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SPECIAL PAPER

Global patterns in the divergence between phylogenetic diversity and species richness in 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 geographical 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 distributional 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 biogeographical 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, while 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 conclusions There is geographical 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 prioritization.

Keywords
biodiversity measures, birds, conservation, Faith's PD, global species richness, phylogenetic diversity

INTRODUCTION

Rapid losses of biodiversity have occurred across the globe over recent decades, driven primarily by human modification of the environment and increasing demand for natural resources (Vitousek *et al.*, 1997; Butchart *et al.*, 2010; Cardinale *et al.*, 2012). Estimates of the current rate of species extinctions are 1000 to 10,000 times higher than background levels, and this is consistent with previous mass extinction events (Leaky & Lewin, 1992; Mace *et al.*, 2000; Barnosky

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et al., 2011). The loss of biodiversity is likely to have profound effects on ecosystem functioning (Loreau *et al.*, 2001), reducing the intrinsic resilience of these systems to environmental change (Peterson *et al.*, 1998; Chapin *et al.*, 2000), and affecting ecosystem processes and the provision of ecosystem services (Tilman *et al.*, 2006; Worm *et al.*, 2006). Consequently, preventing the loss of biodiversity is a global priority (Rands *et al.*, 2010).

Conservation efforts *in situ* usually focus on the preservation of species and, consequently, species richness (SR) is frequently used as the metric of biodiversity for assessing spatial conservation priorities (Gaston, 1996; Gotelli & Colwell, 2001; Fuller *et al.*, 2010). SR, however, is driven largely by common and widespread species, and thus, conservation prioritizations based on this metric will often fail to capture the features of biodiversity that require the greatest conservation focus (Brooks *et al.*, 2006). To address this concern, metrics have been developed that quantify various aspects of species' irreplaceability; such metrics include the number of endemic species or the taxonomic uniqueness of species in a community (Brooks *et al.*, 2006). These metrics aim to better account for the conservation value of individual species based on rarity or their unique evolutionary history (May, 1990; Vane-Wright *et al.*, 1991). While irreplaceability metrics have theoretical appeal, it has often proven difficult to quantify these metrics, in large part due to limitations with data, including incomplete species inventories and lack of robust phylogenies. However, for many of the major taxonomic groups (e.g. birds, mammals), distributional and phylogenetic data have become more widely available, leading to irreplaceability metrics being estimated and used more readily in conservation prioritizations (Heard & Mooers, 2000; Purvis *et al.*, 2000; Isaac *et al.*, 2007).

Phylogenetic diversity (PD) is a measure of the evolutionary relationship between species (Hardy & Senterre, 2007) and provides a metric of biodiversity that accounts for evolutionary distances between co-occurring species (Crozier, 1997). Thus, PD can be used to quantify the taxonomic uniqueness of species in a community and to assess irreplaceability in terms of evolutionary history, functional diversity (Flynn *et al.*, 2011) and evolutionary potential (Faith, 1992; Forest *et al.*, 2007). Such irreplaceability metrics might add value over SR metrics when considered in conservation strategies (Isaac *et al.*, 2007, 2012). Under the assumption that closely related species have a similar evolutionary potential, but more distantly related species differ more in their potential, a community with high PD has a higher chance of containing a subset of species with greater evolutionary potential (Winter *et al.*, 2012). Therefore, a community with high PD might be considered to have a greater potential to be robust to future environmental changes (Faith, 1992).

Patterns of SR and PD tend to be highly correlated across broad spatial scales and earlier studies suggest that SR is, in general, an adequate surrogate for PD (Rodrigues *et al.*, 2005). Yet localized differences between SR and PD, as well as related measures such as phylogenetic endemism and functional diversity, have been found across a range of taxa (Davies *et al.*, 2008; Davies & Buckley, 2011; Fritz & Rahbek, 2012). A global study of amphibians found mismatches between SR and PD, with lower PD than expected (given SR) on remote islands and archipelagos, as well as in regions that have been long isolated, such as Madagascar and Australia (Fritz & Rahbek, 2012). For mammals, lower than expected PD has been identified for some mountain ranges and remote islands, whereas higher than expected PD was found in Sub-Saharan Africa and parts of the Indian subcontinent (Davies & Buckley, 2011).

Observed localized differences between SR and PD could occur for various reasons. Unlike SR patterns, which have been a central topic throughout the history of ecology (Wallace, 1878; Stevens, 1989; Palmer, 1994), exploring patterns of PD has become possible only very recently, due to the availability of comprehensive phylogenies (Cavender-Bares *et al.*, 2009; Roquet *et al.*, 2013). Consequently, the drivers of these PD patterns remain largely unknown. Important historical processes (Losos & Glor, 2003), as well as macroecological changes such as mass migrations (e.g. Great American Biotic Interchange; Webb, 2006) and extinctions, can leave a signature in PD (Mooers & Heard, 1997). Additionally, environmental factors that could affect PD (see Appendix S1a in Supporting Information) include areas of long-term climate stability and areas with a steep altitudinal gradient, both of which could lead to areas acting as climate refugia (Keppel *et al.*, 2012). Ecological transition zones, harbouring communities with great genetic diversity (Petit *et al.*, 2003) could also have higher PD, due to the occurrence of species adapted to different ecological zones within one community. Habitat diversity, which is known to affect SR (Rahbek & Graves, 2001) and to drive diversification (Emerson & Kolm, 2005), could also affect PD. Identifying regions where PD is higher or lower than would be expected given SR (PD relative to the SR within the area, hereafter termed relative PD, or rPD), and exploring environmental correlates of rPD, can help identify communities with high irreplaceability, when assessed in terms of the uniqueness of evolutionary histories.

