1   *Original Article*

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3   *Running header: Global patterns and drivers of avian phylogenetic diversity*

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5   **Global patterns in the divergence between phylogenetic diversity and species richness in**

6   **terrestrial birds**

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Abstract

Aim: The conservation value of sites is often based on species richness (SR). However, metrics of phylogenetic diversity (PD) reflect a community's evolutionary potential and reveal the potential for additional conservation value above that based purely on SR. Although PD is typically correlated with SR, localized differences in this relationship have been found in different taxa. Here, we explore geographic variation in global avian PD. We identify where PD is higher or lower than expected (from SR) and explore correlates of those differences, to find communities with high irreplaceability, in terms of the uniqueness of evolutionary histories.

Location: Global terrestrial

Methods: Using comprehensive avian phylogenies and global distribution data for all extant birds, we calculated SR and Faith's PD, a widely applied measure of community PD, across the terrestrial world. We modelled the relationship between avian PD for terrestrial birds and its potential environmental correlates. Analyses were conducted at a global scale and also for individual biogeographic realms. Potential explanatory variables of PD included SR, long-term climate stability, climatic diversity (using altitudinal range as a proxy), habitat diversity and proximity to neighbouring realms.

Results: We identified areas of high and low relative PD (rPD; PD relative to that expected given SR). Areas of high rPD were associated with deserts and islands, whilst areas of low rPD were associated with historical glaciation. Our results suggest that rPD is correlated with different environmental variables in different parts of the world.

Main conclusion: There is geographic variation in avian rPD, much of which can be explained by putative drivers. However, the importance of these drivers shows pronounced regional variation. Moreover, the variation in avian rPD differs substantially from patterns found for mammals and amphibians. We suggest that PD adds additional insights about the irreplaceability of communities to conventional metrics of biodiversity based on SR, and could be usefully included in assessments of site valuation and prioritisation.

48   **Keywords:** birds, phylogenetic diversity, conservation, Faith's PD, global species richness,

49   biodiversity measures

50   **Introduction**

51   Rapid losses of biodiversity have occurred across the globe over recent decades, driven primarily by

52   human modification of the environment and increasing demand for natural resources (Vitousek *et*

53   *al.*, 1997; Butchart *et al.*, 2010; Cardinale *et al.*, 2012). Estimates of the current rate of species

54   extinctions are 1000 to 10,000 times higher than background levels, and this is consistent with

55   previous mass extinction events (Leaky & Lewin, 1992; Mace *et al.*, 2000; Barnosky *et al.*, 2011). The

56   loss of biodiversity is likely to have profound effects on ecosystem functioning (Loreau *et al.*, 2001),

57   reducing the intrinsic resilience of these systems to environmental change (Peterson *et al.*, 1998;

58   Chapin III *et al.*, 2000), and affecting ecosystem processes and the provision of ecosystem services

59   (Tilman *et al.*, 2006; Worm *et al.*, 2006). Consequently, preventing the loss of biodiversity is a global

60   priority (Rands *et al.*, 2010).

61   Conservation efforts *in situ* usually focus on the preservation of species and, consequently,

62   species richness (SR) is frequently used as the metric of biodiversity for assessing spatial

63   conservation priorities (Gaston, 1996; Gotelli & Colwell, 2001; Fuller *et al.*, 2010). SR, however, is

64   driven largely by common and widespread species, and thus, conservation prioritisations based on

65   this metric will often fail to capture the features of biodiversity that require the greatest

66   conservation focus (Brooks *et al.*, 2006). To address this concern, metrics have been developed that

67   quantify various aspects of species' irreplaceability; such metrics include the number of endemic

68   species or the taxonomic uniqueness of species in a community (Brooks et al. 2006). These metrics

69   aim to better account for the conservation value of individual species based on rarity or their unique

70   evolutionary history (May, 1990; Vane-Wright *et al.*, 1991). While irreplaceability metrics have

71   theoretical appeal, it has often proven difficult to quantify these metrics, in large part due to

72   limitations with data, including incomplete species inventories and lack of robust phylogenies.

73   However, for many of the major taxonomic groups (e.g. birds, mammals), distribution and

74 phylogenetic data have become more widely available, leading to irreplaceability metrics being

75 estimated and used more readily in conservation prioritisations (Heard & Mooers, 2000; Purvis *et al.*,

76 2000; Isaac *et al.*, 2007).

77 Phylogenetic diversity (PD) is a measure of the evolutionary relationship between species

78 (Hardy & Senterre, 2007) and provides a metric of biodiversity that accounts for evolutionary

79 distances between co-occurring species (Crozier, 1997). Thus, PD can be used to quantify the

80 taxonomic uniqueness of species in a community and to assess irreplaceability in terms of

81 evolutionary history, functional diversity (Flynn *et al.*, 2011) and evolutionary potential (Faith, 1992;

82 Forest *et al.*, 2007). Such irreplaceability metrics might add value over SR metrics when considered

83 in conservation strategies (Isaac *et al.*, 2007; Isaac *et al.*, 2012). Under the assumption that closely

84 related species have a similar evolutionary potential, but more distantly related species differ more

85 in their potential, a community with high PD has a higher chance of containing a subset of species

86 with greater evolutionary potential (Winter *et al.*, 2012). Therefore, a community with high PD might

87 be considered to have a greater potential to be robust to future environmental changes (Faith,

88 1992).

89 Patterns of SR and PD tend to be highly correlated across broad spatial scales and earlier

90 studies suggest that SR is, in general, an adequate surrogate for PD (Rodrigues *et al.*, 2005). Yet

91 localised differences between SR and PD, as well as related measures such as phylogenetic

92 endemism and functional diversity, have been found across a range of taxa (Davies *et al.*, 2008;

93 Davies & Buckley, 2011; Fritz & Rahbek, 2012). A global study of amphibians found mismatches

94 between SR and PD, with lower PD than expected (given SR) on remote islands and archipelagos, as

95 well as in regions that have been long isolated, such as Madagascar and Australia (Fritz & Rahbek,

96 2012). For mammals, lower than expected PD has been identified for some mountain ranges and

97 remote islands, whereas higher than expected PD was found in Sub-Saharan Africa and parts of the

98 Indian sub-continent (Davies & Buckley, 2011).

99   Observed localized differences between SR and PD could occur for various reasons. Unlike

100   SR patterns, which have been a central topic throughout the history of ecology (Wallace, 1878;

101   Stevens, 1989; Palmer, 1994), exploring patterns of PD has become possible only very recently, due

102   to the availability of comprehensive phylogenies (Cavender-Bares *et al.*, 2009; Roquet *et al.*, 2013).

103   Consequently, the drivers of these PD patterns remain largely unknown. Important historical

104   processes (Losos & Glor, 2003), as well as macro-ecological changes such as mass migrations (e.g.

105   Great American Biotic Interchange; Webb 2006) and extinctions, can leave a signature in PD (Mooers

106   & Heard, 1997). Additionally, environmental factors that could affect PD (Appendix S1a) include

107   areas of long-term climate stability and areas with a steep altitudinal gradient, both of which could

108   lead to areas acting as climate refugia (Keppel *et al.*, 2012). Ecological transition zones, harbouring

109   communities with great genetic diversity (Petit *et al.*, 2003) could also have higher PD, due to the

110   occurrence of species adapted to different ecological zones within one community. Habitat diversity,

111   which is known to affect SR (Rahbek & Graves, 2001) and to drive diversification (Emerson & Kolm,

112   2005), could also affect PD. Identifying regions where PD is higher or lower than would be expected

113   given SR (PD relative to the SR within the area, hereafter termed relative PD, or rPD), and exploring

114   environmental correlates of rPD, can help identify communities with high irreplaceability, when

115   assessed in terms of the uniqueness of evolutionary histories.

116   Here, for the first time, we: (1) map geographic variation in avian rPD and identify those

117   areas characterised by particularly high or low values; and (2) explore potential environmental

118   correlates of PD, in addition to SR, that might indicate where the macroecological processes of

119   dispersal and diversification differ from the global average (Fritz & Rahbek, 2012). We develop

120   models of PD on a global scale, as well as for individual biological realms. We hypothesise that high

121   rPD should be favoured by relatively stable climates, but that habitat diversity will principally affect

122   SR. High rPD might also arise from opportunities for community interchange (for example at

123   boundaries between realms), or by relative isolation (promoting the persistence of ancient lineages).

124   Conversely, we expect lower rPD on more recently formed land-masses. We expect the drivers of PD

125   to differ between individual biological realms, since many broad-scale, macroecological processes

126   differ between these geographic areas. We discuss the implications of our findings for conservation

127   prioritisation, highlighting differences between biodiversity metrics and between major taxonomic

128   groups.

129

130   **Materials and Methods**

131   *Species distribution data*

132   We estimated the extant species present in each grid cell across the global terrestrial land mass

133   using global breeding range maps for 9227 bird species (BirdLife International & NatureServe, 2012).

