

Global variation in woodpecker species richness shaped by tree availability

Sigrid Kistrup Ilsøe^{1,†}, W. Daniel Kissling^{2,†,*} , Jon Fjeldså³, Brody Sandel⁴ and Jens-Christian Svenning¹



¹Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, DK-8000 Aarhus C, Denmark, ²Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, 1090 GE Amsterdam, The Netherlands, ³Center for Macroecology, Evolution and Climate at Natural History Museum of Denmark, University of Copenhagen, DK-1350 Copenhagen K, Denmark, ⁴Department of Biology, Santa Clara University, Santa Clara, CA 95057, USA

ABSTRACT

Aim Species richness patterns are generally thought to be determined by abiotic variables at broad spatial scales, with biotic factors being only important at fine spatial scales. However, many organism groups depend intimately on other organisms, raising questions about this generalization. As an example, woodpeckers (Picidae) are closely associated with trees and woody habitats because of multiple morphological and ecological specializations. In this study, we test whether this strong biotic association causes woodpecker diversity to be closely linked to tree availability at a global scale.

Location Global.

Methods We used spatial and non-spatial regressions to test for relationships between broad-scale woodpecker species richness and predictor variables describing current and deep-time availability of trees, current climate, Quaternary climate change, human impact, topographical heterogeneity and biogeographical region. We further used structural equation models to test for direct and indirect effects of predictor variables.

Results There was a strong positive relationship between woodpecker species richness and current tree cover and annual precipitation, respectively. Precipitation also showed a strong indirect effect on woodpecker richness via the effects on tree availability. Deep-time tree availability, Quaternary climate change, human influence and other abiotic factors showed weaker direct effects. Human influence had a negative effect on tree availability, and hence a negative indirect effect on woodpecker species richness.

Main conclusions Global species richness of woodpeckers is primarily shaped by current tree cover and precipitation, reflecting a strong biotic association between woodpeckers and trees. Human influence can have a negative effect on woodpecker diversity when humans reduce tree availability. Hence, woodpeckers exemplify how broad-scale diversity patterns are predominantly shaped by a biotic factor, and how climate and human influence can have indirect effects on animal biodiversity via the effects on tree availability and forest cover.

Keywords

arboreal avian guild, biotic modifiers, birds, biodiversity, forests, habitat loss, Piciformes, plant-bird interactions, species-habitat associations, vegetation effects

*Correspondence: W. Daniel Kissling, Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands.

E-mail: wdckissling@gmail.com

†These authors contributed equally to this work.

INTRODUCTION

At broad spatial scales, species richness patterns are generally thought to be determined by abiotic variables (Hawkins *et al.*, 2003). Usually, high species richness is linked to high

contemporary availability of water and ambient energy, reflecting higher resource availability or weaker abiotic filtering of the regional species pool (Wright, 1983; Rahbek & Graves, 2001). Nevertheless, climate is not the only factor influencing species diversity. Biotic factors such as habitat

and resource availability are often thought to primarily limit species distributions and species diversity at fine spatial scales (Pearson & Dawson, 2003; Zhang *et al.*, 2013). This is sometimes referred to as 'Eltonian noise hypothesis' (Soberon & Nakamura, 2009). However, it is now increasingly recognized that biotic associations can affect distributions and diversity patterns not only at local scales but also at regional to continental scales (Heikkinen *et al.*, 2007; Wisz *et al.*, 2013).

Woodpeckers (Piciformes: Picidae) constitute a monophyletic group with an ecology that is closely associated with trees (Short, 1982; Webb & Moore, 2005; Mikusiński, 2006). This biotic association involves morphological specialization to perch and climb on branches and trunks of trees, and retrieving food by drilling and probing into wood, albeit with significant variation in the degree of specialization. Furthermore, all woodpecker species breed in cavities, which they usually excavate themselves in decaying wood. Woodpeckers have colonized virtually all forested and wooded parts of the world. The main exceptions are Australasia, Madagascar and various remote islands, which reflects a reluctance of woodpeckers to cross large expanses of barren land or water (Short, 1982; Winkler & Christie, 2002). The broad-scale drivers of the geographical diversity patterns in woodpeckers have not yet been studied, but the close biotic association with trees suggests that tree availability may shape their species richness patterns at regional, continental and global spatial scales. This is indicated by studies of the acorn woodpecker (*Melanerpes formicivorus*), which show that its distribution is limited by its close biotic association with oaks and their variability in acorn production (Koenig & Haydock, 1999; Freeman & Mason, 2015).

Tree availability could influence woodpecker diversity not just via present-day availability (MacArthur, 1965; Zhang *et al.*, 2013; Stein *et al.*, 2014), but potentially also via its availability across geological time (Jetz & Fine, 2012). Availability and persistence of suitable habitats and biomes over deep geological times can produce high species richness, e.g. due to time for speciation and/or low extinction (Jetz & Fine, 2012). Across geological time scales, tree availability has varied strongly in some regions. For example, the extent of forest cover in Africa contracted strongly during the Neogene, leading to reduced biodiversity and affecting the phylogenetic structure of African palms (Kissling *et al.*, 2012b). Moreover, the strong glacial-interglacial oscillations of the Quaternary have resulted in dramatic dynamics in the extent and distribution of forested areas in many regions (Prentice *et al.*, 2011), with strong effects on species diversity patterns via extinction and speciation processes (e.g. Svenning & Skov, 2007; Sandel *et al.*, 2011).

Today, human impacts can influence woodpecker diversity via effects on resource availability, via effects on overall tree cover, or by affecting specific tree resources and habitat structures such as old trees, large trees, and standing dead trees (Mikusiński, 2006; Drapeau *et al.*, 2009). Habitat loss caused by human activities has been studied widely at broad and fine spatial scales with particular attention to the negative effects

of tree removal and forest management on biodiversity (e.g. Sanderson *et al.*, 2002; Lindenmayer *et al.*, 2012). Forest clearing and management, as well as urbanization and land use intensification, have been found to negatively affect the diversity of woodpeckers at local and regional scales because this reduces the amount of suitable habitat (e.g. Mikusiński & Angelstam, 1998; Myczko *et al.*, 2014).