Here, for the first time, we: (1) map geographical variation in avian rPD and identify those areas characterized by particularly high or low values; and (2) explore potential environmental correlates of PD, in addition to SR, that might indicate where the macroecological processes of dispersal and diversification differ from the global average (Fritz & Rahbek, 2012). We develop models of PD on a global scale, as well as for individual biological realms. We hypothesize that high rPD should be favoured by relatively stable climates, but that habitat diversity will principally affect SR. High rPD might also arise from opportunities for community interchange (e.g. at boundaries between realms), or by relative isolation (promoting the persistence of ancient lineages). Conversely, we expect lower rPD on more recently formed landmasses. We expect the drivers of PD to differ between individual biological realms, as many broad-scale, macroecological processes differ between these geographical areas. We discuss the implications of our findings for conservation prioritization, highlighting differences between biodiversity metrics and between major taxonomic groups.

MATERIALS AND METHODS

Species distributional data

We estimated the extant species present in each grid cell across the global terrestrial landmass using global breeding range maps for 9227 bird species (BirdLife International & NatureServe, 2012). Taxonomic differences between the species' range data and the avian phylogeny used (see below) meant that 420 of the 9227 species were excluded, e.g. species might be recognized as one species in the phylogeny but split into two separate species in the BirdLife taxonomy. Owing to our terrestrial focus, a further 346 seabird species were also excluded. Range data were transferred onto an equal area grid in Behrman projection with a cell size of 1° latitude by 1° longitude at 30°N and 30°S latitude (Orme *et al.*, 2005; Fritz & Rahbek, 2012; Huang *et al.*, 2012). An equal area grid enables spatially unbiased comparisons among grid cells. A species was considered to occur in a cell only if the species' range polygon and grid cell overlap was $\geq$ 10%, a threshold that prevents species being represented in cells in which their occurrence is very limited. For 1287 species with ranges so restricted that they never occur in at least 10% of any cell, their occurrences were derived from the intersection of their range polygons with cells, without applying a 10% threshold. The gridded species' range data were then used to determine species lists for each grid cell across the globe.

Global phylogenetic diversity

To derive PD, we used the first full phylogeny of extant birds (Jetz *et al.*, 2012). These phylogenetic data are provided as 10,000 possible tree topologies in Newick tree format (Olsen, 1990). The phylogenetic data are available based on two taxonomic backbones: those of Hackett *et al.* (2008) and Ericson (Ericson *et al.*, 2006). Here we used the phylogeny based on the Hackett backbone, which is the most recent high-level avian topology available (Hackett *et al.*, 2008).

Several indices are available to measure PD but the most frequently used is Faith's PD (Cadotte *et al.*, 2010). Faith's PD (hereafter just PD) summarizes how much of the branching pattern of a phylogenetic tree is represented in a community, by adding the branch lengths for all members of the community (Faith, 1992). As such, it provides a summary measure of the phylogenetic diversity of a community (Faith, 1992; Barker, 2002). For each terrestrial grid cell globally, we calculated SR and PD. To aid the comparison of PD between cells, the root of the phylogenetic tree was excluded and the tree was pruned, using the 'APE' package in R (Paradis *et al.*, 2004), to the most recent common ancestor of the species within each cell (Faith, 1992). We calculated PD for all terrestrial cells containing at least two species. Grid cells that contain only one species cannot provide a minimum spanning path between two species, resulting in the exclusion of some cells in the Saharan desert and around the poles (Faith, 1992; Barker, 2002). In total, we collected data on avian PD from 17,363 terrestrial grid cells.

A pilot study (See Figure S1 in Supporting Information) showed that 200 randomly chosen potential trees of the avian phylogeny (Jetz *et al.*, 2012) were adequate to reduce the coefficient of variation (from the trees available in this phylogeny) of estimated PD, for individual cells, to below 0.005 for 90% of the test cells. Consequently, we estimated PD for all cells using a random selection of 200 of the possible phylogenetic trees. Previous studies have used different methods to investigate the relationship between PD and SR, including analysing the residuals of the modelled relationship (Davies & Buckley, 2011; Fritz & Rahbek, 2012), or using a null model based on randomized species assemblages, which are then compared to the empirical data; the latter having been used only for studies on a smaller scale (Kluge & Kessler, 2011). Here, we used two approaches. Firstly, we followed the methods of Fritz & Rahbek (2012) and modelled the relationship between PD and SR using local regression with nonparametric smoothing techniques (Forest *et al.*, 2007), utilizing functions from the 'CAIC' package in R (Orme *et al.*, 2009). This allows us to compare our results to previous studies on global patterns of PD that have used a similar approach but for other taxa (Davies & Buckley, 2011; Fritz & Rahbek, 2012). To highlight areas with unusually high or low rPD, we selected the cells with the top and bottom 5% of the residuals from the local regression between PD and SR (Fritz & Rahbek, 2012).