134   Taxonomic differences between the species' range data and the avian phylogeny used (see below),

135   meant that 420 of the 9227 species were excluded, e.g. species might be recognized as one species

136   in the phylogeny but split into two separate species in the BirdLife taxonomy. Owing to our

137   terrestrial focus, a further 346 seabird species were also excluded. Range data were transferred onto

138   an equal area grid in Behrman projection with a cell size of 1° latitude by 1° longitude at 30°N and

139   30°S latitude (Orme *et al.*, 2005; Fritz & Rahbek, 2012; Huang *et al.*, 2012). An equal area grid

140   enables spatially unbiased comparisons among grid cells. A species was considered to occur in a cell

141   only if the species' range polygon and grid cell overlap was ≥ 10%, a threshold that prevents species

142   being represented in cells in which their occurrence is very limited. For 1287 species with ranges so

143   restricted that they never occur in at least 10% of any cell, their occurrences were derived from the

144   intersection of their range polygons with cells, without applying a 10% threshold. The gridded

145   species' range data were then used to determine species lists for each grid cell across the globe.

146   *Global phylogenetic diversity*

147   To derive PD, we used the first full phylogeny of extant birds (Jetz *et al.*, 2012). These phylogenetic

148   data are provided as 10,000 possible tree topologies in Newick tree format (Olsen, 1990). The

149   phylogenetic data are available based on two taxonomic backbones: those of Hackett *et al.* (2008)

150 and Ericson (Ericson *et al.*, 2006). Here we used the phylogeny based on the Hackett backbone,

151 which is the more recent higher-level avian topology available (Hackett *et al.*, 2008).

152   Several indices are available to measure PD but the most frequently used is Faith's PD

153 (Cadotte *et al.*, 2010). Faith's PD (hereafter just PD) summarises how much of the branching pattern

154 of a phylogenetic tree is represented in a community, by adding the branch lengths for all members

155 of the community (Faith, 1992). As such, it provides a summary measure of the phylogenetic

156 diversity of a community (Faith, 1992; Barker, 2002). For each terrestrial grid cell globally, we

157 calculated SR and PD. To aid the comparison of PD between cells, the root of the phylogenetic tree

158 was excluded and the tree was pruned, using the 'APE' package in R (Paradis *et al.*, 2004), to the

159 most recent common ancestor of the species within each cell (Faith, 1992). We calculated PD for all

160 terrestrial cells containing at least two species. Grid cells that contain only one species cannot

161 provide a minimum spanning path between two species, resulting in the exclusion of some cells in

162 the Saharan desert and around the poles (Faith, 1992; Barker, 2002). In total, we collected data on

163 avian PD from 17,363 terrestrial grid cells.

164   A pilot study (See Figure S1 in Supporting Information) showed that 200 randomly chosen

165 potential trees of the avian phylogeny (Jetz *et al.*, 2012) were adequate to reduce the coefficient of

166 variation (from the trees available in this phylogeny) of estimated PD, for individual cells, to below

167 0.005 for 90% of the test cells. Consequently, we estimated PD for all cells using a random selection

168 of 200 of the possible phylogenetic trees. Previous studies have used different methods to

169 investigate the relationship between PD and SR, including analysing the residuals of the modelled

170 relationship (Davies & Buckley, 2011; Fritz & Rahbek, 2012), or using a null model based on

171 randomized species assemblages, which are then compared to the empirical data; the latter having

172 been used only for studies on a smaller scale (Kluge & Kessler, 2011). Here, we used two approaches.

173 Firstly, we followed the methods of Fritz and Rahbek (2012) and modelled the relationship between

174 PD and SR using local regression with nonparametric smoothing techniques (Forest *et al.*, 2007),

175 utilising functions from the 'CAIC' package in R (Orme *et al.*, 2009). This allows us to compare our

176   results to previous studies on global patterns of PD that have used a similar approach but for other

177   taxa (Davies & Buckley, 2011; Fritz & Rahbek, 2012). To highlight areas with unusually high or low

178   rPD, we selected the cells with the top and bottom 5% of the residuals from the local regression

179   between PD and SR (Fritz & Rahbek, 2012).

180

181   Secondly, because when using a local regression with nonparametric smoothing techniques, the

182   residuals can be affected by the surrounding cells, i.e. the rPD value for a grid cell is always relative

183   to the surrounding values within the window of the local regression, which could mask important

184   general relationships, we used an alternative method (Appendix S1c) to check the robustness of the

185   observed patterns in rPD. We ordered the cells of the world by their SR values and divided them into

186   five equal-sized groups. We fitted a generalized (Michaelis-Menten) saturating curve to the PD and

187   SR data from a random data sample (n = 1000) drawn from each the five groups and then predicted

188   to the four left-out groups each time. The process was repeated 50 times, taking new random

189   samples each time. From these predictions we calculated the mean residual value from the fitted

190   generalized saturating curves for each grid cell. Unlike in the locally-weighted regression, the

191   resultant residual is relative to the whole dataset and not just to grid cells with similar SR values.

192   Although the patterns of the residuals from this alternative approach (See Figure S2 in Supporting

193   Information) are less pronounced than those of the locally-weighted regressions (See Figure S3 in

194   Supporting Information) and the transitions between areas of low and high residual are more

195   gradual, the overall pattern remains very similar. Consequently, and for simplicity, we display only

196   results from the locally weighted regression analysis in the main manuscript.

197   *Environmental correlates of rPD*

198   We assessed environmental characteristics that might be associated with geographic variation in

199   rPD. Specifically, we modelled the relationship between PD and SR, including additional covariates to

200   help explain divergence. These additional covariates were: the distance to the nearest neighbouring

201   realm, altitudinal range (considered as a proxy for within-cell climatic diversity), climate stability

202 since the Last Glacial Maximum (LGM, present to 20,000 years ago), climate stability since the last

203 interglacial period (LIG, present to 125,000 years ago), and habitat diversity (Appendix S1a). The

204 derivations of these covariates are described below.

205 We calculated the distance of each grid cell to the nearest neighbouring realm based on an

206 updated version of Wallace's zoogeographic regions of the world (Holt *et al.*, 2013). To calculate the

207 altitudinal range within each cell we used the 30 arc second (approx. 1 x 1 km) GMTED 2010 global

208 elevation data (U.S. Geological Survey, 2012a). Habitat diversity was measured as the number of

209 habitats covering a minimum of 1% of a cell's area, using the USGS vegetation cover data, which

210 comprises 24 different habitat types (U.S. Geological Survey, 2012).

211 Measures of temporal climate stability for two time periods (since the LGM, and since the

212 LIG) were based on modelled palaeo-climatic data (the production of which is detailed in Appendix

213 S1a). The palaeo-climate data were derived from a series of general circulation model (GCM) climate

214 simulations, performed using the HadCM3 version of the Hadley Centre Unified Model (Gordon *et*

215 *al.*, 2000; Pope *et al.*, 2000). Details of the model's configuration are given by Singarayer & Valdes

216 (2010), and the resultant climate data were made available by the Bristol Research Initiative for the

217 Global Environment (BRIDGE, http://www.bridge.bris.ac.uk/).

218 We extracted, as potential explanatory palaeoclimatic variables: (1) the stability of past

219 precipitation, (2) the stability of past temperature, and (3) a bivariate metric based on variation in

220 both of those variables. From these we calculated eight potential palaeoclimate environmental

221 covariates, including stability of: mean temperature, mean precipitation, mean bivariate climate and

222 maximum bivariate climate, for time since both LGM and LIG. We used the potential for maximum

223 values to explain PD because extreme events may drive extinctions (Crowley & North, 1988;

224 Parmesan, 2006). Following Dormann *et al.*, (2013), we avoided combinations of highly correlated

225 climate variables (Pearsons' correlation, $r > 0.70$). Specifically, we used a preliminary model selection

226 approach to select the climate stability variable with the most explanatory power (Appendix S1d),

227 such that no model contained more than one metric of climate stability. Following preliminary data

228   exploration, we included quadratic terms for SR, altitudinal range and climate stability variables, and

229   linear effects for the remaining variables in our models to estimate global PD.

230   To identify global drivers of PD, we fitted general linear models of global PD including all

231   valid combinations of environmental covariates and polynomial terms. The PD values were highly

232   spatially auto-correlated (Moran's I = 0.99), which can affect inference. To minimise the potential

233   impacts of spatial autocorrelation on inference, we designed a blocking method in which models of

234   global PD were built and tested using spatially disaggregated data (See Figure S4 in Supporting

235   Information). This approach substantially reduced the spatial autocorrelation (mean Moran's I across

236   random data subsets = 0.18; Table 1). Using this blocking method we fitted models to 1000 random

237   subsets of the data. In each case, we selected among all competing models using the 'MuMIn'

238   package in R (Bartoń, 2014). Inevitably, this resampling approach resulted in subtly different

239   variable selection for each random subset of data. To identify those parameters with robust and

240   repeatable influences on PD, we recorded the frequency with which individual environmental

241   covariates were selected in the top models across the 1000 subsets. We report the parameter values

242   for those covariates that were included in at least 95% of the top models (See Figure S5 in

243   Supporting Information). Parameters defined as robust by this method were used to predict PD for

244   all terrestrial cells globally.