In this study, we test whether and to what extent the close association between woodpeckers and trees influences global patterns of woodpecker species richness. First, we hypothesize that current and deep-time tree availability are important variables to explain the global variation in woodpecker species richness ('biotic association hypothesis'). This would indicate that biotic factors play an important role in shaping large-scale diversity patterns (Kissling *et al.*, 2007, 2008; Wisz *et al.*, 2013). Second, we hypothesize that climatic effects on broad-scale woodpecker species richness are often indirect, via effects on tree cover ('indirect climate effects hypothesis'). This can be expected if animals strongly depend on plant resources and habitat structures that are in turn determined by climate (Kissling *et al.*, 2008; Zhang *et al.*, 2013; Ferger *et al.*, 2014). Finally, we expect that human activities have a negative impact on woodpecker species richness, mainly because of the effects on tree availability ('human impact hypothesis'). This can be expected given the pervasive influence that humans have on forests and other woody habitats worldwide (Hansen *et al.*, 2013).

MATERIALS AND METHODS

Woodpecker data

We used the species taxonomy of woodpeckers as recognized by BirdLife International and NatureServe (2011). For higher taxonomic levels, we followed Dickinson & Remsen (2013) as well as recent molecular studies of woodpecker phylogenetic relationships (Webb & Moore, 2005; Benz *et al.*, 2006; Fuchs *et al.*, 2007, 2013; Moore *et al.*, 2011; Manegold & Töpfer, 2013). We assigned each species from the family Picidae ($n = 218$ species) to sub-families (Picinae, $n = 186$ species; Jynginae, $n = 2$ species; Picumninae, $n = 29$ species; Nesocitinae, $n = 1$ species), and species in the sub-family Picinae also to the tribes therein: Hemicircinae ($n = 2$ species), Melanerpini ($n = 91$ species), Picini ($n = 77$ species) and Campephilini ($n = 16$ species). For the statistical analyses, we focus on species richness of the whole woodpecker family (Picidae), but also repeat the multi-predictor models (see below) for the sub-family Picinae and its two largest tribes (Melanerpini and Picini) (see Appendix S1 in Supporting Information). The other taxa comprised too few species for meaningful analyses.

Data on global species distributions – representing conservative extent-of-occurrence extrapolations of the world-scale breeding ranges – were compiled from BirdLife International & NatureServe (2011) for the 218 recognized extant woodpecker species. These range maps were overlaid from their

original polygon format onto a cylindrical equal area grid with > 39,900 cells with 110 × 110 km resolution, equivalent to *c.* 1° × 1° near the equator (Kissling *et al.*, 2012a). This spatial resolution is commonly used in macroecological analyses of such expert-based range maps because they tend to predict false presences at finer resolution as a result of variation in landscapes and habitats. Presence of a species in a grid cell was recorded when the species distribution polygon overlapped with the grid cell. We calculated species richness per grid cell for each taxonomic group separately by summing up the presences of all included species. Grid cells with no woodpecker presence or > 50% water were excluded.

Predictor variables

We used 10 predictor variables to explain the broad-scale distribution of woodpecker species richness (Table 1). These variables were related to current and past tree availability (two variables), current climate (three variables), past climate (two variables), human influence (one variable), topographical heterogeneity (one variable), and biogeographical region (one variable). Geoprocessing of data was performed in ARCGIS 10.2 (ESRI, Redland, USA).

Current tree availability

Data on current tree availability (i.e. areas with woody vegetation) were obtained from the vegetation continuous field dataset (DiMiceli *et al.*, 2011), a remotely sensed product derived from the MODerate-resolution Imaging Spectroradiometer (MODIS) sensor on board the NASA's Terra satellite. This product contains proportional estimates for vegetative cover types such as woody vegetation, herbaceous vegetation and bare ground (DiMiceli *et al.*, 2011). For our analyses, we used the global map of percent coverage of tree canopies at 250 m spatial resolution in the year 2010. We calculated the mean percentage of tree cover for each 110 × 110 km grid cell from this product (TREES, Table 1).

Past tree availability

We quantified the past tree availability as the availability of suitable historical biomes over deep geological time (Hist-BIOME, Table 1). This was performed using biome reconstructions from the Last Glacial Maximum (LGM, 0.021 Ma) (Prentice *et al.*, 2011), the middle Pliocene (3.6–2.6 Ma) (Salzmann *et al.*, 2008) and the late Miocene (11.6–7.25 Ma)

Table 1 Predictor variables used to explain geographical variation in species richness of woodpeckers worldwide. The data sources and references for each predictor variable are provided. Data were compiled and aggregated in a cylindrical equal area grid with a grid cell resolution of 110 × 110 km (equivalent to 1° × 1° at equator).

