



Voskamp, A., Baker, D. J., Stephens, P. A., Valdes, P. J., & Willis, S. G. (2017). Global patterns in the divergence between phylogenetic diversity and species richness in terrestrial birds. Journal of Biogeography, 44(4), 709–721. DOI: 10.1111/jbi.12916

Publisher's PDF, also known as Version of record

Link to published version (if available): 10.1111/jbi.12916

Link to publication record in Explore Bristol Research PDF-document

This is the final published version of the article (version of record). It first appeared online via Wiley at http://onlinelibrary.wiley.com/doi/10.1111/jbi.12916/abstract. Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available: http://www.bristol.ac.uk/pure/about/ebr-terms.html

1	Journal of Biogeography
2	SUPPORTING INFORMATION
3	Global patterns in the divergence between phylogenetic diversity and species richness in
4	terrestrial birds
5	Alke Voskamp, David J Baker, Philip A Stephens, Paul J Valdes, Stephen G Willis
6	
7	Appendix S1
8	
9	S1a) Choice of environmental covariates to explain rPD (PD relative to that expected from Species
10	Richness)
11	We selected several potential correlates for phylogenetic diversity (PD) using literature. PD reflects
12	the evolutionary history of communities and can be used to detect the signature of important
13	historical processes (Losos & Glor, 2003). Macro-ecological changes such as mass migrations (e.g.
14	Great American Biotic Interchange; (Webb, 2006)) and extinctions can leave their signature in PD
15	(Mooers & Heard, 1997) and potentially lead to mismatches between PD and Species Richness (SR).
16	Areas of long-term climate stability, for instance, can serve as climate refugia (Keppel et al., 2012)
17	that might allow species to persist during periods of rapid climate change. Such regions have been
18	found to correlate with species endemism and sometimes contain very old species lineages (Fjeldså
19	& Lovette, 1997). The presence of those ancient linages can lead to an increased relative PD (rPD; PD
20	relative to that expected from SR) in these areas. We therefore included climate stability for each
21	grid cell over time as potential correlate for PD. We explored the mean climate stability since the last
22	glacial maximum (LGM) and the last interglacial period (LIG). The climate data were available on two
23	different timescales. Data since the LGM (present to 20,000 years ago) were available in steps of
24	2000 years. Data since the LIG period (present to 125,000 years ago) were available in intervals of
25	4000 years. To represent overall palaeo-climate stability in each cell, we used temperature and
26	precipitation data. We determined mean values of z-transformed temperature and precipitation

27 data in each relevant year. For each consecutive temporal transition, we estimated the mean 28 Euclidean distance between temperature and precipitation in bivariate space. The mean of these 29 Euclidean distances was our measure of overall palaeo-climatic stability. Additionally, we repeated 30 the above calculations for each cell but used the maximum Euclidean distance for the two variables, 31 since extreme events may drive extinction (Crowley & North, 1988; Parmesan, 2006). To estimate 32 stability in temperature and precipitation individually over time, we calculated the standard deviation within each cell for both variables for each of the LIG and LMG climatic datasets. We 33 34 considered temperature and precipitation separately, as well as jointly, as their importance may 35 differ regionally.

36 Mountain ranges have the potential to limit extinctions by providing a high diversity of 37 climates in a local area and, thus, providing localised climatic refugia. SR is especially strongly related 38 to altitudinal range in warmer climates, where it creates a steeper gradient on a small scale (Janzen, 39 1967; Ruggiero & Hawkins, 2008). Unsurprising, mountains harbour half of the currently recognised 40 biodiversity hotspots (Kohler & Maselli, 2009), although this might be partly an artefact, due to 41 lower human impacts in remote mountain regions (Joppa & Pfaff, 2009). Areas such as the northern 42 Andes still harbour ancient lineages of arctic species which have persisted since the late Pliocene or 43 early Pleistocene (Hughes & Eastwood, 2006) and could therefore potentially harbour a high Relative 44 PD. Species in mountain ranges at lower latitudes as the tropical Andes and the Afro and Sino 45 Himalayan montane regions, by contrast, are suggested to have undergone high rates of speciation 46 (Fjeldså et al., 2012). Relatively young mountain areas, such as the Himalayas, which are still rising a 47 centimetre per year (Bilham et al., 1997), and the central Andes, could contain recent species 48 radiations (McGuire et al., 2014). This could be reflected in a low Relative PD due to the occurrence 49 of a great variety of closely related species.