245   To test whether environmental covariates relate to PD in different ways, or to differing

246   degrees, in individual biological realms, we produced models similar to the global models described

247   above but fitted instead to data from the individual realms. We considered only those realms with >

248   500 grid cells, to permit a blocking approach during model fitting. Eight realms satisfied this selection

249   criterion: the Afrotropical, Neotropical, Nearctic, Australian, Saharo-Arabian, Sino-Japanese, Oriental

250   and Palaearctic realms. Each of these realms was split into eight blocks, using the same method as

251   for the global model. Following the same approach as described above for the global data, we

252   identified the best model for each biological realm.

253   For each of the identified best models for the global scale and the individual biological

254   realms, we calculated McFadden's r^2 (McFadden, 1974; Beaujean, 2012) as a measure of the extent

255   to which the model with the lowest Akaike information criterion (AIC) value was an improvement

256   over an alternative model containing only SR. Finally, we compared the predictions of PD from the

257   global model with the predictions of the models based on the individual realms to assess whether

258   the improvement in predictions of PD based on combining predictions from models fitted to the

259   individual realms justifies the increase in complexity over the model fitted to the global data. To do

260   this, we compared the AIC (based on the least squares case, Burnham & Anderson, 2002, p.46) of

261   the global model to that of an amalgamation of the separate realm predictions, for the realms where

262   we could produce estimates using both methods.

263

264   **Results**

265   *Global patterns of SR, PD and rPD*

266   As expected, the correlation between SR (Fig. 1a) and PD (Fig. 1b) is very high for terrestrial bird

267   species across the globe (Fig. 2a; r^2 = 0.973). Nonetheless, the residuals of the LOESS regression have

268   a marked spatial pattern (Fig. 1c, 1d), with clusters of positive and negative residuals that indicate

269   divergence between SR and PD (Fig. 2b). Areas with the most negative rPD (i.e. where PD is lower

270   than expected given SR) include areas of high relief, such as the Himalayas and Andes, and also areas

271   of glacial coverage during the LGM, such as the northern Nearctic and Palaearctic. Extensive areas of

272   high rPD occur on isolated tropical islands including Madagascar and Sri Lanka, and in dryland areas

273   fringing the subtropics. The latter regions include the Sahelian edge of the Afrotropical realm, parts

274   of eastern Africa and central southern Africa, as well as northern Australia and the border between

275   India and Pakistan.

276   *Potential drivers of avian PD*

277　The best global model of avian PD included the variables SR, mean climate stability since the LIG and

278　altitudinal range, and explained 98% (r^2 = 0.982, Table 1, Table 2) of the variation in PD. This model

279　explained one third of the remaining variation in PD when compared to the global model including

280　only SR (r^2 = 0.973, Table 1).

281　　At a realm level, the climate variables included in the best model of PD differed among

282　realms (Table 2). Nonetheless, for all realms, besides the Australian and the Neotropical realm, the

283　best PD models included one of the LIG climate variables. Other variables (apart from SR and climatic

284　variables) included in the best realm models of PD were the distance to the nearest neighbouring

285　realm and altitudinal range, though combinations of variables in the best individual realm models

286　differed. For the Oriental and Saharo-Arabian realms, no additional drivers of PD could be identified

287　in addition to SR.

288　　Overall, the amalgamated realm level models described PD better than the global level

289　model (realm model AIC: 81420, global model AIC: 86716). The residuals of the realm level models

290　(Fig. 3b) have a considerably less pronounced pattern than the residuals of the global level model

291　suggesting that these models are able to explain considerably more of the divergence between PD

292　and SR than the global model (Fig. 3a).

293

294　**Discussion**

295　*Global patterns of avian rPD*

296　Our analyses show that macro-evolutionary processes have left a strong pattern in the phylogenetic

297　diversity of current avian assemblages. We have shown that there is clear spatial patterning in areas

298　where PD diverges from SR, and this suggests that biological and geological processes play a major

299　role in rPD. The spatial pattern observed here for birds differs markedly to those that have been

300　observed previously for other taxa (Davies *et al.*, 2008; Davies & Buckley, 2011; Fritz & Rahbek,

301　2012), indicating that these processes may operate differently across taxonomic groups. Areas of

302　low avian rPD occurred at high latitudes and in areas of high relief associated with the Andes and

303   Himalayan mountain ranges. Areas with particularly high rPD were distributed more widely and

304   include islands and isolated regions, such as Australia and Madagascar, as well as ecological

305   transition zones, such as the Sahel and parts of Central America.

306   We discuss our results in the context of the correlates of rPD identified in this study; the

307   relationship between avian, mammalian and amphibian rPD; the importance of refining our

308   understanding of rPD; and the potential implications for conservation.

309   *Potential drivers of avian PD*

310   As suggested by earlier studies (Rodrigues *et al.*, 2005; Davies & Buckley, 2011; Fritz & Rahbek,

311   2012), SR showed a high correlation with PD; however, additional variables explained much of the

312   remaining variation (rPD). As expected, the importance of the additional environmental variables

313   differed between the individual realms and, consequently, the individual realm models predicted

314   realm-level PD better than a single global model. Areas of very high or low rPD reveal information

315   about the underlying structures of the communities, and indicate if these are taxonomically

316   clustered or over dispersed (Rodrigues *et al.*, 2005; Forest *et al.*, 2007). Unusually high rPD, i.e. a

317   taxonomically over-dispersed assemblage in an area, especially when associated with low SR, can be

318   the result of the existence of old lineages, harbouring unique evolutionary information. These

319   lineages can result from a speciation process with little radiation, or from the extinction of other

320   species in the same clades (Rodrigues *et al.*, 2005). These old lineages occur more frequently in the

321   Neotropical and Afrotropical regions, which harbour large numbers of basal taxa (Wiens &

322   Donoghue, 2004; Hawkins *et al.*, 2006; Hawkins *et al.*, 2007). By contrast, unusually low rPD (i.e., a

323   taxonomically clustered assemblage) is more likely to occur in areas with more recent speciation

324   events (Davies & Buckley, 2011).

325   The environmental predictors tested here were expected, *a priori*, to be important based on

326   macroecological and biogeographic theory. For example, contact zones between realms could

327   positively affect the rPD, because dispersal events from different species pools in neighbouring

328   biogeographic realms into areas in the contact zone are likely to occur. We found that a large

329   proportion of the cells with a high rPD are located within contact regions between biomes, such as in

330   Sahelian Africa. Consequently, the distance to the nearest neighbouring realm was an important

331   driver of the rPD pattern in the Afrotropical realm.

332   Another likely predictor of low rPD that we considered *a priori* was climate stability. It was

333   selected because areas with unstable climates are likely to experience frequent local extinction

334   events, reducing the number of old lineages. The largest clusters of low rPD occur in the two large

335   northern-temperate realms, as well as in some mountain areas at lower latitudes, such as occur in

336   the Andes and the Himalayas. In the Nearctic and Palaearctic, the climatic stability since the LIG is

337   the most important explanatory variable of rPD. Low rPD in areas of climatic instability since the LIG

338   might reflect the impact of past glacial events, and result in a phylogenetically depauperate fauna

339   considering the SR in the area.

340   Altitudinal range was considered a potential driver of both high and low rPD, depending on

341   the age of the mountain range and the local climate stability. High rPD is likely to occur where

342   movement up or down the altitudinal gradient could act as a local buffer against climatic variation,

343   enabling persistence of lineages. Low rPD is likely to be found where mountain ranges are relatively

344   young and provide a centre for relatively recent speciation events. Previous studies have identified

345   mountain ranges as centres for speciation during the Pleistocene period (circa 2.5Ma to 12Ka)

346   (Fjeldså, 2012; Päckert *et al.*, 2012), although there is evidence that some of the younger mountain

347   ranges are approaching ecological saturation and species radiations are slowing down (Price *et al.*,

348   2014). We found greater support for altitudinal range being associated with low rPD, with areas of

349   low rPD in the relatively young Andes and Himalayan mountain ranges. The importance of altitudinal

350   range in explaining rPD in the Neotropical realm model, which contains the Andes, similarly suggests

351   that these mountain ranges may act as centres for recent speciation, resulting in low rPD despite

352   high endemism. Hence, the variables that best explained rPD in this study tend to fit with

353   contemporary evolutionary and geological understanding of how species have evolved and

354   persisted.

