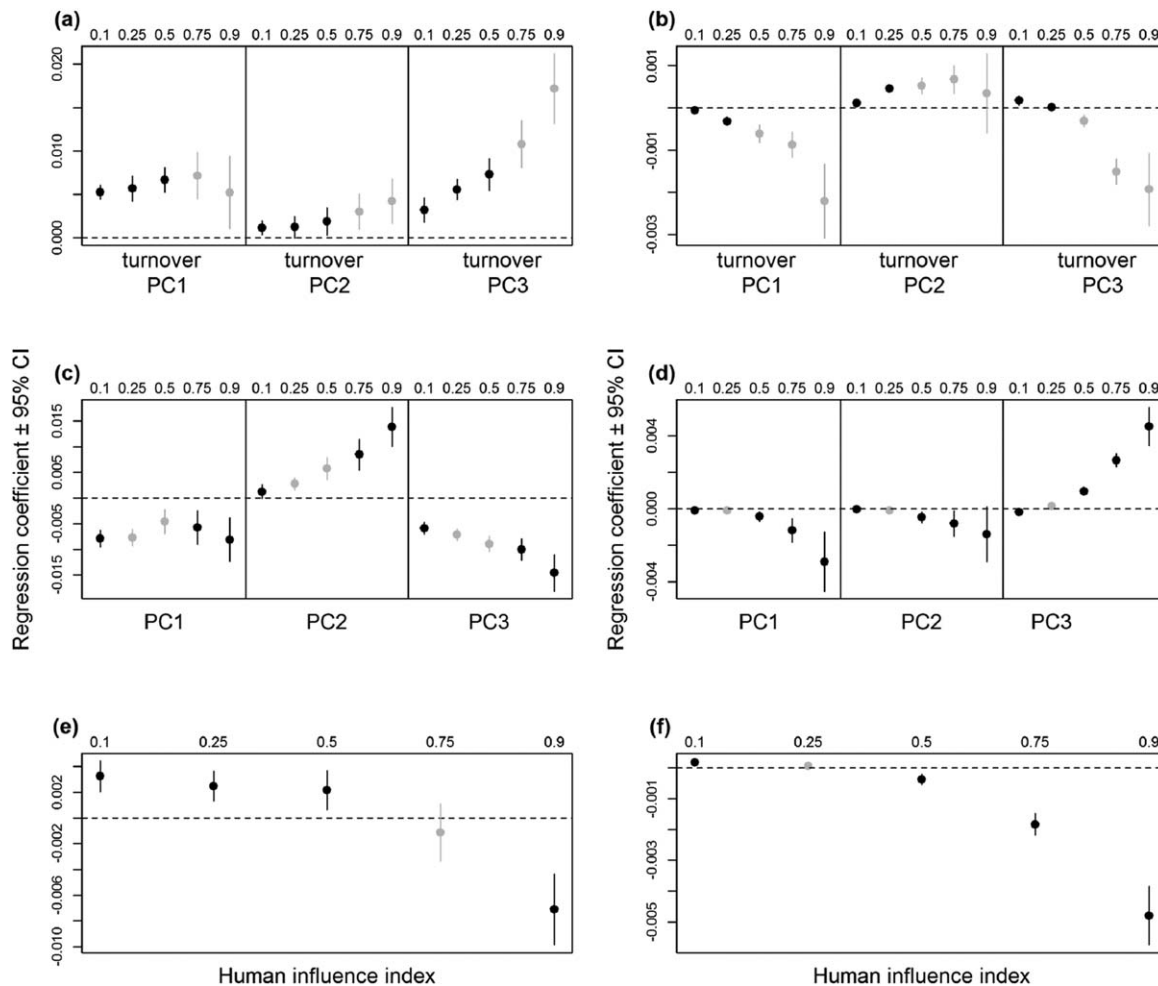


FIGURE 3 Biome-related variations in bird (a) taxonomic and (b) trait turnover. Differences among biomes are shown as contrasts assessed from quantile regressions (quantile shown = .5), taking the 'boreal forests and taiga' (BFT) biome as an arbitrary reference (dashed line). DXS = deserts and xeric shrublands; FGS = flooded grasslands and savannas; MFWS = mediterranean forests, woodlands and scrub; MGS = montane grasslands and shrublands; T = tundra; TBMF = temperate broadleaf and mixed forests; TCF = temperate conifer forests; TGSS = temperate grasslands, savannas and shrublands; TSCF = tropical and subtropical coniferous forests; TSDBF = tropical and subtropical dry broadleaf forests; TSGSS = tropical and subtropical grasslands, savannas and shrublands; TSMBF = tropical and subtropical moist broadleaf forests

& Orme, 2010). Accordingly, neighbourhood trait turnover was dominated by species' habitat, diet and, to a lesser extent, thermal preferences in most regions. Importantly, human influence imposed an upper bound on taxonomic and trait turnover values, as expected under biotic homogenization.

