

## LETTER

# Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients

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### Abstract

Regions worldwide differ markedly in species richness. Here, for birds and mammals worldwide, we directly compare four sets of hypotheses regarding geographical richness gradients: (1) evolutionary, emphasising heterogeneity in diversification rates, (2) historical, related to differences in region ages and sizes, (3) energetic, associated with variation in productive or ambient energy and (4) ecological, reflecting differences in ecological niche diversity. Among highly independent regions, or ‘evolutionary arenas’, we find that richness is weakly influenced by richness-standardised ecological niche diversity, questioning the significance of ecological constraints for producing large-scale diversity gradients. In contrast, we find strong evidence for the importance of region area and its changes over time, together with a role for temperature. These predictors affect richness predominately directly without concomitant positive effects on diversification rates. This suggests that regional richness is governed by historical and evolutionary processes, which promote region-specific accumulation of diversity through time or following asymmetrical dispersal.

### Keywords

Birds, diversification rate, diversity, functional diversity, mammals, species traits.

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## INTRODUCTION

Despite dedicated research, there is still no consensus on the determinants of broad-scale diversity gradients (Ricklefs & Schlüter 1993; Rosenzweig 1995; Hawkins *et al.* 2003; Mittelbach *et al.* 2007). Four main sets of hypotheses are: (1) macroevolutionary, focusing on environmental and geographical heterogeneity in diversification rates (Rohde 1992; Mittelbach *et al.* 2007; Rolland *et al.* 2014), (2) historical, suggesting differences in the ages and sizes of regions as major factors providing greater opportunities for speciation and maintenance of richness (Rosenzweig 1995; Fine & Ree 2006; Jetz & Fine 2012), (3) energetic constraints on capacity, emphasising differences in resource availability (Hawkins *et al.* 2003; Evans *et al.* 2005; Storch *et al.* 2005; Hurlbert & Jetz 2010) and (4) ecological constraints on coexistence, reflecting geographical differences in the variety of available niches or in the amount of ecological divergence among lineages (Ricklefs & Schlüter 1993; Chesson 2000; Rabosky 2009). Although these hypotheses have been regularly tested in isolation, a synthetic study contrasting their relative importance is still lacking.

The association between these hypothesised effects and species richness depends on whether richness has reached a balance between extinction, speciation and dispersal. At equilibrium, we would expect a direct influence of predictors associated with variety of ecological opportunities, or niches, which facilitate coexistence among species in a region. Likewise, fewer energetic constraints (e.g. higher total net primary productivity) may allow lower extinction rates and larger region area may facilitate higher speciation rates (Rosenzweig 1995) both resulting in higher equilibrium richness. If, however, species richness is not at equilibrium, and thus a limit to

regional richness has not been reached (Morlon *et al.* 2010), rates of diversification, dispersal and region age are expected to be key drivers (Wiens 2011). In this case, other predictors may modify richness largely indirectly by altering rates of diversification or dispersal. The major challenge we address in this study is to quantify the direct and indirect ecological and evolutionary mechanisms underlying current variation in species richness.

Net diversification rates (here defined as speciation – extinction) are expected to be positively related to species richness under all non-equilibrium models, unless heterogeneity in dispersal or region age masks these patterns. However, a lack of suitably large and reliable phylogenies has to date limited tests of the ability of diversification rates to explain global richness gradients. Using a clade-based approach, higher diversification rates were found at lower latitudes for birds (Cardillo *et al.* 2005; but see Weir & Schlüter 2007), plants (Davies *et al.* 2004) and mammals (Rolland *et al.* 2014). In contrast, a recent species-level analysis for all birds (Jetz *et al.* 2012) and similar results for a sample for over 200 mammalian genera (Soria-Carrasco & Castresana 2012) suggested at most a limited role for differences in rates of net species production to explain the latitudinal richness gradient. An integrative geographical and regional assessment in the context of alternative mechanisms is, as of yet, missing.