355   The only potential driver of avian PD that was not selected as important in any model was

356   contemporary habitat diversity. This might reflect that habitat diversity mainly drives patterns of SR

357   (Lack, 1969; Bazzaz, 1975). It might also arise because of the use of contemporary habitat diversity

358   data, which does not reflect long-term changes in habitat diversity that might have influenced the

359   current PD pattern.

360   Several of the larger biological realms span multiple ecosystems, such that variables

361   explaining rPD may not operate similarly across the entire area. As we only report variables that are

362   selected in most models, this could result in some important variables that operate in only part of a

363   realm being overlooked. For example, in the Oriental realm, only SR was consistently selected,

364   although long term temperature stability was selected in 76% of models explaining PD. We found

365   that adding this variable significantly improved PD prediction for the Indian subcontinent but not for

366   the rest of the Oriental realm. This suggests that, for some realms, variables influencing PD may be

367   operating over a finer scale than the realm and conducting analyses over smaller sub-regions could

368   highlight locally influential variables that are overlooked by our realm-level analysis.

369   *Mismatch of avian rPD with that of other taxa*

370   The rPD patterns found for birds are very different from those previously identified for amphibians

371   (Fritz & Rahbek, 2012) and mammals (Davies & Buckley, 2011; Safi *et al.*, 2011; Rosauer & Jetz,

372   2015). Strikingly, the patterns of highest and lowest rPD for birds are, to a large extent, the inverse

373   of those found for amphibians. In particular, for birds, areas of low rPD are often located in

374   extensive mainland areas and in mountainous areas such as the Himalayas and the Andes; for

375   amphibians these are areas of high rPD. For amphibians, islands and isolated areas such as Australia,

376   Madagascar, New Guinea and the Caribbean have been identified as having low rPD (Fritz & Rahbek,

377   2012), whereas for birds these tend to be regions of high rPD. Similarly, areas of high rPD for

378   amphibians in the Indo-Chinese realm are identified as regions of lower than expected PD for birds.

379   For birds and mammals, there are also areas where the two taxa show contrasting patterns of rPD.

380   This occurs in islands and isolated areas such as Australia and the Caribbean, as well as Central

381 America, with avian rPD being higher than mammal rPD. Areas such as the Sahel, parts of Eastern

382 and Southern Africa, and parts of the Indian subcontinent show a high rPD for both taxa.

383   Relatively few areas of the world have similarly high rPD for birds, mammals and

384 amphibians. Those that do include parts of South America which lie to the east of the Andes, the

385 Cameroon Highlands and parts of the Eastern Arc mountain range in Africa. Amphibians and birds

386 also both have high rPD in SE Brazil and parts of Indochina. However, outside of Amazonia, the most

387 remarkable thing about rPD patterns of these taxa is their lack of congruence. This may, in part, be a

388 result of the mobility of birds relative to mammals and amphibians, which could facilitate relatively

389 rapid recolonization of newly exposed mountain and arctic sites following glaciation events, and

390 increased colonisation of isolated island sites (Weir & Schluter, 2004). It could explain the different

391 observed patterns among taxa on islands and newly exposed sites, which often show very low rPD

392 for amphibians and mammal but not for birds.

393 *Improving our understanding of rPD*

394 Here, we try to explain rPD through consideration of contemporary niche diversity (current habitat

395 and climate diversity) and longer term climate stability. However, there are other potentially

396 important determinants of PD that we were unable to consider, including short duration extreme

397 events (climatic or tectonic), longer term habitat occurrence and persistence, and

398 isolation/connectivity due to landmass movements. One of our putative niche measures, elevation

399 range (considered a proxy for contemporary climate diversity), may have operated more as a

400 tectonic proxy in our models, by highlighting the youngest land on mainland landmasses, such as the

401 Himalayas and Andes. Assessing directly the role of these longer-term landmass and habitat changes

402 and the impacts of extreme events was not possible in the current study. Future studies of PD would

403 undoubtedly benefit from the inclusion of such measures, should data become available.

404 The phylogeny of Jetz *et al.* (2012) is the best full avian phylogeny currently available. Nevertheless,

405 it has been the focus of academic discussion as a result of the methods used to construct the

406 phylogenetic tree (Ricklefs & Pagel, 2012). Sources of uncertainty include the use of a previously

407   defined backbone, the estimation of branch length by inference from time-dated trees (Venditti *et*

408   *al.*, 2010), as well as local differences in the level to which populations are resolved (see Appendix

409   S1g for a more detailed discussion of the potential sources of uncertainty).

410   Amendments to the avian taxonomy are ongoing, and suggested alterations to the

411   phylogeny of living birds further our understanding of avian phylogenetic history (Appendix S1h).

412   Recent amendments demonstrate the rapid advances in this field (Jarvis *et al.* 2014, Prum *et al.*

413   2015, Rocha *et al*. 2015). Repeating our analyses with alternative full avian phylogenies, when

414   available, will determine how robust the patterns identified here are to updates in taxonomy.

415   Our study gives a first indication of the variables that drive avian rPD patterns on a large

416   scale in different ecoregions of the world, and identifies areas where macro-ecological processes are

417   likely to have affected the underlying structures of species in a community, resulting in a mismatch

418   between SR and PD. Future work could focus on understanding the causes of pattern in rPD at a

419   finer scale. Exploring beta diversity (Whittaker, 1960) across areas with a steep rPD gradient could

420   aid our understanding of how changing species compositions affect rPD, and enable deeper insights

421   into the drivers at a local scale. For example, high rPD might be primarily driven by the occurrence of

422   a small number of old lineages in an area.

423   Studies considering PD for conservation purposes have become more frequent (Rodrigues &

424   Gaston, 2002; Winter *et al.*, 2012; Brooks *et al.*, 2015). These have advocated, for example,

425   conservation that prioritises the protection of unique lineages (Isaac *et al.*, 2007). Nonetheless,

426   phylogenetic information remains under-used (Rodrigues *et al.*, 2011). One difficulty is that

427   biodiversity measures based on phylogenetic information [e.g. PD (Faith, 1992), phylogenetic

428   endemism (Rosauer *et al.*, 2009), and evolutionary distinctiveness (Isaac *et al.*, 2007)] have been

429   found to be inconsistent in their spatial congruence (Daru *et al.*, 2014). A future research priority

430   should be to improve our understanding of the global pattern of rPD among taxa and its relationship

431   with other biodiversity measures, and with current protected area networks, to make phylogenetic

432   information more applicable for conservation practice.

433   *Implications for conservation*

434   Our findings have implications for biodiversity conservation. Aside from the role of rPD in aiding our

435   understanding of historical patterns of evolution, extinction and colonisation, rPD could prove a

436   useful metric to highlight areas of high irreplaceability and added value, in conservation terms. Our

437   study confirms that, across much of the world, SR provides a good proxy for avian PD and, hence,

438   provides a good surrogate for biodiversity (where biodiversity is richness at all diversity scales,

439   including phylogenetic diversity). However, we also identify areas of high (or low) rPD where this

440   relationship is weaker. The areas of high rPD are of particular interest for conservation planning

441   since they indicate a likely high evolutionary potential of a community, in comparison to

442   communities with a similar SR in combination with an average or low rPD value. Interestingly, for

443   birds, we find that many areas prioritised because of endemic species actually have low rPD.

444   Typically, these areas are associated with recent species radiations as seen in, for example, the

445   Andes which have a comparably low rPD. This region harbours many endemic, but closely related,

446   hummingbirds (McGuire *et al.*, 2014). Consequently, such areas might be considered of lower

447   conservation priority than regions with similar SR but higher rPD.

448   Importantly, the lack of overlap between the rPD of birds, amphibians and mammals,

449   compels caution in generalising PD results among taxa. This result is consistent with a recent study

450   by Zupan *et al.*, (2014) which suggests strong divergence between the patterns of PD in vertebrate

451   taxa across Europe. As with SR, it seems that there is no 'silver bullet' indicator taxon that can be

452   used to infer PD across taxa. That habitat diversity was seldom identified as a useful predictor of PD

453   suggests that this, too, would be a poor metric of current PD. Using ecosystem-based metrics (such

454   as habitat/ecosystem richness) as a basis for protecting areas for biodiversity conservation (Brooks

455   *et al.*, 2006) may conserve ecosystem function, and to some extent SR, but would perform rather

456   poorly in representing rPD, as habitat diversity was not included in our global or regional models of

457   PD. Current best-practice to identify terrestrial biodiversity hotspots (such as Conservation

458   International's hotspots or BirdLife International's EBAs) consider endemism but do not yet account

459   for phylogenetic uniqueness. The next challenge for conservation biologists is to combine supertree

460   PD data across a number of key taxa to identify hotspots of biodiversity that represent areas of true

461   phylogenetic diversity and uniqueness, in addition to species diversity, endemism and

462   distinctiveness.