Secondly, because when using a local regression with nonparametric smoothing techniques, the residuals can be affected by the surrounding cells, i.e. the rPD value for a grid cell is always relative to the surrounding values within the window of the local regression, which could mask important general relationships, we used an alternative method (Appendix S1c) to check the robustness of the observed patterns in rPD. We ordered the cells of the world by their SR values and divided them into five equal-sized groups. We fitted a generalized (Michaelis–Menten) saturating curve to the PD and SR data from a random data sample (n = 1000) drawn from each of the five groups and then predicted to the four left-out groups each time. The process was repeated 50 times, taking new random samples each time. From these predictions, we calculated the mean residual value from the fitted generalized saturating curves for each grid cell. Unlike in the locally weighted regression, the resultant residual is relative to the whole dataset and not just to grid cells with similar SR values. Although the patterns of the residuals from this alternative approach (See Figure S2 in Supporting Information) are less pronounced than those of the locally weighted regressions (See Figure S3 in Supporting Information) and the transitions between areas of low and high residual are more gradual, the overall pattern remains very similar. Consequently, and for simplicity, we display only results from the locally weighted regression analysis in the main manuscript.

Environmental correlates of rPD

We assessed environmental characteristics that might be associated with geographical variation in rPD. Specifically, we modelled the relationship between PD and SR, including additional covariates to help explain divergence. These additional covariates were: the distance to the nearest neighbouring realm, altitudinal range (considered as a proxy for within-cell climatic diversity), climate stability since the Last Glacial Maximum (LGM, present to 20,000 years ago), climate stability since the Last Interglacial period (LIG, present to 125,000 years ago) and habitat diversity (Appendix S1a). The derivations of these covariates are described below.

We calculated the distance of each grid cell to the nearest neighbouring realm based on an updated version of Wallace's zoogeographical regions of the world (Holt *et al.*, 2013). To calculate the altitudinal range within each cell, we used the 30 arc second (*c.* 1 × 1 km) GMTED 2010 global elevation data (U.S. Geological Survey, 2012a). Habitat diversity was measured 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, 2012b).

Measures of temporal climate stability for two time periods (since the LGM, and since the LIG) were based on modelled palaeoclimatic data (the production of which is detailed in Appendix S1a). The palaeoclimatic data were derived from a series of general circulation model (GCM) climate simulations, performed using the HadCM3 version of the Hadley Centre Unified Model (Gordon *et al.*, 2000; Pope *et al.*, 2000). Details of the model's configuration are given by Singarayer & Valdes (2010), and the resultant climate data were made available by the Bristol Research Initiative for the Global Environment (BRIDGE, http://www.bridge.bris.ac.uk/).

We extracted, as potential explanatory palaeoclimatic variables: (1) the stability of past precipitation, (2) the stability of past temperature and (3) a bivariate metric based on variation in both of those variables. From these, we calculated eight potential palaeoclimatic environmental covariates, including stability of: mean temperature, mean precipitation, mean bivariate climate and maximum bivariate climate, for time since both LGM and LIG. We used the potential for maximum values to explain PD because extreme events may drive extinctions (Crowley & North, 1988; Parmesan, 2006). Following Dormann *et al.* (2013), we avoided combinations of highly correlated climate variables (Pearsons' correlation, $r > 0.70$). Specifically, we used a preliminary model selection approach to select the climate stability variable with the most explanatory power (Appendix S1d), such that no model contained more than one metric of climate stability. Following preliminary data exploration, we included quadratic terms for SR, altitudinal range and climate stability variables, and linear effects for the remaining variables in our models to estimate global PD.

To identify global drivers of PD, we fitted general linear models of global PD including all valid combinations of environmental covariates and polynomial terms. The PD values were highly spatially auto-correlated (Moran's $I = 0.99$), which can affect inference. To minimize the potential impacts of spatial autocorrelation on inference, we designed a blocking method in which models of global PD were built and tested using spatially disaggregated data (See Figure S4 in Supporting Information). This approach substantially reduced the spatial autocorrelation (mean Moran's I across random data subsets = 0.18; Table 1). Using this blocking method, we fitted models to 1000 random subsets of the data. In each case, we selected among all competing models using the 'MuMIn' package in R (Bartoń, 2014). Inevitably, this resampling approach resulted in subtly different variable selection for each random subset of data. To identify those parameters with robust and repeatable influences on PD, we recorded the frequency with which individual environmental covariates were selected in the top models across the 1000 subsets. We report the parameter values for those covariates that were included in at least 95% of the top models (See Figure S5 in Supporting Information). Parameters, defined as robust by this method, were used to predict PD for all terrestrial cells globally.

To test whether environmental covariates relate to PD in different ways, or to differing degrees, in individual biological realms, we produced models similar to the global models described above but fitted instead to data from the individual realms. We considered only those realms with > 500 grid cells, to permit a blocking approach during model fitting. Eight realms satisfied this selection criterion: the Afrotropical, Neotropical, Nearctic, Australian, Saharo-Arabian, Sino-Japanese, Oriental and Palaearctic realms. Each of these realms was split into eight blocks, using the same method as for the global model. Following the same approach as described above for the global data, we identified the best model for each biological realm.

For each of the identified best models for the global scale and the individual biological realms, we calculated

Table 1 Mean autocorrelation values (Moran's I) for the model fitting data after subsampling and r^2 values for the species richness (SR) only model and the full model (SR plus the additional explanatory variables) for the global scale model and the individual realm models (same as Table 2).