Classical niche-based hypotheses predict that niche partitioning among species presents a key ecological limitation on coexistence (MacArthur 1972). If richness is at equilibrium, more available niches may directly allow more species to coexist. However, also non-equilibria hypotheses predict a relationship between ecological niche diversity and richness, albeit indirectly via diversification rates (Wiens 2011). Hence,

within-region depressed opportunities for ecological differentiation, or low levels of evolutionary divergence in ecological traits among a region's lineages, could impede within-region survival of lineages and impose constraints on diversification (Rabosky 2009; Etienne & Haegeman 2012). Conversely, regions that support and produce lineages with distinct ecological niches may be less constrained and thus experience less inhibited speciation, or lower extinction and thus harbour higher richness. In contrast, a negative ecological divergence – diversification relationship would arise if ecological limitations do not constrain richness, e.g. in the case of non-ecological speciation or coexistence unimpeded by similarity (Schluter 2009; Tobias *et al.* 2014). Higher speciation rates may still increase richness, but result in the accumulation of ecologically overlapping species, e.g. species from recent radiations that have not yet strongly diverged ecologically. Although this connection between ecological niche diversity and diversification rates of regional assemblages is critical for our understanding of biodiversity, it has seldom been examined on a global scale (Ricklefs 2012).

Inference about the processes underlying richness gradients has been impeded by the difficulty of integrating the respective ecological, phylogenetic and spatial components (Pyron & Burbrink 2013; Morlon 2014). Attempts to discern these effects have included macroevolutionary studies focused on select clades, e.g. to demonstrate slowdowns in diversification rate with increased species richness as evidence for ecological constraints on diversification (Phillimore & Price 2008; Rabosky 2009; Kisel *et al.* 2011; Moen & Morlon 2014). But these studies have not explicitly addressed the geographical context of diversification and coexistence. Ecological constraints and regional niche filling would naturally extend beyond select clades to include interactions between species that may be distantly related but ecologically convergent. This requires a sufficiently large phylogenetic scope.

We here assess, jointly for birds and mammals, the variation in richness using historically and climatically well-defined bioregions or 'evolutionary arenas'. While both birds and mammals are endotherms and the global patterns of richness are markedly congruent (Grenyer *et al.* 2006; Hawkins *et al.* 2012), the similarity in relative importance of underlying processes is much less clear (Hawkins *et al.* 2012). Despite a broad overlap in habitats and diets, distinct adaptations, such as powered flight in birds (and bats), rumination and a large range of body sizes in mammals, suggest potential for ecological divergence across biomes. We use a global compilation of best-available species-level ecological traits and phylogenies to directly contrast, for the first time, four major sets of hypotheses underlying global richness gradients of these taxa.

## METHODS

### Species distribution and geographical regions

Geographical studies are inherently non-independent. One way to reduce this problem is to conduct analyses over regions, or putative core 'evolutionary arenas', that are as evolutionarily independent as possible (Rosenzweig *et al.* 2012). We follow Jetz & Fine (2012) and use 32 well-

established bioregions (biomes within the world's main biogeographical realms). As these bioregions are climatically distinct (as opposed to those defined by community dissimilarity), they allow us to directly assess the influence of environmental drivers.

Total species *Richness* (*All*) within each bioregion was determined as the number of species ranges intersecting the bioregion area (Table S1). However, as many of these species will have most of their distribution in other bioregions, the signature of bioregion-specific factors, such as area, age or diversification rate, is likely to diminish. To elicit the signal of processes on the bioregion scale, we additionally calculated patterns for *Resident* species only, defined as species with the majority of their range within the designated bioregion (Jetz & Fine 2012). Assigning each species only to its dominant bioregion also eliminates pseudo-replication and ensures that common and rare species are equally well represented. This procedure produced complete region independence at the species level (Table S1; 100% of the species occur only in one bioregion).