463

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470   **References**

471   Barker, G.M. (2002) Phylogenetic diversity: a quantitative framework for measurement of priority

472   and achievement in biodiversity conservation. *Biological Journal of the Linnean Society*, **76**,

473   165-194.

474   Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C.,

475   McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011) Has the earth's

476   sixth mass extinction already arrived? *Nature*, **471**, 51-57.

477   Bartoń, K. (2014) *MuMIn: Multi-model inference*. Available at: http://CRAN.R-

478   project.org/package=MuMIn (accessed 01.10.2014)

479   Bazzaz, F.A. (1975) Plant species diversity in old-field successional ecosystems in southern Illinois.

480   *Ecology*, **56**, 485-488.

481   Beaujean, A.A. (2012) *BaylorEdPsych: R package for Baylor University educational psychology*

482   *quantitative courses. R package version 0.5.*, R Foundation for Statistical Computing, Vienna,

483   Austria. Available at: http://CRAN.R-project.org/package=BaylorEdPsych.

484   BirdLife International & NatureServe (2012) *Bird species distribution maps of the world*, BirdLife

485   International, Cambridge, UK & NatureServe, Arlington, USA.

486   Brooks, T.M., Cuttelod, A., Faith, D.P., Garcia-Moreno, J., Langhammer, P. & Pérez-Espona, S. (2015)

487   Why and how might genetic and phylogenetic diversity be reflected in the identification of

488   key biodiversity areas? *Philosophical Transactions of the Royal Society B: Biological Sciences*,

489   **370**, 1471-2970.

490   Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F.,

491   Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006) Global biodiversity conservation

492   priorities. *Science*, **313**, 58-61.

493   Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical*

494   *information-theoretic approach*. Springer, New York.

495   Butchart, S.H.M., Walpole, M., Collen, B. et al. (2010) Global biodiversity: Indicators of recent

496   declines. *Science*, **328**, 1164-1168.

497   Cadotte, M.W., Jonathan Davies, T., Regetz, J., Kembel, S.W., Cleland, E. & Oakley, T.H. (2010)

498   Phylogenetic diversity metrics for ecological communities: integrating species richness,

499   abundance and evolutionary history. *Ecology Letters*, **13**, 96-105.

500   Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace,

501   G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie,

502   A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*,

503   **486**, 59-67.

504   Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community

505   ecology and phylogenetic biology. *Ecology Letters*, **12**, 693-715.

506   Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U.,

507   Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S. (2000) Consequences of changing

508   biodiversity. *Nature*, **405**, 234-242.

509   Crowley, T.J. & North, G.R. (1988) Abrupt climate change and extinction events in earth history.

510   *Science*, **240**, 996-1002.

511   Crozier, R.H. (1997) Preserving the information content of species: genetic diversity, phylogeny, and

512   conservation worth. *Annual Review of Ecology and Systematics*, **28**, 243-268.

513   Daru, B.H., van der Bank, M. & Davies, T.J. (2014) Spatial incongruence among hotspots and

514   complementary areas of tree diversity in southern Africa. *Diversity and Distributions*, 1 - 12.

515   Davies, T.J. & Buckley, L.B. (2011) Phylogenetic diversity as a window into the evolutionary and

516   biogeographic histories of present-day richness gradients for mammals. *Philosophical*

517   *Transactions of the Royal Society B: Biological Sciences*, **366**, 2414-2425.

518   Davies, T.J., Fritz, S.A., Grenyer, R., Orme, C.D.L., Bielby, J., Bininda-Emonds, O.R.P., Cardillo, M.,

519   Jones, K.E., Gittleman, J.L., Mace, G.M. & Purvis, A. (2008) Phylogenetic trees and the future

520   of mammalian biodiversity. *Proceedings of the National Academy of Sciences*, **105**, 11556-

521   11563.

522   Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B.,

523   Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B.,

524   Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of

525   methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**,

526   27-46.

527   Emerson, B.C. & Kolm, N. (2005) Species diversity can drive speciation. *Nature*, **434**, 1015-1017.

528   Ericson, P.G.P., Anderson, C.L., Britton, T., Elzanowski, A., Johansson, U.S., Källersjö, M., Ohlson, J.I.,

529   Parsons, T.J., Zuccon, D. & Mayr, G. (2006) Diversification of Neoaves: integration of

530   molecular sequence data and fossils. *Biology Letters*, **2**, 543-547.

531   Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1-

532   10.

533   Fjeldså, J. (2012) Diversification of the neotropical avifauna: disentangling the geographical patterns

534   of persisting ancient taxa and phylogenetic expansions. *Ornitologia Neotropical* **23**, 13-27.

535   Flynn, D.F.B., Mirotchnick, N., Jain, M., Palmer, M.I. & Naeem, S. (2011) Functional and phylogenetic

536   diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology*, **92**, 1573-

537   1581.

538   Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Balmford, A., Manning,

539   J.C., Proches, S., van der Bank, M., Reeves, G., Hedderson, T.A.J. & Savolainen, V. (2007)

540   Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature*, **445**, 757-

541   760.

542   Fritz, S.A. & Rahbek, C. (2012) Global patterns of amphibian phylogenetic diversity. *Journal of*

543   *Biogeography*, **39**, 1373-1382.

544 Fuller, R.A., McDonald-Madden, E., Wilson, K.A., Carwardine, J., Grantham, H.S., Watson, J.E.M.,

545   Klein, C.J., Green, D.C. & Possingham, H.P. (2010) Replacing underperforming protected

546   areas achieves better conservation outcomes. *Nature*, **466**, 365-367.

547 Gaston, K.J. (1996) Species richness: measure and measurement. *Biodiversity: a Biology of Numbers*

548   *and Difference* (ed. by K.J. Gaston), pp. 77 - 113. Blackwell Science, Oxford.

549 Gordon, C., Cooper, C., Senior, C.A., Banks, H., Gregory, J.M., Johns, T.C., Mitchell, J.F.B. & Wood,

550   R.A. (2000) The simulation of SST, sea ice extents and ocean heat transports in a version of

551   the Hadley Centre coupled model without flux adjustments. *Climate Dynamics*, **16**, 147-168.

552 Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the

553   measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.

554 Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox,

555   W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S.,

556   Sheldon, F.H., Steadman, D.W., Witt, C.C. & Yuri, T. (2008) A phylogenomic study of birds

557   reveals their evolutionary history. *Science*, **320**, 1763-1768.

558 Hardy, O.J. & Senterre, B. (2007) Characterizing the phylogenetic structure of communities by an

559   additive partitioning of phylogenetic diversity. *Journal of Ecology*, **95**, 493-506.

560 Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2006) Special paper: post-eocene

561   climate change, niche conservatism, and the latitudinal diversity gradient of new world

562   birds. *Journal of Biogeography*, **33**, 770-780.

563 Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo , C.A. & Soeller, S.A. (2007) Climate, niche conservatism,

564   and the global bird diversity gradient. *The American Naturalist*, **170**, 16-27.

565 Heard, S.B. & Mooers, A.O. (2000) Phylogenetically patterned speciation rates and extinction risks

566   change the loss of evolutionary history during extinctions. *Proceedings of the Royal Society*

567   *of London. Series B: Biological Sciences*, **267**, 613-620.

568 Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H.,

569   Graham, C.H., Graves, G.R., Jønsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J.,

570   Fjeldså, J. & Rahbek, C. (2013) An update of Wallace's zoogeographic regions of the world.

571   *Science*, **339**, 74-78.

572   Huang, S., Davies, T.J. & Gittleman, J.L. (2012) How global extinctions impact regional biodiversity in

573   mammals. *Biology Letters*, **8**, 222-225.

574   Isaac, N.J.B., Redding, D.W., Meredith, H.M. & Safi, K. (2012) Phylogenetically-informed priorities for

575   amphibian conservation. *PLoS ONE*, **7**, e43912.

576   Isaac, N.J.B., Turvey, S.T., Collen, B., Waterman, C. & Baillie, J.E.M. (2007) Mammals on the EDGE:

577   conservation priorities based on threat and phylogeny. *PLoS ONE*, **2**, e296.

578   Jarvis, E.D., Mirarab, S., Aberer, A.J. et al. (2014) Whole-genome analyses resolve early branches in

579   the tree of life of modern birds. *Science*, **346**, 1320-1331.

580   Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in

581   space and time. *Nature*, **491**, 444-448.

582   Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T.,

583   Hopper, S.D. & Franklin, S.E. (2012) Refugia: identifying and understanding safe havens for

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

585   Kluge, J. & Kessler, M. (2011) Phylogenetic diversity, trait diversity and niches: species assembly of

586   ferns along a tropical elevational gradient. *Journal of Biogeography*, **38**, 394-405.

587   Lack, D. (1969) The number of bird species on islands. *Bird Study*, 193- 209.

588   Leaky, R. & Lewin, R. (1992) *The sixth extinction: patterns of life and the future of humankind*.

589   doubleday, New York.