Consistent with the biome hypothesis, trait turnover was high in deserts but low in tropical biomes. All traits, and notably those related to resource use (habitat preference and, to a lesser extent, dietary preference), showed low turnover rates around the Amazon Basin and in Southeast Asia in spite of high levels of endemism and resource specialization (Del Hoyo et al., 2013). Hence, tropical bird assemblages are relatively homogeneous in traits at the regional scale, which could be explained by the concurring effects of tropical niche conservatism,



**FIGURE 4** Environmental effects on (a,c,e) bird taxonomic turnover and (b,d,f) trait turnover as estimated from quantile regressions with five quantiles. Estimates and 95% confidence intervals (CIs) based on a Gaussian approximation are represented for each tested variable: environmental turnover on three principal component axes (turnover PC1, PC2 and PC3); regional environmental conditions reflected by these axes (PC1, PC2 and PC3) and human impact quantified by the human influence index. Coefficients corresponding to quantiles that were not retained by an Akaike information criterion selection procedure are displayed in grey

predominance of high rates of local radiation, and low dispersal in the tropics (Barnagaud et al., 2014; Salisbury, Seddon, Cooney, & Tobias, 2012; Wiens & Donoghue, 2004). These processes have been related to long-term climatic stability and high resource availability in the tropical zone (Wiens & Donoghue, 2004). In line with this interpretation, taxonomic turnover increased while trait turnover decreased towards warm and wet current climatic conditions. Turnover calculated at finer resolution (for instance, considering different classes of frugivores or measurements related to bill size and coloration) would probably yield more positive correlations between taxonomic and trait turnover if local specialization on resources and biotic interactions underpin geographical distributions in tropical bird assemblages (Dehling et al., 2014). At the other extreme of the climatic gradient, arctic tundra was also characterized by high taxonomic turnover, but the lowest trait turnover of all biomes. This was especially true for dietary and habitat preferences, suggesting strong effects of environmental filtering and post-glacial recolonization events (Villéger et al., 2013).

Taxonomic turnover increased with topographic heterogeneity, whereas trait turnover decreased. The strong zonation of climatic and resource conditions in mountains triggers increases in beta diversity attributable to changes in species richness and species segregation under the joint effects of thermal and habitat preferences (Dobrovolski, Melo, Cassemiro, & Diniz-Filho, 2012; Melo, Rangel, & Diniz-Filho, 2009; Swenson et al., 2010). Such patterns are hardly visible at the spatial resolution of our study because a single bird assemblage in a mountainous area encompasses the whole range of traits from typical lowland species to alpine specialists. Consequently, studies within biomes using finer trait classifications and a higher spatial resolution of species assemblages would probably give different results (Belmaker & Jetz, 2013; McKnight et al., 2007). Although there was no evidence for temperature-mediated turnover along altitudinal gradients, turnover in thermal preferences was higher along biome borders, especially at high latitudes, the southern border of the Amazonian forest and between the eastern Sahara and savannahs. This supports the hypothesis of a



relationship between habitat and thermal niches mediated by biogeographical history (Barnagaud et al., 2012).

As one of multiple forms of biotic homogenization, human-mediated global change reorganizes bird diversity into more taxonomically and functionally redundant assemblages (Baiser & Lockwood, 2011; Meynard et al., 2011; Solar et al., 2015). Our results were in line with this and, furthermore, showed that human influence was the strongest where taxonomic and trait turnover were highest, such as in assemblages composed of range-restricted or specialist species, which usually exhibit low resilience to disturbance (Salisbury et al., 2012) and are more likely to go extinct (Sekercioglu, 2011). This is notably the case in deserts and the arctic, where HII is comparably low (Sanderson et al., 2002), suggesting that small levels of anthropogenic disturbance have a disproportionate impact on species-poor assemblages. At a global scale, the magnitude of human influence on bird turnover was comparable to that of environmental and biogeographical gradients, as observed in other taxa or at finer spatial scales (Šizling et al., 2016). Our results therefore support the hypothesis that a few thousand years of human imprint on the earth have become a major process structuring biodiversity patterns at macroecological scales (Ellis, 2015).