Range maps for mammals were based on the IUCN assessment (<http://www.iucnredlist.org/>) and range maps for birds compiled from the best available sources for a given broad geographical region or taxonomic group (Belmaker & Jetz 2011) with updates as in Jetz *et al.* (2012). We included all non-marine birds (breeding ranges only) and all terrestrial mammals, including volant species. Spatial scale is likely to influence the perception of ecological and evolutionary patterns (Belmaker & Jetz 2011). We thus repeated the analyses but instead of bioregions we used regionalisation delimitations based on maximising assemblage dissimilarity (Appendix 1).

### Phylogenies

The complete phylogenetic tree for birds was based on (Jetz *et al.* 2012), which includes the posterior distribution of species-level phylogenies representing the underlying reconstruction uncertainty. Species without genetic information (3330) were placed within their clade using taxonomic information and branching times sampled from a pure birth model of diversification. The mammal trees follow Kuhn *et al.* (2011) which builds on prior work by Bininda-Emonds *et al.* (2007) and Fritz *et al.* (2009).

### Diversification rates

We calculated the species-level lineage net diversification rate for every species following (Jetz *et al.* 2012; cf. Supplementary Methods 1.2.2 for individual lineage-level analyses). *DivRate* is calculated as the inverse of its Equal Splits measure:

$$DivRate_i = \left( \sum_{j=1}^{N_i} l_j \frac{1}{2^{j-1}} \right)^{-1}$$

where *DivRate<sub>i</sub>* is the diversification rate of species *i*, *N<sub>i</sub>* is the number of edges on the path from species *i* to the root, and *l<sub>j</sub>* = length of the edge *j*. As demonstrated in (Jetz *et al.* 2012), *DivRate* aims to capture clade-wide net diversification estimates in birth-only and homogeneous birth-death trees, and still performed well for a simulated set of non-homogeneous

trees with linear density-dependence plus extinction. Estimating extinctions from molecular phylogenies is notoriously difficult. *DivRate* is unable to account for the extinctions of whole clades in select parts of the tree and most reliably measures speciation.

We considered several alternative ways of calculating *DivRate* (Appendix 1). All methods returned similar results and exact *DivRate* metric specification did not affect our main conclusions (Figs. S1, S2). We therefore restrict our main presentation of results to *DivRate* estimated using the entire phylogenetic tree (Jetz *et al.* 2012), but restrict the *DivRate* calculation to below the most ancient node of species in the region. We used the rate values calculated from a posterior distribution of 100 trees. We then calculated the median diversification rate of each regional assemblage as an estimate of its *DivRate* (Table S1).

### Historical predictors

Regions that have been large over long time are expected to have accumulated and retained more species than those that are small and young (Rosenzweig 1995; Fine & Ree 2006; Jetz & Fine 2012). The influence of region size and age on *Richness* may be direct, by providing longer time for species to accumulate or by lowering extinction and elevating speciation rates when the region is at equilibrium (e.g. larger regions allow greater opportunities for *in situ* speciation through vicariance). Under non-equilibrium dynamics, we predict similar mechanisms will lead to an indirect positive association between region size and age and *Richness* via higher *DivRate* (Kisel *et al.* 2011).

For each bioregion, we used an estimate of time-integrated area (*TimeArea*) as detailed and provided in Jetz & Fine (2012) ('wet' interpretation). Specifically, this variable represents the integrated areal extent of a bioregion over 55 million years, or simply the sum of the area estimated for each of the 55 one million-year periods. For analyses with regions based on maximal dissimilarity (which do not necessarily correspond to integral biomes, making it difficult to reconstruct their past environment), we only used current-day region area (*Area*) as variable. Both *Area* and *TimeArea* were  $\log_{10}$  transformed.