Abbreviations	Predictor variables (units)	Data source (reference)
<i>Current tree availability</i>		
TREES	Mean percentage tree canopy cover (%)	Vegetation continuous field data set (DiMiceli <i>et al.</i> , 2011)
<i>Past tree availability</i>		
HistBIOME	Historical biome availability, i.e., number of time periods (Miocene, Pliocene, Quaternary) in which suitable woodpecker habitats (biomes with trees) were present (categorical): zero, one, two, three	Calculated in ARCGIS, based on biome reconstructions from Pound <i>et al.</i> (2011) (Miocene), Salzmann <i>et al.</i> (2008) (Pliocene) and Prentice <i>et al.</i> (2011) (Last Glacial Maximum)
<i>Current climate</i>		
PREC	Annual precipitation (mm yr ⁻¹)	WORLDCLIM data set (Hijmans <i>et al.</i> , 2005)
PREC SEAS	Precipitation seasonality: coefficient of variation of monthly precipitation values (mm)	WORLDCLIM data set (Hijmans <i>et al.</i> , 2005)
TEMP	Annual mean temperature (°C × 10)	WORLDCLIM dataset (Hijmans <i>et al.</i> , 2005)
<i>Past climate</i>		
QUA TEMP	Difference in mean temperature between Last Glacial Maximum and present (°C × 10)	Calculated with data from PIMP 2 project (Braconnot <i>et al.</i> , 2007) and WORLDCLIM (Hijmans <i>et al.</i> , 2005), all downloaded from WorldClim
QUA PREC	Difference in annual precipitation between Last Glacial Maximum and present (mm yr ⁻¹)	Calculated with data from PIMP 2 project (Braconnot <i>et al.</i> , 2007) and WORLDCLIM (Hijmans <i>et al.</i> , 2005), all downloaded from WorldClim
<i>Topographical heterogeneity</i>		
TOPO	Topographical heterogeneity: range in elevation (m)	Global Land Cover Characterization Database (https://lta.cr.usgs.gov/glcc/globdoc2_0)
<i>Human influence</i>		
HUMAN	Human influence index: global map of human influence per 1 km ² (range in scale from 0 to 65)	Sanderson <i>et al.</i> (2002)
<i>Biogeographical region</i>		
REGION	Region (categorical): Afrotropical, Nearctic, Neotropical, Oriental, Palaearctic, Panamanian, Saharo-Arabian, Sino-Japanese	Terrestrial zoogeographical realms (Holt <i>et al.</i> , 2013)

(Pound *et al.*, 2011). The different biome reconstructions use slightly different vegetation classifications (Salzmann *et al.*, 2008; Pound *et al.*, 2011; Prentice *et al.*, 2011). From all biome reconstructions, any biome that represented forested habitats or savannas was classified as suitable woodpecker habitat (for biome classes see Appendix S2 in Supporting Information). We reclassified them with the value 1 (suitable) whereas all non-suitable biomes were reclassified with the value 0 (non-suitable). For each 110 × 110 km grid cell we then identified whether biomes classified as suitable woodpecker habitat were available at each time epoch. We summed this per grid cell to quantify the temporal availability of woodpecker habitats, with values ranging from no suitable habitat available in any epoch (value 0) to suitable habitat available in all three time periods (value 3).

Current climate

Climate data were retrieved from WORLDCLIM 1.4 (www.worldclim.org; Hijmans *et al.*, 2005), a global set of layers with a spatial resolution of *c.* 1 km². From the original resolution, we calculated mean values of each climate variable for each 110 × 110 km grid cell. We represented current climate with annual mean temperature (TEMP), total annual precipitation (PREC) and precipitation seasonality (PREC SEAS) (Table 1). Other climate data (e.g. temperature seasonality and mean temperature of the coldest quarter) were also considered, but they showed high correlations with the other climate variables (Spearman rank $r > 0.85$). We therefore excluded them in the statistical analysis (see below).

Past climate

We assessed the importance of past climate by capturing Quaternary glacial-interglacial oscillations, i.e. quantifying the differences (anomalies) between the current climate and the LGM (Kissling *et al.*, 2012c). Two past climate variables were calculated, namely the anomaly in precipitation (QUA PREC) and the anomaly in annual mean temperature (QUA TEMP) (Table 1). This was performed by subtracting the LGM value in each 110 × 110 km grid cell from the present-day climate value. Positive anomaly values indicate a higher precipitation or temperature in the present than in the past whereas negative anomaly values indicate the opposite. For LGM climates, we used the mean values across two climate simulations, namely the Community Climate System Model 3 (CCSM3) and the Model for Interdisciplinary Research on Climate 3.2 (MIROC3.2), derived from the Paleoclimatic Modelling Intercomparison Project (PMIP2; <https://pmip2.lsce.ipsl.fr/>) (Braconnot *et al.*, 2007).

Topographical heterogeneity

Topographical heterogeneity is an important predictor of species richness because it captures steep climatic and habitat

gradients which promote spatial turnover of species (Stein *et al.*, 2014). We quantified topographical heterogeneity (TOPO, Table 1) as elevational range for each 110 × 110 km grid cell, based on data from the GTOPO-30 digital elevation model with a spatial resolution of 0.05°. Data were downloaded from the Global Land Cover Characterization Database at https://lta.cr.usgs.gov/glcc/globdoc2_0.

Human influence

We used the human influence index (HII) (Sanderson *et al.*, 2002) as a measure of anthropogenic impact. The HII is a global map of human imprint created from nine global data layers covering human population pressure (population density), human land use and infrastructure (including settlements and built-up areas, night-time lights, agricultural land cover, mixed-use cover, roads and railways), and human accessibility (estimated as proximity to roads, railroads, navigable rivers and coastlines). It largely refers to the year 2000 and quantifies human impact per 1 km², with values ranging from 0 to 65. Data were downloaded from the archives of the Wildlife Conservation Society (available at <http://sedac.ciesin.columbia.edu/data/collection/wildareas-v2>). We extracted the mean HII values per 110 × 110 km grid cell (HUMAN, Table 1). Hence, a 110 × 110 km grid cell that is characterized by high human population density, large urban centres and/or agricultural activities will show a high mean HII, whereas those dominated by undisturbed and inaccessible habitats will show a low HII value.

Biogeographical region

We included a categorical variable to capture idiosyncratic regional effects on woodpecker species richness (REGION, Table 1). We used the region definition of Holt *et al.* (2013) and assigned each 110 × 110 km grid cell to one of seven biogeographical regions (Table 1). We then used REGION in a multi-predictor regression model to test for differences in woodpecker species richness amongst biogeographical regions whilst simultaneously accounting for present-day environmental conditions and paleo-climatic changes (see below).

Alternative predictor variables for current and past tree availability

To assess the sensitivity of our current and past tree availability measures (TREES, HistBIOME), we also calculated a number of alternative predictor variables for both categories. Four alternative variables of current tree availability described various proportions tree cover per grid cell, i.e. proportion of ≥ 50%, ≥ 60%, ≥ 70 or ≥ 80% tree cover (rather than using the mean percentage of tree cover, as in TREES). Similarly, 13 alternative variables were quantified for past tree availability, including time-integrated area of deep-time tree availability, continuous tree availability across all three time epochs (late Miocene, middle Pliocene and

LGM), tree availability in a specific epoch, or in the same way as HistBIOME (i.e. as temporal availability of suitable biomes in none, one, two or three epochs) but excluding savannah biomes (for details see Appendix S2).