## 5 | CONCLUSION

Although patterns of bird taxonomic turnover have been studied at various spatial scales (Buckley & Jetz, 2007; Gaston et al., 2007), our study brings major advances. First, we separated turnover from gradients in species and trait diversity, and could therefore more adequately address hypotheses that were previously tested globally using beta diversity as a surrogate of turnover (Gaston et al., 2007; Koleff, Lennon, & Gaston, 2003). Second, we showed that humans set a bound to diversity gradients, providing macroecological evidence of biotic homogenization at a global scale. Our results should stimulate further assessments of how processes operating at multiple time scales, including anthropogenic ones, shape present-day turnover of biodiversity across our planet.

## DATA ACCESSIBILITY

Bird extent of occurrence data can be freely retrieved at <http://www.birdlife.org/datazone/info/spcdownload>. All environmental variables can be retrieved freely on the Internet at the URL provided in the main text. The species-traits matrix is available upon request from the authors.

## ACKNOWLEDGMENTS

This study is a contribution by the Center for Informatics Research on Complexity in Ecology (CIRCE), funded by the Aarhus University Research Foundation under the AU Ideas programme. We are grateful to the Université Libre de Bruxelles for allowing access to its computation cluster. We thank Simon Chamailé-Jammes for advice on quantile regression. We are grateful to dozens of volunteers and students, especially Monte Neate-Clegg, Joshua Horns, Evan

Buechley, Jason Socci, Sherron Bullens, Debbie Fisher, David Hayes, Beth Karpas and Kathleen McMullen, for their dedicated help with the world bird ecology database. J.-C.S. also considers this work a contribution to his VILLUM Investigator project 'Biodiversity Dynamics in a Changing World' funded by VILLUM FONDEN. W.D.K. acknowledges a University of Amsterdam starting grant, and Ç.H.S. acknowledges University of Utah and Koç University support. We thank Ana Santos and two anonymous referees for their constructive comments on an earlier version of this article.

## ORCID

Jean-Yves Barnagaud  <http://orcid.org/0000-0002-8438-7809>

## REFERENCES

- Ackerly, D. D., & Cornwell, W. K. (2007). A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. *Ecology Letters*, *10*, 135–145.
- Antonelli, A., Nylander, J. A. A., Persson, C., & Sanmartín, I. (2009). Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences USA*, *106*, 9749–9754.
- Araújo, M. B., Nogués-Bravo, D., Diniz-Filho, J. A. F., Haywood, A. M., Valdes, P. J., & Rahbek, C. (2008). Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, *31*, 8–15.
- Baiser, B., & Lockwood, J. L. (2011). The relationship between functional and taxonomic homogenization. *Global Ecology and Biogeography*, *20*, 134–144.
- Barnagaud, J.-Y., Devictor, V., Jiguet, F., Barbet-Massin, M., Le Viol, I., & Archaux, F. (2012). Relating habitat and climatic niches in birds. *PLoS One*, *7*, e32819.
- Barnagaud, J.-Y., Kissling, W. D., Sandel, B., Eiserhardt, W. L., Şekercioglu, Ç. H., Enquist, B. J., & Svenning, J. C. (2014). Ecological traits influence the phylogenetic structure of bird species co-occurrences worldwide. *Ecology Letters*, *17*, 811–820.
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143.
- Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, *21*, 1223–1232.
- Baselga, A., & Leprieur, F. (2015). Comparing methods to separate components of beta diversity. *Methods in Ecology and Evolution*, *6*, 1069–1079.
- Belmaker, J., & Jetz, W. (2013). Spatial scaling of functional structure in bird and mammal assemblages. *The American Naturalist*, *181*, 464–478.
- Belmaker, J., Sekercioglu, C. H., & Jetz, W. (2011). Global patterns of specialization and coexistence in bird assemblages. *Journal of Biogeography*, *39*, 193–203.
- Birdlife International & NatureServe. (2012). *Bird species distribution maps of the world*. Version 2.0. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA.
- Blanchet, S., Grenouillet, G., Beauchard, O., Tedesco, P. A., Leprieur, F., Dürr, H. H., ... Brosse, S. (2010). Non-native species disrupt the worldwide patterns of freshwater fish body size: Implications for Bergmann's rule. *Ecology Letters*, *13*, 421–431.