	Moran's I	r^2 SR only model	r^2 full model
Global	0.136	0.973	0.982
Afrotropical	0.118	0.980	0.989
Australian	0.156	0.913	0.988
Nearctic	0.154	0.900	0.955
Neotropical	0.14	0.937	0.946
Palaearctic	0.135	0.965	0.971
Sino-Japanese	0.230	0.971	0.983

McFadden's r^2 (McFadden, 1974; Beaujean, 2012) as a measure of the extent to which the model with the lowest Akaike information criterion (AIC) value was an improvement over an alternative model containing only SR. Finally, we compared the predictions of PD from the global model with the predictions of the models based on the individual realms to assess whether the improvement in predictions of PD based on combining predictions from models fitted to the individual realms justifies the increase in complexity over the model fitted to the global data. To do this, we compared the AIC (based on the least squares case, Burnham & Anderson, 2002, p. 46) of the global model to that of an amalgamation of the separate realm predictions, for the realms where we could produce estimates using both methods.

RESULTS

Global patterns of SR, PD and rPD

As expected, the correlation between SR (Fig. 1a) and PD (Fig. 1b) is very high for terrestrial bird species across the globe (Fig. 2a; $r^2 = 0.973$). Nonetheless, the residuals of the LOESS regression have a marked spatial pattern (Fig. 1c, 1d), with clusters of positive and negative residuals that indicate divergence between SR and PD (Fig. 2b). Areas with the most negative rPD (i.e. where PD is lower than expected given SR) include areas of high relief, such as the Himalayas and Andes, and also areas of glacial coverage during the LGM, such as the northern Nearctic and Palaearctic. Extensive areas of high rPD occur on isolated tropical islands including Madagascar and Sri Lanka, and in dry land areas fringing the subtropics. The latter regions include the Sahelian edge of the Afrotropical realm, parts of eastern Africa and central southern Africa, as well as northern Australia and the border between India and Pakistan.

Potential drivers of avian PD

The best global model of avian PD included the variables SR, mean climate stability since the LIG and altitudinal range, and explained 98% ($r^2 = 0.982$, Table 1, Table 2) of the variation in PD. This model explained one-third of the remaining variation in PD when compared to the global model including only SR ($r^2 = 0.973$, Table 1).