590   Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston,

591   M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem

592   functioning: current knowledge and future challenges. *Science*, **294**, 804-808.

593   Losos, J.B. & Glor, R.E. (2003) Phylogenetic comparative methods and the geography of speciation.

594   *Trends in Ecology & Evolution*, **18**, 220-227.

595   Mace, G.M., Balmford, A., Boitani, L., Cowlishaw, G., Dobson, A.P., Faith, D.P., Gaston, K.J.,

596   Humphries, C.J., Vane-Wright, R.I., Williams, P.H., Lawton, J.H., Margules, C.R., May, R.M.,

597   Nicholls, A.O., Possingham, H.P., Rahbek, C. & van Jaarsveld, A.S. (2000) It's time to work

598   together and stop duplicating conservation efforts. *Nature*, **405**, 393-393.

599   May, R.M. (1990) Taxonomy as destiny. *Nature*, **347**, 129-130.

600   McFadden, D. (1974) Conditional logit analysis of qualitative choice behaviour. *Frontiers in*

601   *econometrics* (ed. by P. Zarembka), pp. 105 - 142. Academic Press, New York.

602   McGuire, Jimmy A., Witt, Christopher C., Remsen Jr, J.V., Corl, A., Rabosky, Daniel L., Altshuler,

603   Douglas L. & Dudley, R. (2014) Molecular phylogenetics and the diversification of

604   hummingbirds. *Current Biology*, **24**, 910-916.

605   Mooers, A.O. & Heard, S.B. (1997) *Infering evolutionary process from phylogenetic treeshape*.

606   University of Chicago Press, Chicago, IL.

607   Olsen, G. (1990) *Gary Olsen's interpretation of the "Newick's 8:45" tree format standard*. Available

608   at: http://evolution.genetics.washington.edu/phylip/newick_doc.html(accessed 01.10.2014)

609   Orme, C.D.L., Freckleton, R.P. & Thomas, G.H. (2009) *CAIC: comparative analyses using independent*

610   *contrasts. R package version 1.0.4.*, R Foundation for Statistical Computing ,Vienna, Austria.

611   Available at: http://r-forge.r-project.org/projects/caic

612   Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.-

613   S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston,

614   K.J. & Owens, I.P.F. (2005) Global hotspots of species richness are not congruent with

615   endemism or threat. *Nature*, **436**, 1016-1019.

616   Päckert, M., Martens, J., Sun, Y.-H., Severinghaus, L.L., Nazarenko, A.A., Ting, J., Töpfer, T. & Tietze,

617   D.T. (2012) Horizontal and elevational phylogeographic patterns of Himalayan and South

618   East Asian forest passerines (Aves: Passeriformes). *Journal of Biogeography*, **39**, 556-573.

619   Palmer, M. (1994) Variation in species richness: towards a unification of hypotheses. *Folia*

620   *Geobotanica et Phytotaxonomica*, **29**, 511-530.

621   Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R

622   language. *Bioinformatics*, 289 - 290.

623   Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review*

624   *of Ecology, Evolution, and Systematics*, **37**, 637-669.

625   Peterson, G., Allen, C.R. & Holling, C.S. (1998) Ecological resilience, biodiversity, and scale.

626   *Ecosystems*, **1**, 6-18.

627   Petit, R.J., Aguinagalde, I., de Beaulieu, J.-L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi,

628   S., Grivet, D., Lascoux, M., Mohanty, A., Müller-Starck, G., Demesure-Musch, B., Palmé, A.,

629   Martín, J.P., Rendell, S. & Vendramin, G.G. (2003) Glacial refugia: hotspots but not melting

630   pots of genetic diversity. *Science*, **300**, 1563-1565.

631   Pope, V.D., Gallani, M.L., Rowntree, P.R. & Stratton, R.A. (2000) The impact of new physical

632   parametrizations in the Hadley Centre climate model: HadAM3. *Climate Dynamics*, **16**, 123-

633   146.

634   Price, T.D., Hooper, D.M., Buchanan, C.D., Johansson, U.S., Tietze, D.T., Alstrom, P., Olsson, U.,

635   Ghosh-Harihar, M., Ishtiaq, F., Gupta, S.K., Martens, J., Harr, B., Singh, P. & Mohan, D. (2014)

636   Niche filling slows the diversification of Himalayan songbirds. *Nature*, **509**, 222-225.

637   Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M. & Lemmon, A.R. (2015)

638   A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing.

639   *Nature*, **526**, 569-573.

640   Purvis, A., Agapow, P.-M., Gittleman, J.L. & Mace, G.M. (2000) Nonrandom extinction and the loss of

641   Evolutionary History. *Science*, **288**, 328-330.

642   Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness.

643   *Proceedings of the National Academy of Sciences*, **98**, 4534-4539.

644   Rands, M.R.W., Adams, W.M., Bennun, L., Butchart, S.H.M., Clements, A., Coomes, D., Entwistle, A.,

645   Hodge, I., Kapos, V., Scharlemann, J.P.W., Sutherland, W.J. & Vira, B. (2010) Biodiversity

646   conservation: challenges beyond 2010. *Science*, **329**, 1298-1303.

647 Ricklefs, R.E. & Pagel, M. (2012) Evolutionary biology: birds of a feather. *Nature*, **491**, 336-337.

648 Rocha, T.C., Sequeira, F., Aleixo, A., Rêgo, P.S., Sampaio, I., Schneider, H. & Vallinoto, M. (2015)

649   Molecular phylogeny and diversification of a widespread Neotropical rainforest bird group:

650   the Buff-throated Woodcreeper complex, Xiphorhynchus guttatus/susurrans (Aves:

651   Dendrocolaptidae). *Molecular Phylogenetics and Evolution*, **85**, 131-140.

652 Rodrigues, A.S.L. & Gaston, K.J. (2002) Maximising phylogenetic diversity in the selection of networks

653   of conservation areas. *Biological Conservation*, **105**, 103-111.

654 Rodrigues, A.S.L., Brooks, T.M. & Gaston, K.J. (2005) Integrating phylogenetic diversity in the

655   selection of priority areas for conservation: does it make a difference? *Phylogeny and*

656   *Conservation* (ed. by A. Purvis, J.L. Gittleman and T.M. Brooks), pp. 101 - 116. Cambridge

657   University Press, Cambridge.

658 Rodrigues, A.S.L., Grenyer, R., Baillie, J.E.M., Bininda-Emonds, O.R.P., Gittlemann, J.L., Hoffmann, M.,

659   Safi, K., Schipper, J., Stuart, S.N. & Brooks, T. (2011) Complete, accurate, mammalian

660   phylogenies aid conservation planning, but not much. *Philosophical Transactions of the*

661   *Royal Society B: Biological Sciences*, **366**, 2652-2660.

662 Roquet, C., Thuiller, W. & Lavergne, S. (2013) Building megaphylogenies for macroecology: taking up

663   the challenge. *Ecography*, **36**, 013-026.

664 Rosauer, D.A.N., Laffan, S.W., Crisp, M.D., Donnellan, S.C. & Cook, L.G. (2009) Phylogenetic

665   endemism: a new approach for identifying geographical concentrations of evolutionary

666   history. *Molecular Ecology*, **18**, 4061-4072.

667 Rosauer, D.F. & Jetz, W. (2015) Phylogenetic endemism in terrestrial mammals. *Global Ecology and*

668   *Biogeography*, **24**, 168-179.

669 Safi, K., Cianciaruso, M.V., Loyola, R.D., Brito, D., Armour-Marshall, K. & Diniz-Filho, J.A.F. (2011)

670   Understanding global patterns of mammalian functional and phylogenetic diversity.

671   *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 2536-2544.

672   Singarayer, J.S. & Valdes, P.J. (2010) High-latitude climate sensitivity to ice-sheet forcing over the last

673   120kyr. *Quaternary Science Reviews*, **29**, 43-55.

674   Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in

675   the tropics. *The American Naturalist*, **133**, 240-256.

676   Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a decade-long

677   grassland experiment. *Nature*, **441**, 629-632.

678   U.S. Geological Survey (2012a) *Global 30 arc-second elevation (GTOPO30)* Available at:

679   http://lpdaac.usgs.gov (accessed 01.05.2014)

680   U.S. Geological Survey (2012b) *Global land cover (GlobCover)*, Land Processes Distributed Active

681   Archive Center (LP DAAC), located at USGS/EROS, Sioux Falls, SD. Available at:

682   http://lpdaac.usgs.gov.

683   Vane-Wright, R.I., Humphries, C.J. & Williams, P.H. (1991) What to protect?—systematics and the

684   agony of choice. *Biological Conservation*, **55**, 235-254.

685   Venditti, C., Meade, A. & Pagel, M. (2010) Phylogenies reveal new interpretation of speciation and

686   the Red Queen. *Nature*, **463**, 349-352.