Ecological transitions between ecosystems can be important zones of differentiation and speciation caused by species adaptations (Smith *et al.*, 1997). Those transition zones are well known to harbour high species richness and biodiversity (Odum, 1971) and have been related to genetic diversity within taxa (Petit *et al.*, 2003). They can accommodate species from two or more realms,
each of which may have experienced very different evolutionary histories. Hence, such regions could
potentially contain high Relative PD. However, high speciation rates have also been recorded in
some ecological transition zones (Schilthuizen, 2000), which would result in a low Relative PD.

Habitat diversity was selected because SR has often been related to it. A study of South American breeding birds found that up to 51% percent of the variation in species richness could be explained by the number of ecosystems within a 1° grid cell (Rahbek & Graves 2001). We measured habitat richness as the number of habitats covering a minimum of 1% of a cell's area, using the USGS vegetation cover data, which comprises 24 different habitat types (U.S. Geological Survey, 2012). We do expect habitat diversity to affect SR rather than PD.

64 S1b) Using a subset of the 10,000 available trees to estimate PD per cell

Due to computational limitations we used of a subset of the 10,000 available trees. To determine 65 how many trees were necessary to produce a stable estimate of PD for a cell we undertook a pilot 66 67 analysis on 20 randomly chosen cells from across the world. The species richness for these cells 68 varied between 16 and 387 species per cell. We calculated PD values for each cell, using a random 69 subset of 1000 trees (Rubolini et al., 2015) out of the 10,000 phylogenetic trees from Jetz et al. 70 (2012). We then calculated the change in the coefficient of variance of PD values per cell as more 71 trees were added. We determined that using 200 of 1000 trees resulted in a coefficient of variance 72 below 0.005 for 90% of the cells, i.e. the precision in PD increased to only a small extent if more than 73 200 trees were considered. Therefore, we subsequently calculated mean PD for all cells using 200 74 randomly chosen trees from the 10,000 available trees (Figure S1).



75

Figure S1: The coefficient of variation (for 20 randomly chosen grid cells) for PD plotted against the
number of trees used to calculate PD. The black line indicates the coefficient of variation threshold
of 0.005. Coloured lines and points represent data for individual cells. Cells had a SR between 16 and
219 species.

81 S1 c) Alternative modelling method to investigate the relationship between SR and PD

82 To analyse the relationship between species richness (SR) and phylogenetic diversity (PD) we used a 83 locally weighted regression (LOESS). The method was chosen to make the results of this study 84 comparable to previously published similar work (Fritz & Rahbek, 2012). It is assumed to be "akin to 85 using the global relationship between species richness and phylogenetic diversity as a simple null 86 model, in order to account for sampling effects arising from different levels of species richness 87 among grid cells" (Fritz & Rahbek, 2012). Using this method it is difficult to disentangle potential real 88 effects from sampling effects and there for the assumption that the modelled association reflects a 89 null relationship could be untrue. The given rPD value for a grid cell is always relative to the 90 surrounding values within the window of the LOESS regression. To double check the pattern of the 91 residuals of the LOESS regression, we have split the data into five blocks based on their SR. We have fitted a generalized (Michaelis- Menten) saturating curve to a random data sample (n=1000) of each 92 93 of the blocks and then predicted to the whole dataset. We repeated this process 50 times, taking 94 new random samples each time. We then took the average residual value from the fitted curve for 95 each grid cell. This gives us an average residual value for each grid cell that is not relative to only 96 those grid cells with similar SR values but the whole dataset. We then compared the residuals of the 97 LOESS regression (Figure S3) and the average residuals from the predictions of the generalized 98 saturating curve (Figure S2).