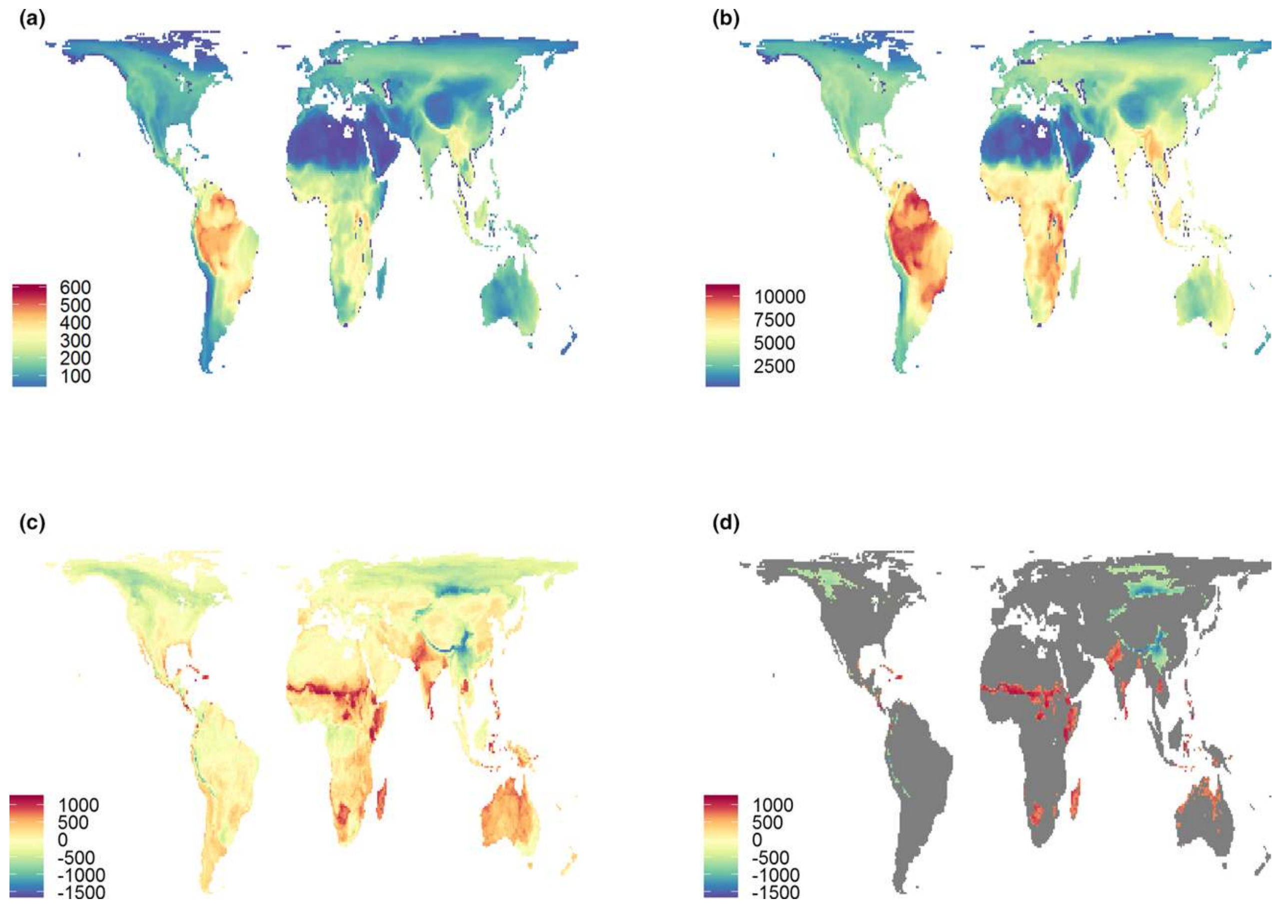

Figure 1 Global maps (Behrman projection) showing (a) global avian species richness, (b) global avian phylogenetic diversity (calculated using Faith's (1992) phylogenetic diversity), (c) residuals of the local regression (LOESS) between avian species richness (SR) and phylogenetic diversity (PD) and (d) global areas containing the highest or lowest 5% of the residuals, with cells that do not fall in the top or bottom 5% masked in grey. In the latter two graphs, red indicates unusually high PD given the SR, and blue unusually low PD given the SR. [Colour figure can be viewed at wileyonlinelibrary.com]

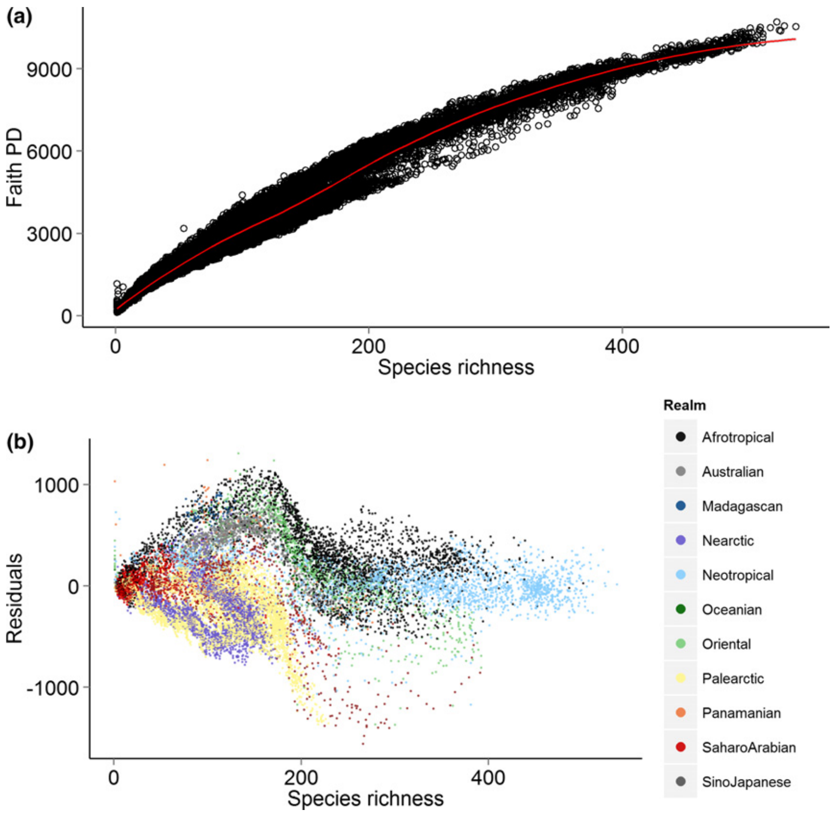

Figure 2 (a) The global relationship between avian species richness (SR) and phylogenetic diversity (PD); the red line was fitted to the data using local regression with nonparametric smoothing techniques; (b) residuals of the local regression plotted against avian species richness, coloured by realm. [Colour figure can be viewed at wileyonlinelibrary.com]

At a realm level, the climate variables included in the best model of PD differed among realms (Table 2). Nonetheless, for all realms, besides the Australian and the Neotropical realm, the best PD models included one of the LIG climate variables. Other variables (apart from SR and climatic variables) included in the best realm models of PD were the distance to the nearest neighbouring realm and altitudinal range, though combinations of variables in the best individual realm models differed. For the Oriental and Saharo-Arabian realms, no additional drivers of PD could be identified in addition to SR.

Overall, the amalgamated realm-level models described PD better than the global level model (realm model AIC: 81420, global model AIC: 86716). The residuals of the realm-level models (Fig. 3b) have a considerably less pronounced pattern than the residuals of the global level model suggesting that these models are able to explain considerably more of the divergence between PD and SR than the global model (Fig. 3a).

DISCUSSION

Global patterns of avian rPD

Our analyses show that macroevolutionary processes have left a strong pattern in the phylogenetic diversity of current avian assemblages. We have shown that there is clear spatial patterning in areas where PD diverges from SR, and this suggests that biological and geological processes play a major role in rPD. The spatial pattern observed here for birds differs markedly to those that have been observed previously for other taxa (Davies *et al.*, 2008; Davies & Buckley, 2011; Fritz & Rahbek, 2012), indicating that these processes may operate differently across taxonomic groups. Areas of low avian rPD occurred at high latitudes and in areas of high relief associated with the Andes and Himalayan mountain ranges. Areas with particularly high rPD were distributed more widely and include islands and isolated regions, such as Australia and Madagascar, as well as ecological transition zones, such as the Sahel and parts of Central America.