Statistical analysis

In a first step, we included all 10 predictor variables (Table 1) in ordinary least square (OLS) multiple regression models to explain variation in species richness of woodpeckers worldwide (family Picidae). We run similar analyses for sub-family Picinae and tribes Melanerpini and Picini (Appendix S1). For all included variables, variance inflation factors (VIF) were < 10 , indicating acceptable levels of collinearity. A stepwise, backward model selection based on the Akaike information criteria (AIC) (Burnham & Anderson, 2002) further indicated that the model with all 10 predictor variables was the most parsimonious model. We therefore used all 10 predictor variables in each multiple regression model.

To test for spatial autocorrelation, we calculated Moran's I (using the four nearest neighbours) for the residuals of the OLS models. Since Moran's I values of model residuals were statistically significant, we fitted spatial simultaneous autoregressive (SAR) models to account for residual autocorrelation. We used the SAR error model (Kissling & Carl, 2008) with a spatial weights matrix defined by the four nearest neighbours of each cell ($k = 4$) and a row-standardizing scheme. Because of the computational intractability of applying SAR models to large datasets (i.e. with > 7000 – 8000 grid cells) we used a bootstrapping approach where 10% of the sample size (i.e. 734–830 grid cells) were randomly subsampled 100 times (following Kissling *et al.*, 2012a). We then calculated mean values of coefficients and other model criteria across the 100 bootstrap samples. More details and sensitivity analyses of this bootstrapping approach are found in the Appendix S2 of Kissling *et al.* (2012a).

In all statistical models, we \log_{10} -transformed the response variable (species richness) to improve normality of the residuals. We further \log -transformed TOPO and PREC, and square-root-transformed TREES and PREC SEAS. We also used a nonparametric curve fitter (lowess) to explore nonlinearity in the relationships between predictors and the response. However, in the final regression models no polynomial terms were used. All continuous variables were scaled to a mean of zero and variance of 1 before the analysis to make model coefficients comparable. For both OLS and SAR models, we report the R^2 values (i.e. variance explained by the environmental predictor variables, referred to as R^2_{ENV}), the AIC values and the Moran's I values. For the SAR models, we additionally report the R^2_{FULL} which reflects the variation explained by the full SAR model (including both environment and space) (Kissling & Carl, 2008). All SAR coefficients, R^2_{PRED} , R^2_{FULL} , AIC and Moran's I are mean values across the 100 bootstrap samples (see above).

In a second step, we used structural equation models (SEMs) to test for direct and indirect effects of predictor

variables (Grace, 2006). Similar to previous macroecological implementations of SEMs (e.g. Kissling *et al.*, 2007, 2008; Sandom *et al.*, 2013; Zhang *et al.*, 2013; Ferger *et al.*, 2014), we constructed a SEM with paths from all predictor variables to both TREES and woodpecker species richness (only family Picidae) as well a path between TREES and woodpecker species richness. Direct effects are reflected by the standardized partial regression coefficient of paths between a predictor variable and a response variable (here TREES or woodpecker species richness) whereas indirect effects correspond to paths that go from an abiotic variable through TREES to woodpecker species richness. To explore the influence of spatial autocorrelation on inference from SEMs, we recalculated the standardized partial regression coefficients by using SAR error models with either TREES or woodpecker species richness as response variable (compare Kissling *et al.*, 2008). We implemented a similar bootstrapping approach as above and calculated the mean values across the 100 bootstrap samples. Beyond the global SEM we further explored regional variation by implementing separate SEMs for each biogeographical region. We followed the region classification from Holt *et al.* (2013) and assigned each grid cell to one of these regions. For the regional SEMs, no bootstrapping approach was needed because sample sizes (number of grid cells) were always < 2500 .

Statistical analyses were performed with the R SOFTWARE 3.2.2 (The R Foundation for Statistical Computing, <https://www.r-project.org/>) and RSTUDIO 0.99.902 (RStudio Inc., <https://www.rstudio.com/>). Spatial and SEM analyses were implemented with the R packages 'spdep' 0.5-74 (R. Bivand, <https://cran.r-project.org/web/packages/spdep/index.html>) and 'semPlot' 1.0.1 (S. Epskamp, <https://cran.r-project.org/web/packages/semPlot/semPlot.pdf>).

RESULTS

Woodpecker species richness

Species richness of woodpeckers (family Picidae) peaked in tropical and subtropical South America and Southeast Asia, with localized peaks in Afromontane areas (Fig. 1). These hotspots of species richness were also reflected in the sub-family Picinae and the tribe Picini (Appendix S1, Fig. S1-1). However, the tribe Melanerpini contributed noticeably to woodpecker diversity at high latitudes, especially in the coniferous forest biome of North America and in two areas in the Eastern and Western Palaearctic (Appendix S1, Fig. S1-1). The tribe Melanerpini further contributes to the high woodpecker diversity in the Sino-Himalayan mountains, along the western rift valley of Africa and in the tropical Andes (Appendix S1, Fig. S1-1).