- Braconnot, P., Otto-Bliesner, B., Harrison, S., Joussaume, S., Peterchmitt, J.-Y., Abe-Ouchi, A., ... Zhao, Y. (2007). Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum – Part 1: Experiments and large-scale features. *Climate of the Past*, 3, 261–277.
- Buckley, L. B., & Jetz, W. (2007). Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1167–1173.
- Buckley, L. B., & Jetz, W. (2008). Linking global turnover of species and environments. *Proceedings of the National Academy of Sciences USA*, 105, 17836–17841.
- Caley, M. J., & Schluter, D. (1997). The relationship between local and regional diversity. *Ecology*, 78, 70–80.
- Capinha, C., Essl, F., Seebens, H., Moser, D., & Pereira, H. M. (2015). The dispersal of alien species redefines biogeography in the Anthropocene. *Science*, 348, 1248–1251.
- De Bello, F., Thuiller, W., Lepš, J., Choler, P., Clément, J.-C., Macek, P., ... Lavorel, S. (2009). Partitioning of functional diversity reveals the scale and extent of trait convergence and divergence. *Journal of Vegetation Science*, 20, 475–486.
- Dehling, D. M., Fritz, S. A., Töpfer, T., Päckert, M., Estler, P., Böhning-Gaese, K., & Schleuning, M. (2014). Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. *Ecography*, 37, 1047–1055.
- Del Hoyo, J., Elliott, A., & Sargatal, J. (2013). *Handbook of the birds of the world*. Barcelona, Spain: Lynx Edicions.
- Dobrovolski, R., Melo, A. S., Cassemiro, F. A. S., & Diniz-Filho, J. A. F. (2012). Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 21, 191–197.
- Ellis, E. C. (2015). Ecology in an anthropogenic biosphere. *Ecological Monographs*, 85, 287–331.
- Eskildsen, A., Carvalheiro, L. G., Kissling, W. D., Biesmeijer, J. C., Schweiger, O., & Høye, T. T. (2015). Ecological specialization matters: Long-term trends in butterfly species richness and assemblage composition depend on multiple functional traits. *Diversity and Distributions*, 21, 792–802.
- Faurby, S., & Svenning, J.-C. (2015). Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Diversity and Distributions*, 21, 1155–1166.
- Ficetola, G. F., Mazel, F., & Thuiller, W. (2017). Global determinants of zoogeographical boundaries. *Nature Ecology & Evolution*, 1, 0089.
- Gaston, K. J., Davies, R. G., Orme, C. D. L., Olson, V. A., Thomas, G. H., Ding, T.-S., ... Blackburn, T. M. (2007). Spatial turnover in the global avifauna. *Proceedings of the Royal Society B: Biological Sciences*, 274, 1567–1574.
- Haberl, H., Erb, K. H., Krausmann, F., Gaube, V., Bondeau, A., Plutzer, C., ... Fischer-Kowalski, M. (2007). Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. *Proceedings of the National Academy of Sciences USA*, 104, 12942–12947.
- Hortal, J., Rodríguez, J., Nieto-Díaz, M., & Lobo, J. M. (2008). Regional and environmental effects on the species richness of mammal assemblages. *Journal of Biogeography*, 35, 1202–1214.
- Kissling, W. D., Baker, W. J., Balslev, H., Barfod, A. S., Borchsenius, F., Dransfield, J., ... Svenning, J.-C. (2012). Quaternary and pre-quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography*, 21, 909–921.
- Kissling, W. D., Sekercioglu, C. H., & Jetz, W. (2012). Bird dietary guild richness across latitudes, environments and biogeographic regions. *Global Ecology and Biogeography*, 21, 328–340.
- Koenker, R. (2016). *quantreg: Quantile Regression*. R package version 5.29. <https://CRAN.R-project.org/package=quantreg>
- Koenker, R., & Machado, J. A. F. (1999). Goodness of fit and related inference processes for quantile regression. *Journal of the American Statistical Association*, 94, 1296–1310.
- Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, 72, 367–382.
- Koleff, P., Lennon, J. J., & Gaston, K. J. (2003). Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography*, 12, 483–498.
- Kraft, N. J. B., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., ... Myers, J. A. (2011). Disentangling the drivers of  $\beta$  diversity along latitudinal and elevational gradients. *Science*, 333, 1755–1758.
- Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16, 545–556.
- Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, 23, 1324–1334.
- Leprieux, F., Tedesco, P. A., Hugueny, B., Beauchard, O., Dürr, H. H., Brosse, S., & Oberdorff, T. (2011). Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters*, 14, 325–334.
- McKnight, M. W., White, P. S., McDonald, R. I., Lamoreux, J. F., Sechrest, W., Ridgely, R. S., & Stuart, S. N. (2007). Putting beta-diversity on the map: Broad-scale congruence and coincidence in the extremes. *PLoS Biology*, 5, e272.
- Melo, A. S., Rangel, T. F. L. V. B., & Diniz-Filho, J. A. F. (2009). Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography*, 32, 226–236.
- Meynard, C. N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F., & Mouquet, N. (2011). Beyond taxonomic diversity patterns: How do  $\alpha$ ,  $\beta$  and  $\gamma$  components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Global Ecology and Biogeography*, 893–903.
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., ... Kassem, K. R. (2001). Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience*, 51, 933–938.
- Pautasso, M., Böhning-Gaese, K., Clergeau, P., Cueto, V. R., Dinetti, M., Fernández-Juricic, E., ... Cantarello, E. (2011). Global macroecology of bird assemblages in urbanized and semi-natural ecosystems. *Global Ecology and Biogeography*, 20, 426–436.
- Pavoine, S., & Bonsall, M. B. (2011). Measuring biodiversity to explain community assembly: A unified approach. *Biological Reviews*, 86, 792–812.
- Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., & Daniel, H. (2009). On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. *Oikos*, 118, 391–402.
- Pigot, A. L., Owens, I. P. F., & Orme, C. D. L. (2010). The environmental limits to geographic range expansion in birds. *Ecology Letters*, 13, 705–715.
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, 7, 1–15.
- Salisbury, C. L., Seddon, N., Cooney, C. R., & Tobias, J. A. (2012). The latitudinal gradient in dispersal constraints: Ecological specialisation drives diversification in tropical birds. *Ecology Letters*, 15, 847–855.

- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The human footprint and the last of the wild. *Bioscience*, *52*, 891–904.
- Sekercioglu, Ç. H. (2011). Functional extinctions of bird pollinators cause plant declines. *Science*, *331*, 1019–1020.
- Şekerciöglü, Ç. H., Daily, G. C., & Ehrlich, P. R. (2004). Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences USA*, *101*, 18042–18047.
- Šizling, A. L., Pokorný, P., Juričková, L., Horáčková, J., Abraham, V., Šizlingová, E., ... Kunin, W. (2016). Can people change the ecological rules that appear general across space? *Global Ecology and Biogeography*, *25*, 1072–1184.
- Solar, R. R. C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A. C., Thomson, J. R., ... Gardner, T. A. (2015). How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters*, *18*, 1108–1118.
- Svenning, J.-C., Normand, S., & Skov, F. (2008). Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography*, *31*, 316–326.
- Swenson, N. G., Anglada-Cordero, P., & Barone, J. A. (2010). Deterministic tropical tree community turnover: Evidence from patterns of functional beta diversity along an elevational gradient. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 877–884.
- Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. *Oikos*, *118*, 3–17.
- Ulrich, W., Soliveres, S., Maestre, F. T., Gotelli, N. J., Quero, J. L., Delgado-Baquerizo, M., ... Zaady, E. (2014). Climate and soil attributes determine plant species turnover in global drylands. *Journal of Biogeography*, *41*, 2307–2319.
- Villéger, S., Grenouillet, G., & Brosse, S. (2013). Decomposing functional  $\beta$ -diversity reveals that low functional  $\beta$ -diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography*, *22*, 671–681.
- Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, *19*, 639–644.
- Wildlife Conservation Society & Center for International Earth Science Information Network - CIESIN - Columbia University. (2005). Last of the Wild Project, Version 2, 2005 (LWP-2): Last of the Wild Dataset (Geographic). <http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-last-of-the-wild-geographic>
- Zhao, M., Heinsch, F. A., Nemani, R. R., & Running, S. W. (2005). Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote Sensing of Environment*, *95*, 164–176.

## BIOSKETCH

The Center for Informatics Research on Complexity in Ecology (CIRCE) was established at Aarhus University in 2012 to study the importance of complexity in ecosystem function and responses to environmental change, analysing large ecological datasets using advanced statistical and mechanistic modelling. CIRCE focuses on three major complexity factors: species interactions, dispersal and environmental variability (<http://projects.au.dk/circe-center-for-informatics-research-on-complexity-in-ecology/>).

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Barnagaud J-Y, Kissling WD, Tsirogianis C, et al. Biogeographical, environmental and anthropogenic determinants of global patterns in bird taxonomic and trait turnover. *Global Ecol Biogeogr.* 2017;26:1190–1200. <https://doi.org/10.1111/geb.12629>