We discuss our results in the context of the correlates of rPD identified in this study; the relationship between avian, mammalian and amphibian rPD; the importance of refining our understanding of rPD; and the potential implications for conservation.

Potential drivers of avian PD

As suggested by earlier studies (Rodrigues *et al.*, 2005; Davies & Buckley, 2011; Fritz & Rahbek, 2012), SR showed a high correlation with PD; however, additional variables explained much of the remaining variation (rPD). As expected, the importance of the additional environmental variables differed between the individual realms and, consequently, the individual realm models predicted realm-level PD better than a single global model. Areas of very high or low rPD reveal information about the underlying structures of the communities, and indicate if these are taxonomically clustered or

Table 2 Variables used to model phylogenetic diversity (PD) on a global scale and in the individual realms. Standardized coefficients are given for all variables that have been used in a model. Variables which have been consistently selected for the best model (variables that were in the best model after model selection 95% of the time) are marked with an asterisk. Variables which have not been used in any of the models were excluded from the table (habitat diversity, mean short-term climate stability, maxium short-term climate stability).

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*	–	–	–	–	–	–	–	–	–	–	–	–
Maximum 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*

overdispersed (Rodrigues *et al.*, 2005; Forest *et al.*, 2007). Unusually high rPD, i.e. a taxonomically overdispersed assemblage in an area, especially when associated with low SR, can be the result of the existence of old lineages, harbouring unique evolutionary information. These lineages can result from a speciation process with little radiation, or from the extinction of other species in the same clades (Rodrigues *et al.*, 2005). These old lineages occur more frequently in the Neotropical and Afrotropical regions, which harbour large numbers of basal taxa (Wiens & Donoghue, 2004; Hawkins *et al.*, 2006, 2007). By contrast, unusually low rPD (i.e. a taxonomically clustered assemblage) is more likely to occur in areas with more recent speciation events (Davies & Buckley, 2011).

The environmental predictors tested here were expected, *a priori*, to be important based on macroecological and biogeographical theory. For example, contact zones between realms could positively affect the rPD because dispersal events from different species pools in neighbouring biogeographical realms into areas in the contact zone are likely to occur. We found that a large proportion of the cells with a high rPD are located within contact regions between biomes, such as in Sahelian Africa. Consequently, the distance to the nearest neighbouring realm was an important driver of the rPD pattern in the Afrotropical realm.

Another likely predictor of low rPD that we considered *a priori* was climate stability. It was selected because areas with unstable climates are likely to experience frequent local extinction events, reducing the number of old lineages. The largest clusters of low rPD occur in the two large northern-temperate realms, as well as in some mountain areas at lower latitudes, such as in the Andes and the Himalayas. In the Nearctic and Palaearctic, the climatic stability since the LIG is the most important explanatory variable of rPD. Low rPD in areas of climatic instability since the LIG might reflect the impact of past glacial events, and result in a phylogenetically depauperate fauna considering the SR in the area.

Altitudinal range was considered a potential driver of both high and low rPD, depending on the age of the mountain range and the local climate stability. High rPD is likely to occur where movement up or down the altitudinal gradient could act as a local buffer against climatic variation, enabling persistence of lineages. Low rPD is likely to be found where mountain ranges are relatively young and provide a centre for relatively recent speciation events. Previous studies have identified mountain ranges as centres for speciation during the Pleistocene period (*c.* 2.5 Ma to 12 Ka) (Fjeldså, 2012; Päckert *et al.*, 2012), although there is evidence that some of the younger mountain ranges are approaching ecological saturation and species radiations are slowing down (Price *et al.*, 2014). We found greater support for altitudinal range being associated with low rPD, with areas of low rPD in the relatively young Andes and Himalayan mountain ranges. The importance of altitudinal range in explaining rPD in the Neotropical realm model, which contains the Andes, similarly suggests that these mountain ranges may act as centres