Alternative predictor variables for current and past tree availability

We compared the variable of current tree availability (TREES) with four alternative measures, and the variable of

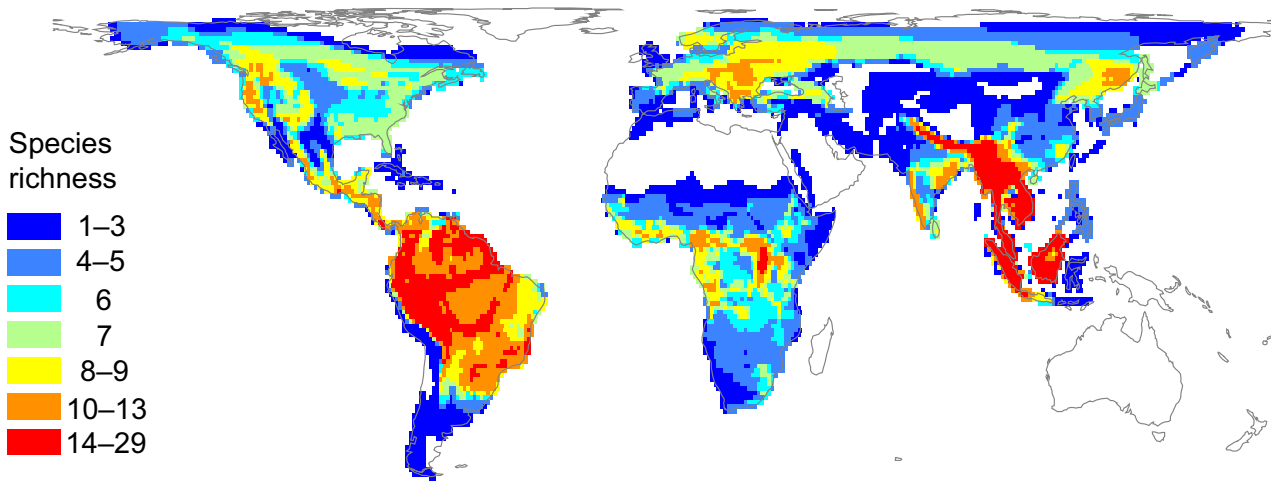


Figure 1 Global geographical variation in species richness of woodpeckers (family Picidae). Blue colours indicate areas with low species richness and red colours high species richness. Grey lines outline land areas. Data are shown with Behrmann projection, in a 110×110 km grid cell resolution (equivalent to $1^\circ \times 1^\circ$ at equator) using quantile classification.

past tree availability (HistBIOME) with 13 alternative measures (see Appendix S2). Spearman rank correlations between these and species richness revealed that TREES showed the strongest correlation (mean $r = 0.273$, $n = 4$ woodpecker groups) amongst all current tree availability measures (Table S2-1 in Appendix S2). Similarly, the best past tree availability measure was HistBIOME (mean $R^2 = 0.141$, $n = 4$ woodpecker groups, Table S2-2 in Appendix S2). Below, we therefore used TREES and HistBIOME in the multi-predictor models to test the biotic association hypothesis.

Effects of tree availability

In both OLS and SAR models, TREES together with PREC were the most important predictor variables to explain woodpecker species richness in the family Picidae (Table 2). Both predictor variables showed a positive relationship with species richness (Fig. 2), suggesting that more woodpecker species are found in areas with high percentage of tree canopy cover and high precipitation. Similar results were obtained for the sub-family Picinae and the tribes Melanerpini and Picini (Appendix S1, Table S1-1). The only important differences were that TEMP was a key predictor for the predominantly tropical tribe Picini, and TOPO a consistent but weak predictor for the tribe Melanerpini (Appendix S1, Table S1-1). The global SEM for the family Picidae also supported the idea that TREES has a strong direct effect on woodpecker diversity (std. coef. = 0.409; Fig. 3a). The effect was similar in strength to the direct effect of PREC, but all other predictor variables showed considerably smaller direct effects on woodpecker species richness (std. coef. ≤ 0.071 ; Fig. 3a). The regional SEMs revealed that TREES had a particularly strong effect (std. coef. > 0.5) on woodpecker species richness in the Nearctic, Palearctic and the Saharo-Arabian region (Fig. 3b). In other regions, the TREES effect

was less pronounced (std. coef. < 0.3 ; Fig. 3b). There was no apparent relationship between the regional effect of TREES in the global SEM (Fig. 3b) and the mean or range of TREES values in a particular region (results not shown). Overall, the results supported the hypothesis that current tree availability is an important predictor variable to explain global woodpecker diversity ('biotic association hypothesis').

Past tree availability (HistBIOME) showed a statistically significant effect in the OLS models for the family Picidae (Table 2) as well as for the sub-family Picinae and the tribes Melanerpini and Picini (Appendix S1, Table S1-1). In particular, a higher species richness of woodpeckers was related to areas that had tree habitats available over 2–3 epochs compared to areas without deep-time availability of tree habitats. However, the effect of HistBIOME was not statistically significant in the SAR models although the strength of the coefficients of different time epochs was consistent with the non-spatial OLS models (Table 2, Appendix S1 Table S1-1).

Direct and indirect effects of climate

Amongst climatic variables, PREC was always amongst the most important predictors for all taxonomic woodpecker groups (Table 2, Appendix S1 Table S1-1), showing strong positive relationships with species richness (Fig. 2). TEMP only showed a strong positive relationship with species richness of the tribe Picini (Appendix S1 Table S1-1). The global SEM for the family Picidae revealed that PREC not only had a strong direct effect on woodpecker richness (std. coef. = 0.409; Fig. 3a), but also a strong indirect effect on woodpecker richness via TREES (indirect effect = $0.749 \times 0.409 = 0.306$; Fig. 3a). Other predictor variables also showed indirect effects on woodpecker richness via TREES that were at least similar in strength to their direct effects (Fig. 3a, Appendix S3 in Supporting Information). This supported the

Table 2 Coefficients from ordinary least squares (OLS) and sub-sampled spatial autoregressive (SAR) error models to explain global species richness of woodpeckers (family Picidae). All continuous variables were scaled before the analysis to make coefficients comparable. The two most important continuous predictor variables (with the highest coefficients) are highlighted with boldface type. R^2_{ENV} = variance explained by the environmental variables; R^2_{FULL} = variance explained of the environmental and spatial component (only SAR); Moran's I = Moran's I value to indicate residual spatial autocorrelation. The values for REGION and HistBIOME are relative to the categories 'Afrotropical' and 'Zero', respectively. Abbreviations of predictor variables are described in Table 1. Significance levels: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; NS, not significant.