687   Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of earth's

688   ecosystems. *Science*, **277**, 494-499.

689   Wallace, A.R. (1878) *Tropical nature: and other essays*. Macmillan and Company.

690   Webb, S.D. (2006) The great american biotic interchange: patterns and processes. *Annals of the*

691   *Missouri Botanical Garden*, **93**, 245-257.

692   Weir, J.T. & Schluter, D. (2004) Ice sheets promote speciation in boreal birds. *Proceedings of the*

693   *Royal Society of London B: Biological Sciences*, **271**, 1881-1887.

694   Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological*

695   *Monographs*, **30**, 279 - 338.

696   Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in*

697   *Ecology & Evolution*, **19**, 639-644.

698   Winter, M., Devictor, V. & Schweiger, O. (2012) Phylogenetic diversity and nature conservation:

699   where are we? *Trends in ecology & evolution*, **28**, 199-204.

700   Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K.,

701   Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J. & Watson, R. (2006) Impacts

702   of biodiversity loss on ocean ecosystem services. *Science*, **314**, 787-790.

703   Zupan, L., Cabeza, M., Maiorano, L., Roquet, C., Devictor, V., Lavergne, S., Mouillot, D., Mouquet, N.,

704   Renaud, J. & Thuiller, W. (2014) Spatial mismatch of phylogenetic diversity across three

705   vertebrate groups and protected areas in Europe. *Diversity and Distributions*, **20**, 674-685.

706

707 **SUPPORTING INFORMATION**

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

709 **Appendix S1** Supplementary methods and supplementary figures

710 **Biosketch**

711 All authors except PJV are members of the Conservation Ecology Group

712 (www.conservationecology.org) at Durham, which applies ecological approaches to issues of interest

713 to conservation biology. AV is a PhD student in the group working on global species distributions and

714 their underlying ecological and evolutionary processes. AV is supervised by SGW and PAS. AV and

715 DJB performed the analyses and, with SGW and PAS, wrote the manuscript. PJV is a climatologist,

716 working on contemporary and palaeo climatology.

717

718 Editor: Fumin Lei
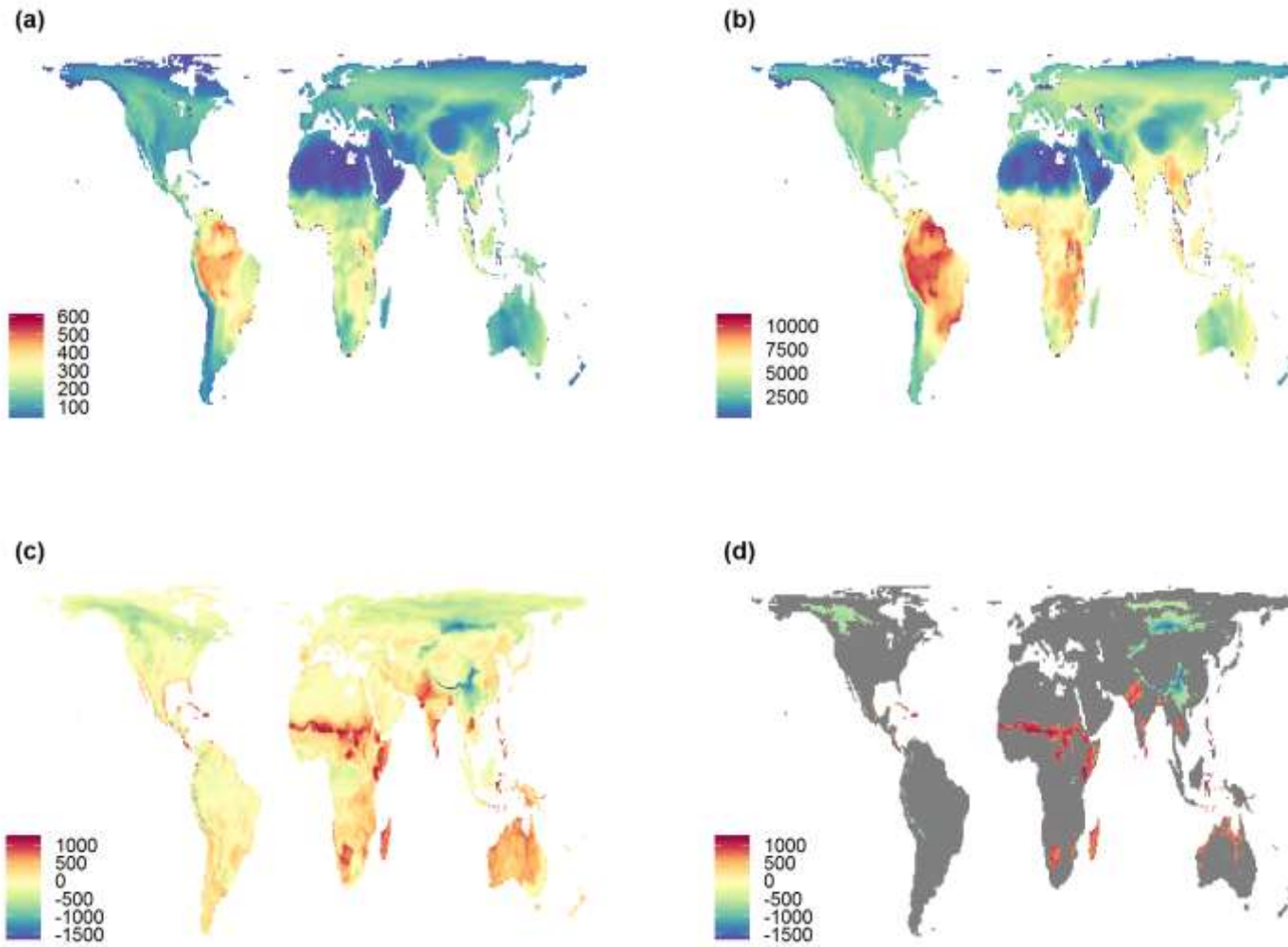
719 **Figure legends**

720 **Figure 1:** Global maps (Behrman projection) showing (a) global avian species richness, (b) global

721 avian phylogenetic diversity (calculated using Faith's (1992) phylogenetic diversity), (c) residuals of

722 the local regression (LOESS) between avian species richness (SR) and phylogenetic diversity (PD) and

723 (d) global areas containing the highest or lowest 5% of the residuals, with cells that do not fall in the

724 top or bottom 5% masked in grey. In the latter two graphs, red indicates unusually high PD given the

725 SR, and blue unusually low PD given the SR.

726

727 **Figure 2:** (a) The global relationship between avian species richness (SR) and phylogenetic diversity

728 (PD); the red line was fitted to the data using local regression with nonparametric smoothing

729 techniques; (b) residuals of the local regression plotted against avian species richness, coloured by

730 realm.

731

732 **Figure 3:** (a) The residuals of the global model to predict phylogenetic diversity (PD) and (b) the

733 residuals of stitched models per realm. Realms with less than 500 cells and realms where no drivers

734 for the PD pattern other than species richness (SR) could be identified were excluded from the

735 individual realm analysis and are masked grey.

736

737   **Figure 1**

738

739 **Figure 2**

(a)

(b)