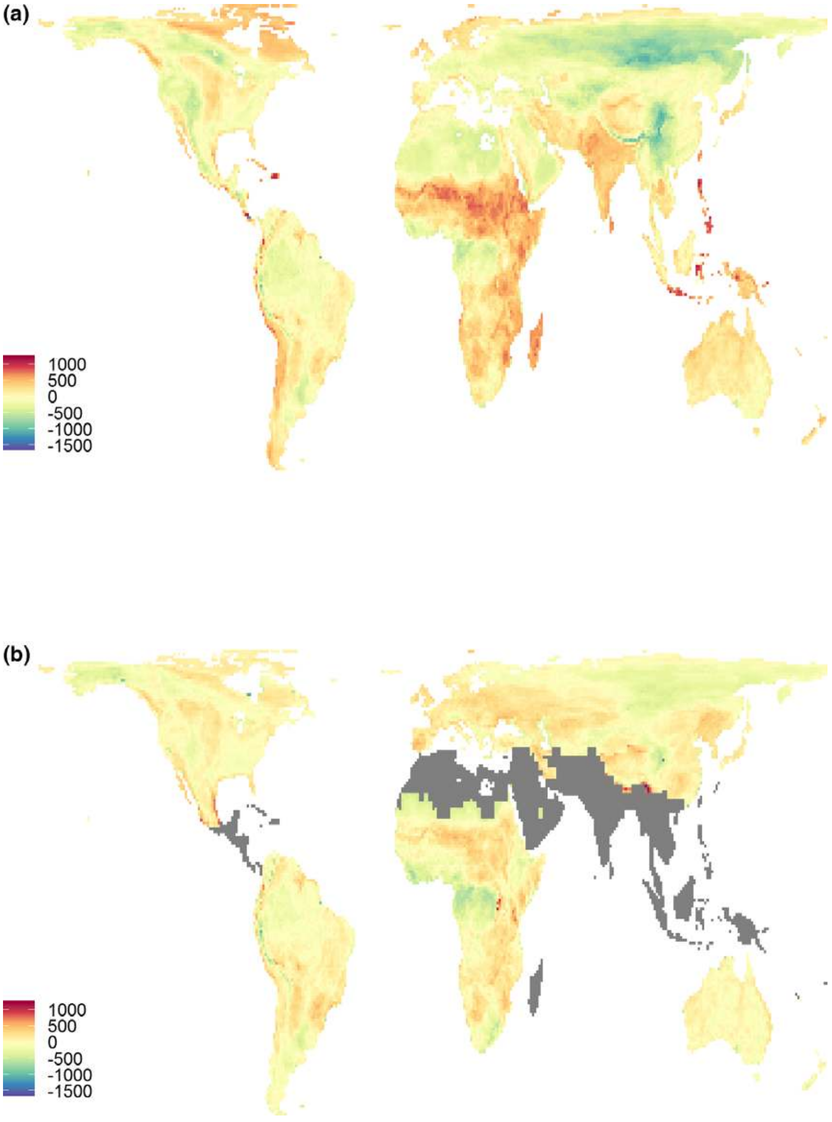

Figure 3 (a) The residuals of the global model to predict phylogenetic diversity (PD) and (b) the residuals of stitched models per realm. Realms with less than 500 cells and realms where no drivers for the PD pattern other than species richness (SR) could be identified were excluded from the individual realm analysis and are masked grey. [Colour figure can be viewed at wileyonlinelibrary.com]

for recent speciation, resulting in low rPD despite high endemism. Hence, the variables that best explained rPD in this study tend to fit with contemporary evolutionary and geological understanding of how species have evolved and persisted.

The only potential driver of avian PD that was not selected as important in any model was contemporary habitat diversity. This might reflect that habitat diversity mainly drives patterns of SR (Lack, 1969; Bazzaz, 1975). It might also arise because of the use of contemporary habitat diversity data, which does not reflect long-term changes in habitat diversity that might have influenced the current PD pattern.

Several of the larger biological realms span multiple ecosystems, such that variables explaining rPD may not operate similarly across the entire area. As we only report variables that are selected in most models, this could result in some important variables that operate in only part of a realm being overlooked. For example, in the Oriental realm, only SR was consistently selected, although long-term temperature stability was selected in 76% of models explaining PD. We found that adding this variable significantly improved PD prediction for the Indian subcontinent but not for the rest of the Oriental realm. This suggests that, for some realms, variables influencing PD may be operating over a finer scale than the realm and conducting analyses over smaller subregions could highlight locally influential variables that are overlooked by our realm-level analysis.

Mismatch of avian rPD with that of other taxa

The rPD patterns found for birds are very different from those previously identified for amphibians (Fritz & Rahbek, 2012) and mammals (Davies & Buckley, 2011; Safi *et al.*, 2011; Rosauer & Jetz, 2015). Strikingly, the patterns of highest and lowest rPD for birds are, to a large extent, the inverse of those found for amphibians. In particular, for birds, areas of low rPD are often located in extensive mainland areas and in mountainous areas such as the Himalayas and the Andes;

for amphibians, these are areas of high rPD. For amphibians, islands and isolated areas such as Australia, Madagascar, New Guinea, and the Caribbean have been identified as having low rPD (Fritz & Rahbek, 2012), whereas for birds, these tend to be regions of high rPD. Similarly, areas of high rPD for amphibians in the Indo-Chinese realm are identified as regions of lower than expected PD for birds. For birds and mammals, there are also areas where the two taxa show contrasting patterns of rPD. This occurs in islands and isolated areas such as Australia and the Caribbean, as well as Central America, with avian rPD being higher than mammal rPD. Areas such as the Sahel, parts of Eastern and Southern Africa, and parts of the Indian subcontinent show a high rPD for both taxa.

Relatively few areas of the world have similarly high rPD for birds, mammals and amphibians. Those that do include parts of South America which lie to the east of the Andes, the Cameroon Highlands and parts of the Eastern Arc mountain range in Africa. Amphibians and birds also both have high rPD in SE Brazil and parts of Indochina. However, outside of Amazonia, the most remarkable thing about rPD patterns of these taxa is their lack of congruence. This may, in part, be a result of the mobility of birds relative to mammals and amphibians, which could facilitate relatively rapid recolonization of newly exposed mountain and arctic sites following glaciation events, and increased colonization of isolated island sites (Weir & Schluter, 2004). It could explain the different observed patterns among taxa on islands and newly exposed sites, which often show very low rPD for amphibians and mammal but not for birds.

Improving our understanding of rPD

Here, we try to explain rPD through consideration of contemporary niche diversity (current habitat and climate diversity) and longer term climate stability. However, there are other potentially important determinants of PD that we were unable to consider, including short duration extreme events (climatic or tectonic), longer term habitat occurrence and persistence, and isolation/connectivity due to landmass movements. One of our putative niche measures, elevation range (considered a proxy for contemporary climate diversity), may have operated more as a tectonic proxy in our models, by highlighting the youngest land on mainland landmasses, such as the Himalayas and Andes. Assessing directly the role of these long-term landmass and habitat changes and the impacts of extreme events was not possible in the current study. Future studies of PD would undoubtedly benefit from the inclusion of such measures, should data become available.