Predictor variables	OLS	SAR
Intercept	-0.341***	-0.294 NS
TREES	0.391***	0.301***
HistBIOME		
One	-0.051 NS	0.009 NS
Two	0.118**	0.147 NS
Three	0.259***	0.221 NS
PREC	0.332***	0.308***
PREC SEAS	0.104***	-0.033 NS
TEMP	0.080***	0.171 NS
QUA TEMP	-0.024*	-0.017 NS
QUA PREC	0.021**	0.029 NS
TOPO	0.024**	0.053 NS
HUMAN	0.105***	0.069 NS
REGION		
Nearctic	0.519***	0.493 NS
Neotropical	0.358***	0.291 NS
Oriental	0.279***	0.017 NS
Palaeartic	0.236***	0.059 NS
Panamanian	-0.053 NS	0.053 NS
Saharo-Arabian	-0.575***	-0.481 NS
Sino-Japanese	-0.328***	-0.072 NS
R^2_{ENV}	0.656	0.621
R^2_{FULL}	-	0.806
Moran's I	0.777***	-0.021 NS

idea that climatic factors influence broad-scale woodpecker species richness indirectly via tree cover ('indirect climate effects hypothesis').

Direct and indirect effects of human influence

The global SEM for the family Picidae showed a weak, positive effect of HUMAN on woodpecker species richness (std. coef. = 0.071; Fig. 3a). However, this direct effect varied in magnitude and direction per biogeographical region (Fig. 4a). In the Afrotropical, Nearctic, Neotropical, Palaeartic and Sino-Japanese region the influence of humans on woodpecker species richness was positive, and particularly pronounced in the Northern hemisphere (Palaeartic and Nearctic; Fig. 4a). Instead, in the Oriental and Panamanian region the direct effect was negative (Fig. 4a). Interestingly, there was a negative effect of HUMAN on TREES (std. coef. = -0.177; Fig. 3a), suggesting a human-induced

reduction of current tree availability. This negative effect resulted in an overall negative indirect effect of HUMAN on woodpecker richness via TREES (indirect HUMAN effect: $-0.177 * 0.409 = -0.072$; Fig. 3a), indicating a decline in woodpecker richness because of human-induced habitat loss. The negative effect of HUMAN on TREES was consistently observed in all biogeographical regions except the Saharo-Arabian one (Fig. 4b).

DISCUSSION

We tested whether the close biotic association between woodpeckers and trees influences the global distribution of woodpecker species richness and found strong evidence that this is indeed the case. Current percentage of tree cover and annual precipitation were the most important predictor variables for woodpecker diversity. Moreover, climate (especially precipitation) and other non-climatic predictor variables showed pronounced effects on tree cover, thereby indirectly influencing woodpecker diversity. This was particularly true for human influence, which had a negative effect on tree availability and hence an indirect negative effect of woodpeckers. Thus, global species richness patterns of woodpeckers are primarily shaped by tree availability, often with indirect climatic and non-climatic effects via tree cover. These results exemplify how broad-scale diversity patterns can be primarily shaped by a biotic factor.

Tree availability

Current mean percentage tree cover (TREES) was a key predictor variable for all four taxonomic woodpecker groups. This result supported the 'biotic association hypothesis'. All taxonomic woodpecker groups showed positive relationships between species richness and TREES, indicating that more woodpecker species are found in areas with dense tree cover than in areas with sparse tree cover. Most woodpeckers prefer dense thickets or old-growth forest (Winkler & Christie, 2002). Especially forests with high amounts of dead wood and cavities for nesting or roosting are preferred (Cockle *et al.*, 2011; Nappi *et al.*, 2015). This can explain the positive trend with tree cover found in this study. The slightly less important role of TREES for the species richness of Picini may occur because of its distribution being largely limited to tropical rainforests. The distribution of this biome is primarily controlled by temperature and precipitation (Greve *et al.*, 2011).

Our results match current knowledge on woodpeckers and their close association with trees on which they depend for feeding and nesting. Although most woodpecker species prefer forest, others inhabit areas with sporadic tree cover (for example savanna, human settlements) or even arid regions with very scattered trees, where woodpeckers may be associated with columnar cacti, or feed on the ground (Winkler & Christie, 2002). Nevertheless, even the ground-foraging and ground-nesting Andean flicker (*Colaptes rupicola*), a species that is widely distributed in treeless habitats in the Andean

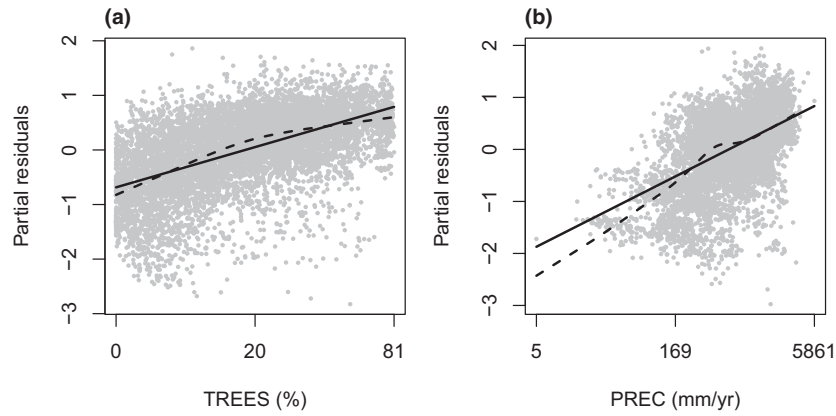
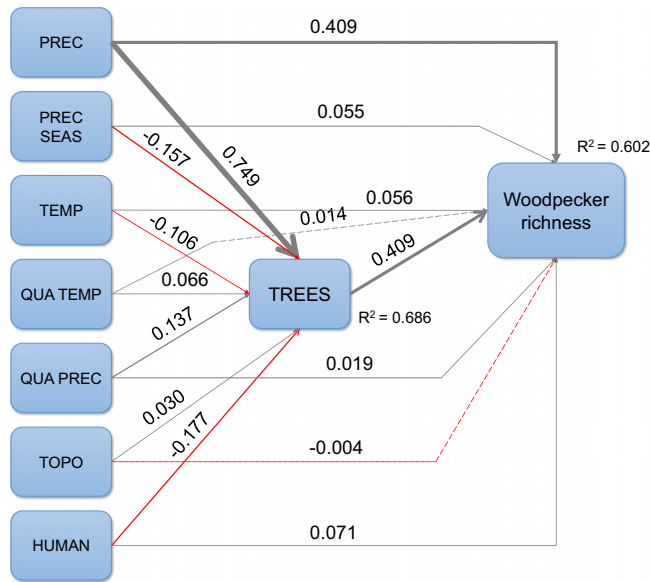