### Environmental predictors

Bioregion-typical temperature estimates (*Temp*) were based on average annual temperatures for 1961–1990 at native 10-min resolution (New *et al.* 2002). For estimates of annual Net Primary Productivity (*NPP*; grams Carbon  $\text{m}^{-2} \text{year}^{-1}$ ), we used an average from 17 global models at a spatial resolution of 0.5 degrees (Cramer *et al.* 1999).

### Ecological divergence

#### Data

To calculate ecological niche diversity, we compiled extensive data on ecologically important trait variables that describe the role that species play within a community (Belmaker & Jetz 2013; Wilman *et al.* 2014). For both birds and mammals, we used the same six trait categories: diet, body mass, activity

cycle, the degree to which the species is fossorial, foraging height and aquatic/terrestrial foraging. As these traits describe species-level attributes; they do not accommodate intraspecific variation, which is likely to be low relative to interspecific differences. We feel these traits quantify important information regarding the likelihood of species occupying similar ecological niches. While it may be possible to gain more accurate information for specific small clades, it is unlikely that data resolution for all birds or mammals will improve considerably in the near future. For a complete description of the data, see Appendix 1.

#### Metric calculation

Calculating trait diversity from a combination of both ordinal and continuous variables required that we first constructed a trait distance matrix. We used Gower dissimilarity and equal weighting of the traits, but results were robust to changes in weighting (Table S2). We formed a dendrogram based on UP-GMA clustering of the distance matrix and used the sum of dendrogram branch lengths. For more information, see Appendix 1.

#### *NicheDiv<sub>n</sub>*

We estimate 'Eltonian' assemblage-level ecological differentiation, using ecological traits or 'niche diversity' (*NicheDiv*, often also called 'functional diversity') of all species associated with a region. Many indices of trait diversity are strongly linked to the number of species within an assemblage. Thus, we calculated *NicheDiv<sub>n</sub>*, which is *NicheDiv* rarefied to  $n$  species. *NicheDiv<sub>n</sub>* captures the average contribution of  $n$  species to total *NicheDiv*, thus facilitating comparisons between assemblages that differ in richness (Nipperess & Matsen 2013). Small *NicheDiv<sub>n</sub>* thus indicates low trait diversity relative to the number of species present. *NicheDiv<sub>n</sub>* provides an estimate of how separate in trait values species are and thus characterises ecological niche differentiation.

For *Resident* species, we used  $n = 10$  which resulted in a small loss of bioregions for both birds and mammals (two and three, respectively). When using *All* species and for the regionalisation based on dissimilarity, we used  $n = 40$ . The value of  $n$  had little effect on the *NicheDiv<sub>n</sub>* ranking of the assemblages (Fig. S3).

### Analyses

We examined the direct relationship between our four predictors and *Richness* using general linear models. Within multiple predictor models, we used hierarchical partitioning to assess the average contribution of each predictor to the variance in species richness over all possible models using the R package 'relaimpo'. Because of the strong independence of sampling units, both in terms of response (no overlap in species) and predictors (by definition each bioregion is environmentally highly distinct from neighbouring bioregions), the usual concerns that spatial autocorrelation will cause a spurious relationship between measured variables is reduced. All predictors displayed low pairwise correlations (Fig. S4).

We examined indirect effects on *Richness* using structural equation modelling. Due to the large number of possible