The phylogeny of Jetz *et al.* (2012) is the best full avian phylogeny currently available. Nevertheless, it has been the focus of academic discussion as a result of the methods used to construct the phylogenetic tree (Ricklefs & Pagel, 2012). Sources of uncertainty include the use of a previously defined backbone, the estimation of branch length by inference from time-dated trees (Venditti *et al.*, 2010), as well as local differences in the level to which populations are resolved (see Appendix S1g for a more detailed discussion of the potential sources of uncertainty).

Amendments to the avian taxonomy are ongoing, and suggested alterations to the phylogeny of living birds further our understanding of avian phylogenetic history (Appendix S1h). Recent amendments demonstrate the rapid advances in this field (Jarvis *et al.*, 2014; Prum *et al.*, 2015; Rocha *et al.*, 2015). Repeating our analyses with alternative full avian phylogenies, when available, will determine how robust the patterns identified here are to updates in taxonomy.

Our study gives a first indication of the variables that drive avian rPD patterns on a large scale in different ecoregions of the world, and identifies areas where macroecological processes are likely to have affected the underlying structures of species in a community, resulting in a mismatch between SR and PD. Future work could focus on understanding the causes of pattern in rPD at a finer scale. Exploring beta diversity (Whittaker, 1960) across areas with a steep rPD gradient could aid our understanding of how changing species compositions affect rPD, and enable deeper insights into the drivers at a local scale. For example, high rPD might be primarily driven by the occurrence of a small number of old lineages in an area.

Studies considering PD for conservation purposes have become more frequent (Rodrigues & Gaston, 2002; Winter *et al.*, 2012; Brooks *et al.*, 2015). These have advocated, for example, conservation that prioritizes the protection of unique lineages (Isaac *et al.*, 2007). Nonetheless, phylogenetic information remains underused (Rodrigues *et al.*, 2011). One difficulty is that biodiversity measures based on phylogenetic information [e.g. PD (Faith, 1992), phylogenetic endemism (Rosauer *et al.*, 2009) and evolutionary distinctiveness (Isaac *et al.*, 2007)] have been found to be inconsistent in their spatial congruence (Daru *et al.*, 2015). A future research priority should be to improve our understanding of the global pattern of rPD among taxa and its relationship with other biodiversity measures, and with current protected area networks, to make phylogenetic information more applicable for conservation practice.

Implications for conservation

Our findings have implications for biodiversity conservation. Apart from the role of rPD in aiding our understanding of historical patterns of evolution, extinction and colonization, rPD could prove a useful metric to highlight areas of high irreplaceability and added value, in conservation terms. Our study confirms that, across much of the world, SR provides a good proxy for avian PD and, hence, provides a good surrogate for biodiversity (where biodiversity is richness at all diversity scales, including phylogenetic diversity). However, we also identify areas of high (or low) rPD where this relationship is weaker. The areas of high rPD are of particular interest for conservation planning as they indicate a likely high evolutionary potential of a community, in comparison to communities with a similar SR in combination with an average or low rPD value. Interestingly, for birds, we find that many areas prioritized because of endemic species actually have low rPD. Typically, these areas are associated with recent species radiations as seen in, for example, the Andes which have a comparably low rPD. This region harbours many endemic, but closely related, hummingbirds (McGuire *et al.*, 2014). Consequently, such areas might be considered of lower conservation priority than regions with similar SR but higher rPD.

Importantly, the lack of overlap between the rPD of birds, amphibians and mammals, compels caution in generalizing PD results among taxa. This result is consistent with a recent study by Zupan *et al.* (2014) which suggests strong divergence between the patterns of PD in vertebrate taxa across Europe. As with SR, it seems that there is no 'silver bullet' indicator taxon that can be used to infer PD across taxa. That habitat diversity was seldom identified as a useful predictor of PD suggests that this, too, would be a poor metric of current PD. Using ecosystem-based metrics (such as habitat/ecosystem richness) as a basis for protecting areas for biodiversity conservation (Brooks *et al.*, 2006) may conserve ecosystem function, and to some extent SR, but would perform rather poorly in representing rPD, as habitat diversity was not included in our global or regional models of PD. Current best-practice to identify terrestrial biodiversity hotspots (such as Conservation International's hotspots or BirdLife International's EBAs) consider endemism but do not yet account for phylogenetic uniqueness. The next challenge for conservation biologists is to combine supertree PD data across a number of key taxa to identify hotspots of biodiversity that represent areas of true phylogenetic diversity and uniqueness, in addition to species diversity, endemism and distinctiveness.

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SUPPORTING INFORMATION

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

Appendix S1 Supplementary methods and supplementary figures.

BIOSKETCH

All authors except P.J.V. are members of the Conservation Ecology Group (www.conservationecology.org) at Durham, which applies ecological approaches to issues of interest to conservation biology. A.V. is a PhD student in the group working on global species distributions and their underlying ecological and evolutionary processes. A.V. is supervised by S.G.W. and P.A.S. A.V. and D.J.B. performed the analyses and, with S.G.W. and P.A.S., wrote the manuscript. P.J.V. is a climatologist, working on contemporary and palaeoclimatology.

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