Figure 2 Partial residual plots showing the relationships between species richness of woodpeckers (family Picidae) and (a) annual precipitation (PREC) and (b) mean percentage tree cover (TREES). These relationships were derived from the ordinary least squares (OLS) model of Table 2. Plots show the effect of each predictor variable (PREC or TREES) when all other predictor variables have been statistically accounted for. Hence, these partial residual plots show the relation $r + b \cdot x$, where r represents the partial residuals of PREC or TREES and b is the regression coefficient estimate for PREC or TREES (x). Each dot represents one grid cell. Solid lines represent the fitted models and dotted lines represent a nonparametric curve fitter (lowess).

(a) Global SEM



(b) Regional effect of TREES

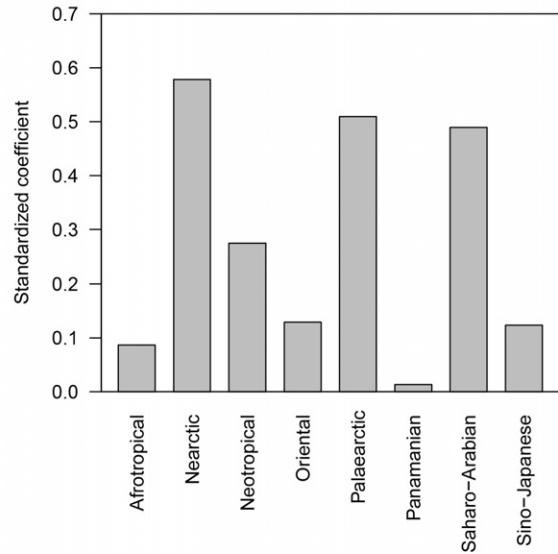


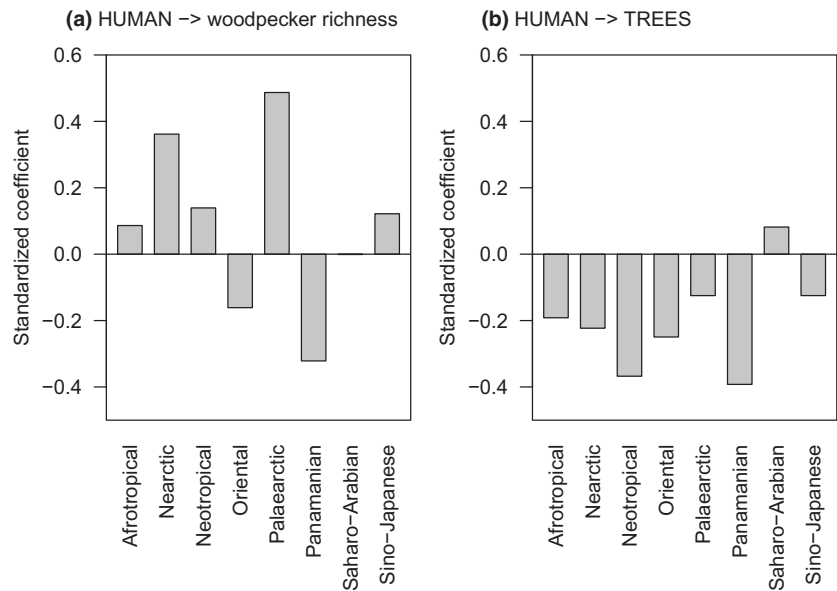
Figure 3 Effect of percentage tree canopy cover (TREES) on woodpecker species richness globally and within regions. (a) Global structural equation model (SEM) representing the effect of TREES on woodpecker species richness (family Picidae), and the direct and indirect effects of current climate (PREC, PREC SEAS, TEMP), past climate change (QUA TEMP, QUA PREC), topography (TOPO), and human influence (HUMAN) on both variables. Arrows (grey, positive; red, negative) represent standardized partial regression coefficients (direct effects), with line thickness being proportional to coefficient strength. (b) Regional variation in the effect of TREES on woodpecker species richness. Illustrated are the effects (i.e. standardized partial regression coefficients) of TREES on woodpecker species richness (family Picidae) from SEMs implemented separately for each biogeographical region. For details of the SEMs see Appendix S3.

highland, is most abundant in mosaic habitats of high-altitude woodlands where it sometimes excavates nest-holes in trees (Fjelds , 1991). In the mesic tropical forest biomes, high species diversity for Picidae, Picinae and Picini (and the tribe Campephilini, not shown separately) corresponds well with high productivity environments, which are characterized

by high precipitation. In the Afrotropics, many woody habitats are strongly seasonal, and woodpecker diversity strongly corresponds to precipitation seasonality in this region (Appendix S3 Fig. S3-2).