Figure S2: The residuals of the generalized (Michaelis- Menten) saturating curve. Red indicating
areas of unusually high PD given the SR and blue indicating unusually low PD given the SR.



116 *Figure S3:* The residuals of the LOESS regression. Red indicating areas of unusually high PD given the

117 SR and blue indicating unusually low PD given the SR.

119 S1d) Selecting the climate variable for the global and the realm model

120 Several climate variables were highly correlated (Pearsons' correlation, r > 0.70), so they were not 121 used in combination to explain PD. Instead, we first sequentially produced models of PD including all 122 potential response variables, but only one of the climate variables each time. For each combination 123 of model explanators (i.e. each with a different climate variable) we used a model selection 124 approach (Burnham & Anderson, 2002; Burnham et al., 2011), calculating the mean AIC across a 1000 random subsamples (using the AICcmodavg package in R; (Mazerolle, 2014). The random 125 126 samples were drawn using the blocking method described in supplementary material S1e. The 127 climate variable contained in the model set that had the lowest mean AIC were used for all 128 subsequent modelling.

129 S1e) Blocking method used to draw sub samples for the models

To minimise potential effects of spatial autocorrelation in analyses of PD, we used a blocking method that divided the globe into 36 sub-blocks containing an equal number of cells. The 36 sub-blocks were divided into two groups in a checkerboard pattern (*Figure S4*). For modelling, we repeatedly drew random subsets of ten percent of the grid cells from each block, using blocks from only one of the two checkerboard groups each time (datasets were drawn equally from the two checkerboard groups). This resulted in approximately 1700 randomly selected cells being drawn broadly from across the globe, for each iteration of the global model.





138 *Figure S4:* The 36 blocks across three latitudinal bands used for data subsampling – see methods.



140 *S1f)* Selecting variables for the final model

- 141 After selecting the best climate variable the full model was run over 1000 randomly selected subsets
- and only those variables which were consistently in the best model were kept for the final model
- 143 (Figure S5)



Figure S5: The mean coefficients (+/- 95% confidence intervals) of the full global model including: habitat diversity, neighbouring realm distance, altitudinal range, and mean climate stability (over 125 ka). Numbers alongside points indicate how often each variable was in the best model across 1000 randomly selected subsets of data. SR has been excluded from the graph to show the coefficients of the other variables more distinct.

150

151 *S1g*) *Critical discussion of the used phylogeny*

152 The phylogeny by Jetz et al. (2012) has been focus of academic discussion due to the methods used to compose it. Using a previously defined backbone (which included 158 major bird clades in the 153 154 case of the backbone based on Hacket et al. (2008) that we used) to define the tree's outline might 155 result in restricted variation in higher order relatedness between avian species. It is possible that 156 avian evolution might be better described by another tree (Ricklefs & Pagel, 2012), and amendments 157 to phylogenetic trees are frequently proposed. Furthermore, the uncertainty around estimating 158 branch length, inferred from time-dated trees (Venditti et al., 2010), can introduce additional bias 159 (Ricklefs & Pagel, 2012). Spatial differences in the degree to which bird populations are distinguished 160 at the species level contribute another potential source of uncertainty. Areas such as North America 161 and Europe, with finely distinguished populations, may contain artefactually inflated species 162 diversification compared to areas with less resolved populations (Ricklefs & Pagel, 2012). All three of 163 these sources of uncertainty could affect the total branch length calculated for a community and, 164 therefore, affect the observed pattern of avian PD.