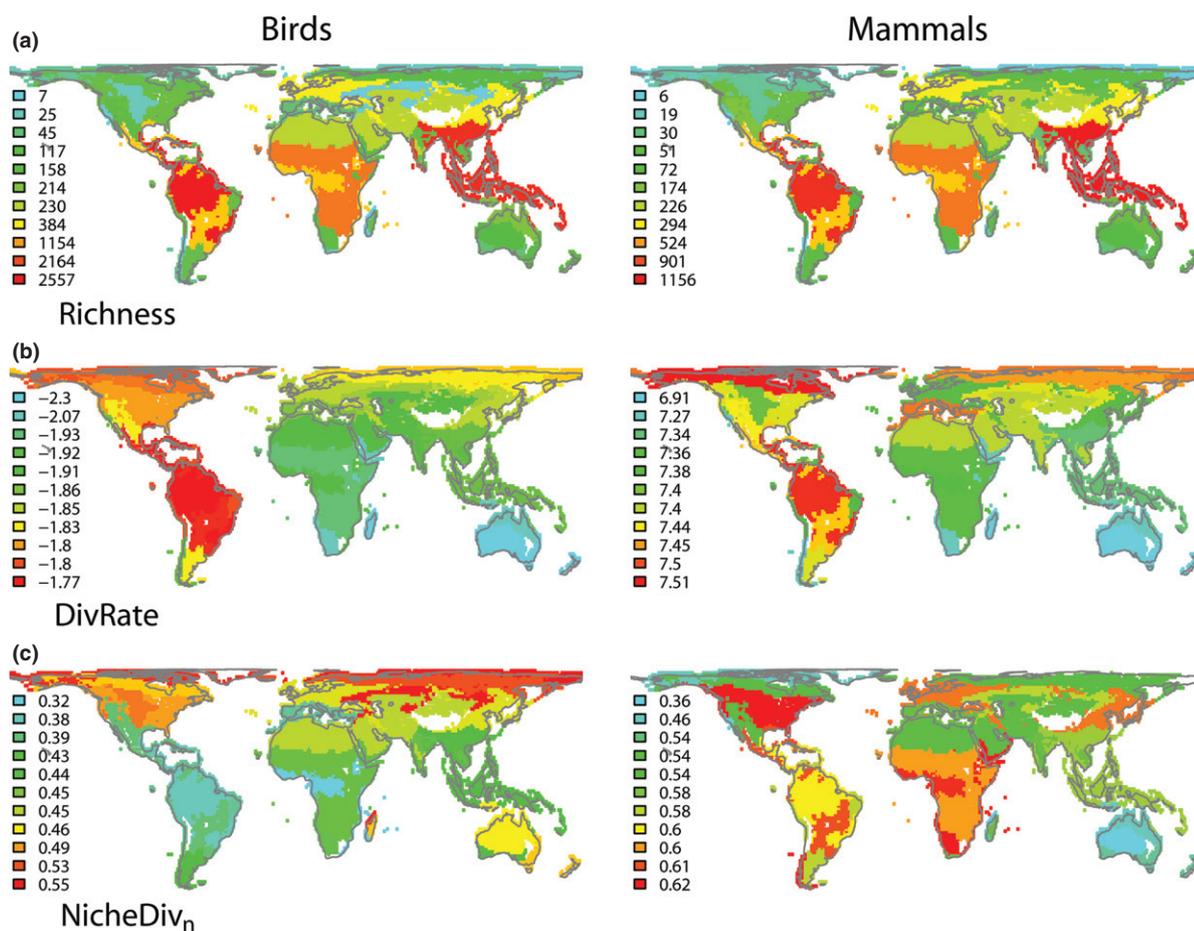
relations between predictors and the small number of data points, we chose to focus on several key relationships. First, we focused on the direct and indirect effects of *DivRate* and *NicheDiv<sub>n</sub>* on *Richness*. We modelled an indirect influence of *NicheDiv<sub>n</sub>* on *DivRate*, corresponding to a putative increase in diversification rate in the face of additional ecological opportunities. While we are aware that the direction of causality may become reversed, with *DivRate* influencing *NicheDiv<sub>n</sub>*, as high diversification rate may result in more redundant species and hence lower *NicheDiv<sub>n</sub>*, this had little influence on the results. Second, to model the direct and indirect effect of energy we chose to include either *NPP* or *Temp*, but not both of them, in the model. Finally, we used region *Area* or *TimeArea* to control for the region history. Region history may have an additional indirect influence on *Richness* by influencing *DivRate* (Kisel *et al.* 2011). Interactions, such as an interaction between region *TimeArea* and *DivRate* or energy (Storch *et al.* 2005; Hurlbert & Jetz 2010) were evaluated but found to be weak (Fig. S5). Structural equation modelling was performed in R using the package ‘lavvan’.