Past tree availability (HistBIOME) had a positive influence on woodpecker species richness, although the effect was not

Figure 4 Effects of human influence (HUMAN) on (a) woodpecker species richness and (b) percentage tree canopy cover (TREES). Results were obtained from structural equation models (SEM) similar to Fig. 3, but implemented separately for each biogeographical region. The standardized coefficients in (a) represent the direct effects of HUMAN on woodpecker species richness. The standardized coefficients in (b) represent the direct effects of HUMAN on TREES, and therefore indirectly the effect on woodpecker species richness. For details of the SEMs see Appendix S3.



statistically significant in the SAR models (Table 2, Appendix S1 Table S1-1). Persistent tree availability throughout deep geological time has been suggested to support high species richness (Jetz & Fine, 2012; Kissling *et al.*, 2012b). The specialized morphology and ecology of woodpeckers (Bock, 1999) together with the species diversity hotspots in tropical and subtropical forests (Fig. 1) suggests that woodpeckers should have benefitted from a stable climatic environment during deep-time history. The weak effect of habitat availability during the Neogene and the Quaternary could indicate that woodpeckers – many of which are good fliers (Winkler & Christie, 2002) – have effectively tracked the changing climate and the dramatic changes in expanding forest habitats, such as those after the LGM (Normand *et al.*, 2011). The lack of a strong effect of HistBIOME in the SAR models (compared to the OLS models) may, however, also in part reflect its coarse spatial structure because models accounting for spatial autocorrelation may shift the importance of variables towards more fine-scaled predictors (Diniz-Filho *et al.*, 2003).

Climate and other abiotic factors

We expected mostly indirect effects of climatic variables on the geographical variation in woodpecker species richness worldwide ('indirect climate effects hypothesis'). High availability of water and ambient energy is a common predictor of high species richness on broad spatial scales (Wright, 1983; Rahbek & Graves, 2001; Kissling *et al.*, 2012a). The influence of climate (especially precipitation) on woodpecker diversity is partly reflected in a direct effect of water-energy availability, maybe as an abiotic limitation on woodpeckers (Hawkins *et al.*, 2003). However, there is also a strong indirect effect possibly reflecting abiotic limitations on their food and habitat (Kissling *et al.*, 2008; Zhang *et al.*, 2013). Effects

of climate during the Quaternary (QUA PREC and QUA TEMP, Table 2 and Table S3-1 in Appendix S3) were weak, contrasting with evidence that long-term-stable climates support high species richness in other organism groups (Svenning & Skov, 2007; Kissling *et al.*, 2012c).

The weak effect of topographical heterogeneity (TOPO) on global woodpecker diversity contrasts with the expectation that habitat complexity increases avian species diversity by providing more niches (MacArthur, 1965; Rahbek & Graves, 2001; Zhang *et al.*, 2013; Stein *et al.*, 2014). This result may be caused by the strong influence of TREES, which may reduce the relative importance of other broad-scale habitat factors. However, species richness of the tribe Melanerpini peaked in mountainous parts of the world (Appendix S1, Fig. S1-1), and TOPO was a good predictor for this tribe. Other factors operating on local spatial scales (e.g. tree mortality related to outbreak of insect pests, local landslides, or avalanches) might also shape the species richness pattern of this group by maintaining a dynamic and disturbed habitat (Fjelds  & Irestedt, 2009). Melanerpini contains many small and moderate-sized species that are rather weak excavators, but can probe into dead and decaying wood when created by the mentioned processes for tree mortality (Bock, 1999; Martin *et al.*, 2004). Such fine-scaled factors could potentially contribute to the broad-scaled diversity pattern in Melanerpini.

Human influence

Human influence (HUMAN) as measured by the HII showed a positive (albeit weak) direct effect on woodpecker species richness, and a negative effect on tree availability, thereby indirectly reducing woodpecker diversity. Several cases of negative impacts from the human activities on woodpecker distributions and species richness have been reported, often

caused by the loss of large and old trees (Lindenmayer *et al.*, 2012) which are particularly important for woodpeckers (Mikusiński, 2006; Drapeau *et al.*, 2009). One of the most well-known examples is the extinction of the Ivory-billed Woodpecker (*Campephilus principalis*) because of loss of important habitat structures and tree cover (Mikusiński, 2006; Drapeau *et al.*, 2009). More generally, the decline of woodpecker species richness and abundance has been associated with intensive land use and pronounced levels of habitat loss and fragmentation (Mikusiński & Angelstam, 1998; Schmiegelow & Mönkkönen, 2002; Cockle *et al.*, 2011; Myczko *et al.*, 2014). For instance, across Europe woodpecker species richness is low in highly developed countries with a long history of intensive land use and a high degree of urbanization (Mikusiński & Angelstam, 1998). Our observed direct positive effect of HUMAN on woodpecker diversity is therefore rather counterintuitive and contrasts with our initial prediction. Although several woodpecker species live near and in human settlements and can benefit from human activities (Winkler & Christie, 2002; Morrison & Chapman, 2005), urbanization and intense land use are usually negatively correlated with species richness and abundance of woodpeckers (Myczko *et al.*, 2014). The reported direct positive effect of HUMAN on woodpecker diversity is, however, in line with the commonly reported positive relationship between human population density and high biodiversity (e.g. Luck, 2007). Such a spatial congruence between people and woodpecker species richness could be caused by the coarse resolution of our dataset (110 × 110 km grid cells), and we suggest more detailed studies of human impact on woodpecker distributions and abundances using high-resolution data across broad spatial extents.

CONCLUSIONS

Global patterns of species richness in woodpeckers are strongly shaped by current tree cover, supplemented by current climate. The strong influence of current tree availability on broad-scale woodpecker diversity is most likely caused by the narrow association between the morphologically and ecologically highly specialized woodpeckers and their woody habitats. We here provide a new example of a broad-scale species richness pattern shaped primarily by a biotic association (guild-habitat association). To fully understand what shapes species diversity on broad geographical scales, studies on groups with specific morphology and ecology are important, as they may show specific biotic needs for habitat or resource availability that could be overshadowed when analysing multiple groups combined.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Results for sub-family Picinae and tribes Melanerpini and Picini.

Appendix S2 Alternative predictor variables for current and past tree availability.

Appendix S3 Global and regional structural equation models.

BIOSKETCH

The author team is broadly interested in understanding the distribution of life on Earth, and has specific expertise in macro- and community ecology, biogeography, taxonomy and diversification of birds, ecoinformatics, physical geography and geospatial analyses.

Author contributions: J.-C.S., S.K.I. and W.D.K. conceived the ideas; W.D.K. collected the data; B.S., S.K.I. and W.D.K. analysed the data; and W.D.K. and S.K.I. wrote the manuscript with input from all the authors.

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