740
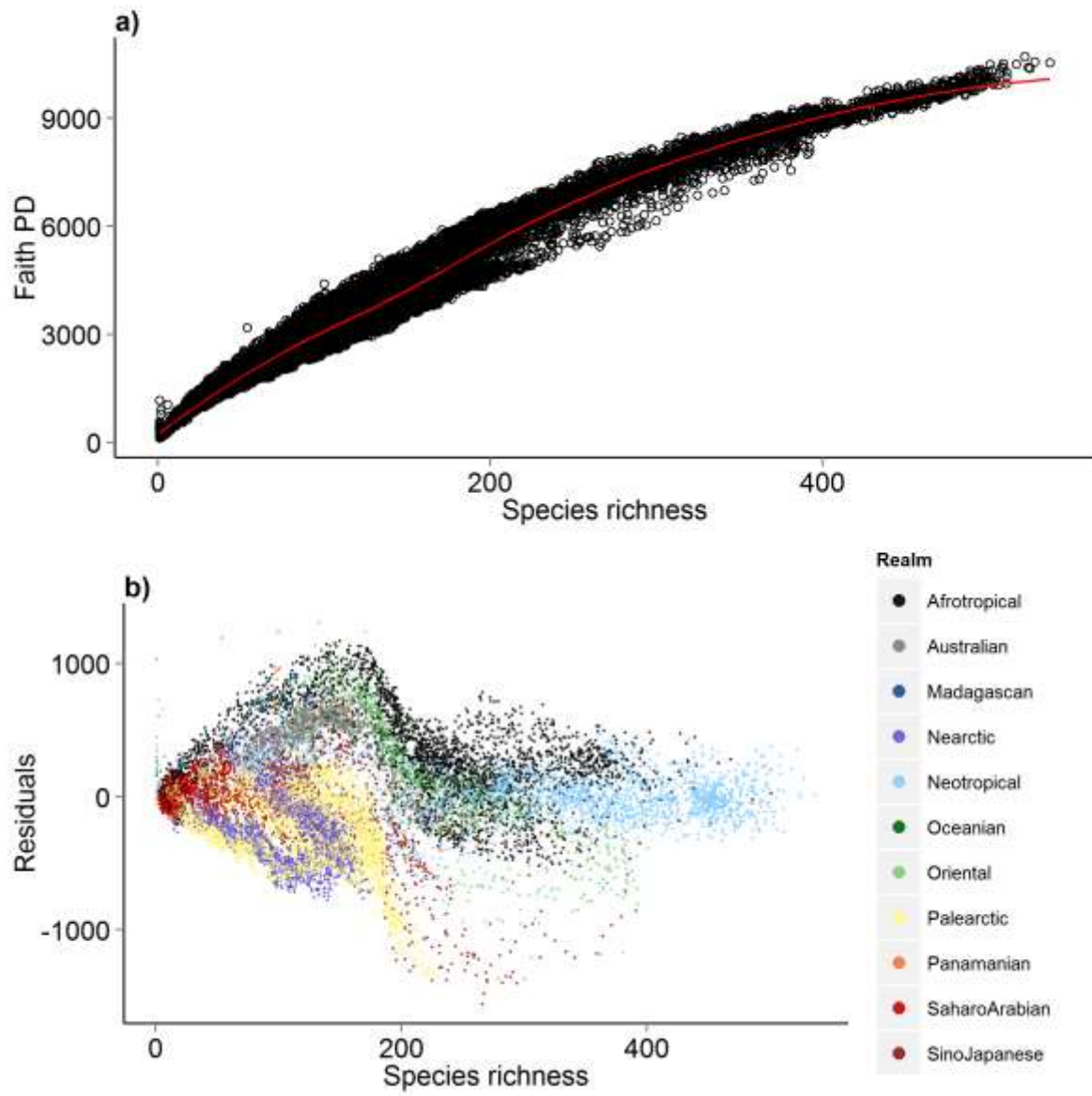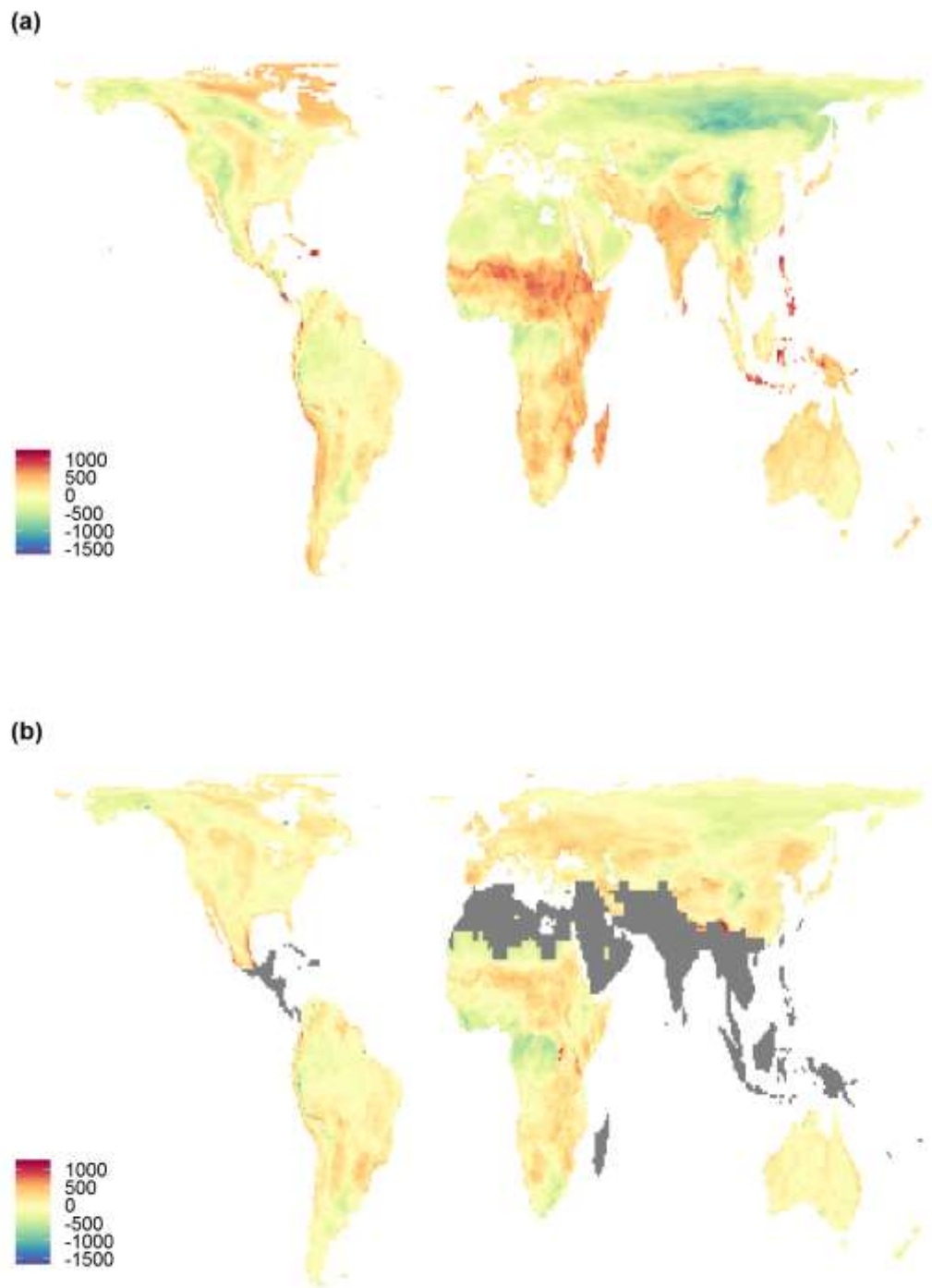
Figure 3

742 **Table legends**

743 **Table 1:** Mean autocorrelation values (Moran's I) for the model fitting data after subsampling and r^2

744 values for the species richness (SR) only model and the full model (SR plus the additional explanatory

745 variables) for the global scale model and the individual realm models (same as Table 2).

746

747 **Table 2:** Variables used to model phylogenetic diversity (PD) on a global scale and in the individual

748 realms. Standardized coefficients are given for all variables that have been used in a model.

749 Variables which have been consistently selected for the best model (variables that were in the best

750 model after model selection 95% of the time) are marked with an asterisk. Variables which have not

751 been used in any of the models were excluded from the table (habitat diversity, mean short-term

752 climate stability, max-short term climate stability).

753

754 **Table 1**

	Moran's I	r2 SR only model	r2 full model
755			
756 Global	0.136	0.973	0.982
757 Afrotropical	0.118	0.980	0.989
758 Australian	0.156	0.913	0.988
759 Nearctic	0.154	0.900	0.955
760 Neotropical	0.140	0.937	0.946
761 Palaearctic	0.135	0.965	0.971
762 Sino Japanese	0.230	0.971	0.983

763

Table 2

Variable	Global		Afrotropical		Australian		Neotropical		Nearctic		Palaearctic		Sino Japanese	
Term used	Quadratic	Linear	Quadratic	Linear	Quadratic	Linear	Quadratic	Linear	Quadratic	Linear	Quadratic	Linear	Quadratic	Linear
Distance to neighbouring realm	-	-0.014	-	-0.052*	-	-0.045*	-	0.022	-	0.081	-	-0.058	-	0.008*
Altitudinal range	0.006*	-0.041*	0.001	-0.018	0.007	-0.021	-0.003*	-0.038*	0.083*	-0.116*	0.028	-0.058	-0.012*	-0.098*
Mean long term climate stability	0.036*	-0.073*	-	-	-	-	-	-	-	-	-	-	-	-
Max long term climate stability	-	-	-	-	-	-	-	-	0.080*	-0.270*	-	-	-	-
Long term precipitation stability	-	-	0.010	-0.023	-	-	-	-	-	-	-	-	-0.026*	0.090*
Short term precipitation stability	-	-	-	-	0.024	0.016	-	-	-	-	-	-	-	-
Long term temperature stability	-	-	-	-	-	-	-	-	-	-	0.068*	-0.071*	-	-
Short term temperature stability	-	-	-	-	-	-	-0.014	-0.011	-	-	-	-	-	-
Species richness	0.144*	0.965*	-0.182*	1.005*	-0.083*	0.987*	-0.132*	0.973*	-0.054*	0.937*	-0.067*	0.985*	-0.140*	1.014*