166 *S1h*) Ongoing amendments to the avian taxonomy

167 Research in the field of avian taxonomy is ongoing, and the rapid advances are demonstrated through recent amendments. For instance, the recently published genomes of 48 species 168 169 representing all Neoaves by Jarvis et al. (2014), resulted in a rearrangement of some of the early 170 branches in the tree of life. Since then, Prum et al. (2015) have published a comprehensive 171 phylogeny, based on more species (198) but sampling only genetic regions rather than whole 172 genomes. The latter contradicts some of Jarvis et al.'s (2014) findings, as with, for example, the 173 splitting of Neoaves into five rather than two groups. Advances are also continuously made on 174 subsets of the avian phylogenetic tree (e.g. Rocha et al. (2015)). Such work will inevitably lead to a 175 more accurate tree of all living birds, which will refine the global geographic patterns of avian PD and 176 rPD we observe. The backbone that we used in this study (Hackett et al. 2008) is broadly similar to 177 the most recent phylogeny of Prum et al. (2015) for terrestrial birds (our focal species). Moreover, 178 among the many possible trees that the phylogeny of Jetz (2012) produces, variance in PD resulting 179 from applying different potential trees was small (Figure S6 Appendix S1i).

181 S1i) Variance among the 200 phylogenetic trees sampled per grid cell

- 182 We explored the variance around the derived PD values from the 200 randomly chosen phylogenetic
- trees per cell. Only 5% of the grid cells have a coefficient of variance of 0.06 or higher, these are
- 184 mainly located in areas with very low species richness.



- 185
- 186 *Figure S6:* The coefficient of variation for the mean PD derived from the 200 trees within each grid
- 187 cell. Dark blue indicating cells with a low coefficient of variation, light blue areas indicating a higher
- 188 coefficient of variation.

189 References

- Bilham, R., Larson, K. & Freymueller, J. (1997) GPS measurements of present-day convergence across
 the Nepal Himalaya. *Nature*, **386**, 61-64.
- Burnham, K., Anderson, D. & Huyvaert, K. (2011) AIC model selection and multimodel inference in
- behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, **65**, 23-35.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer, New York.
- Crowley, T.J. & North, G.R. (1988) Abrupt climate change and extinction events in earth history.
 Science, 240, 996-1002.
- Fjeldså, J. & Lovette, J. (1997) Geographical patterns of old and young species in African forest biota:
 the significance of specific montane areas as evolutionary centres. *Biodiversity & Conservation*, 6, 325-346.
- Fjeldså, J., Bowie, R.C.K. & Rahbek, C. (2012) The Role of mountain ranges in the diversification of
 birds. *The Annual Review of Ecology, Evolution and Systematics*, 43, 249-265.
- Fritz, S.A. & Rahbek, C. (2012) Global patterns of amphibian phylogenetic diversity. *Journal of Biogeography*, **39**, 1373-1382.
- 206 Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox,
- W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S.,
 Sheldon, F.H., Steadman, D.W., Witt, C.C. & Yuri, T. (2008) A Phylogenomic study of birds
 reveals their evolutionary history. *Science*, **320**, 1763-1768.
- Hughes, C. & Eastwood, R. (2006) Island radiation on a continental scale: exceptional rates of plant
 diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences*,
 103, 10334-10339.
- Janzen, D.H. (1967) Why mountain passes are higher in the tropics. *The American Naturalist*, **101**,

214 233-249.

- Jarvis, E.D., Mirarab, S., Aberer, A.J. et al. (2014) Whole-genome analyses resolve early branches in
 the tree of life of modern birds. *Science*, **346**, 1320-1331.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in
 space and time. *Nature*, **491**, 444-448.
- Joppa, L.N. & Pfaff, A. (2009) High and far: biases in the location of protected areas. *PLoS ONE*, 4, e8273.
- Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T.,
 Hopper, S.D. & Franklin, S.E. (2012) Refugia: identifying and understanding safe havens for

biodiversity under climate change. *Global Ecology and Biogeography*, **21**, 393-404.

- Kohler, T. & Maselli, D. (2009) Mountains and climate change: from understanding to action. In.
 Geographica Bernensia, Bern.
- Losos, J.B. & Glor, R.E. (2003) Phylogenetic comparative methods and the geography of speciation.
 Trends in Ecology & Evolution, **18**, 220-227.
- 228 Mazerolle, M.J. (2014) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c).
- Available at: http://CRAN.R-project.org/package=AICcmodavg (accessed 01.10. 2014).
- 230 McGuire, Jimmy A., Witt, Christopher C., Remsen Jr, J.V., Corl, A., Rabosky, Daniel L., Altshuler,
- Douglas L. & Dudley, R. (2014) Molecular phylogenetics and the diversification of
 hummingbirds. *Current Biology*, 24, 910-916.
- 233 Mooers, A.O. & Heard, S.B. (1997) *Infering evolutionary process from phylogenetic treeshape*.
 234 University of Chicago Press, Chicago, IL.
- 235 Odum, E.P. (1971) *Fundamentals of ecology*. Saunders, W.B., Philadelphia, PA.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review* of Ecology, Evolution, and Systematics, **37**, 637-669.
- Petit, R.J., Aguinagalde, I., de Beaulieu, J.-L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi,
- 239 S., Grivet, D., Lascoux, M., Mohanty, A., Müller-Starck, G., Demesure-Musch, B., Palmé, A.,

- 240 Martín, J.P., Rendell, S. & Vendramin, G.G. (2003) Glacial refugia: hotspots but not melting
 241 pots of genetic diversity. *Science*, **300**, 1563-1565.
- 242 Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M. & Lemmon, A.R. (2015)
- A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing.
 Nature, **526**, 569-573.
- Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness.
 Proceedings of the National Academy of Sciences, **98**, 4534-4539.
- 247 Ricklefs, R.E. & Pagel, M. (2012) Evolutionary biology: birds of a feather. *Nature*, **491**, 336-337.
- Rocha, T.C., Sequeira, F., Aleixo, A., Rêgo, P.S., Sampaio, I., Schneider, H. & Vallinoto, M. (2015)
 Molecular phylogeny and diversification of a widespread Neotropical rainforest bird group:
 the buff-throated woodcreeper complex, Xiphorhynchus guttatus/susurrans (Aves:
 Dendrocolaptidae). *Molecular Phylogenetics and Evolution*, **85**, 131-140.
- Rubolini, D., Liker, A., Garamszegi, L.Z., Moeller, A.P. & Saino, N. (2015) Using the BirdTree. org
 website to obtain robust phylogenies for avian comparative studies: a primer. In. *Current Zoology*, **61**, 959–965.
- Ruggiero, A. & Hawkins, B.A. (2008) Why do mountains support so many species of birds? *Ecography*, **31**, 306-315.
- 257 Schilthuizen, M. (2000) Ecotone: speciation-prone. *Trends in Ecology & Evolution*, **15**, 130-131.
- Smith, T.B., Wayne, R.K., Girman, D.J. & Bruford, M.W. (1997) A Role for ecotones in generating
 rainforest biodiversity. *Science*, **276**, 1855-1857.
- U.S. Geological Survey (2012) *Global land cover (GlobCover)*, Land Processes Distributed Active
 Archive Center (LP DAAC), located at USGS/EROS, Sioux Falls, SD. Available at:
 <u>http://lpdaac.usgs.gov</u>.
- Venditti, C., Meade, A. & Pagel, M. (2010) Phylogenies reveal new interpretation of speciation and
 the Red Queen. *Nature*, 463, 349-352.

Webb, S.D. (2006) The great american biotic interchange: patterns and processes. *Annals of the Missouri Botanical Garden*, 93, 245-257Crowley, T.J. & North, G.R. (1988) Abrupt Climate
 Change and Extinction Events in Earth History. *Science*, 240, 996-1002.