## RESULTS

Avian and mammalian *Richness* are highly congruent among bioregions ( $r = 0.89$ ,  $P < 0.001$ ) and exhibits clear temperate-tropical differences (Fig. 1). In contrast, *DivRate* does not exhibit a clear latitudinal trend (Fig. 1). In both birds and mammals the main gradient was, instead, East–West, with particularly high rates in the Neotropics.

We estimate assemblage-level ecological differentiation using ecological trait or ‘niche’ diversity (*NicheDiv*), standardised using rarefaction to be richness-independent (*NicheDiv<sub>n</sub>*). We find that in both groups the highest *NicheDiv<sub>n</sub>* is not associated with areas of the highest richness or total *NicheDiv* (Fig. S6). There are also strong clade differences: mammalian *NicheDiv<sub>n</sub>* is highest in southern Africa and temperate South America, while bird *NicheDiv<sub>n</sub>* is highest in the northern Palearctic and on islands such as Madagascar (Fig. 1).

We examine the direct and indirect associations between *NicheDiv<sub>n</sub>*, *DivRate* and *Richness* using structural equation models. Both bird and mammal *Richness* is only very weakly directly associated with *NicheDiv<sub>n</sub>*. We do find an association



**Figure 1** Global patterns of species *Richness*, *DivRate* and our measure of ecological niche diversity (*NicheDiv<sub>n</sub>*) for birds and mammal. *DivRate* is calculated as the inverse of the Equal Splits measure and represented in units of  $\log(\text{million years}^{-1})$ . *NicheDiv<sub>n</sub>* (*NicheDiv* rarefied to  $n$  species; here  $n = 10$ ) is a richness-independent metric of multivariate trait space filled by an assemblage and is an estimate of the species density in ecological niche space. We use *Resident* species only, defined as species with the majority of their range within the designated bioregion, which produces complete region independence at the species level. Patterns were calculated for 32 well-established, geographically and climatically distinct bioregions. We excluded biomes for which we did not have information on past environments such as montane ecoregions.

between  $NicheDiv_n$  and  $DivRate$ , but the directionality is inconsistent between taxa (positive  $DivRate$  to  $NicheDiv_n$  association for mammals, negative association for birds; Fig. 2). The partial relationships between  $DivRate$  and  $NicheDiv_n$  vary little when adding region size and history ( $TimeArea$ ; compare Fig. 2b and c). The direct association between  $DivRate$  and  $Richness$  was positive but surprisingly small and dependent on the specific model formulation (compare Fig. 2b and c). Thus,  $DivRate$  was more strongly associated with  $Richness$  before  $TimeArea$  was added as a predictor. The direct influence of  $Temp$  on  $Richness$  was strong and positive. However, the indirect influence of either  $Temp$  or  $NPP$  on  $Richness$  via  $NicheDiv_n$  or  $DivRate$  was generally small or even negative (Figs. 2, S7). Of the variables examined, both  $TimeArea$  and  $Area$  explain the highest percentage of variance in  $Richness$  for both birds and mammals (Figs. 3, S8). These patterns were similar when using *All* species as opposed to *Resident* species only (Fig. S9).

We extend these analyses to finer grains that less strictly capture independent evolutionary units (240 regions, species counted in every region they intersect; Figs. S10, S11). We find a much stronger effect of  $NPP$  at this grain while  $Temp$

is relatively less important. For mammals,  $NicheDiv_n$  also displays a stronger and positive effect at this scale (Fig. S10). In contrast, the influence of  $DivRate$  on  $Richness$  diminishes and becomes generally small and even negative. The prime effect of region  $Area$  on  $Richness$  remains at this scale as well.

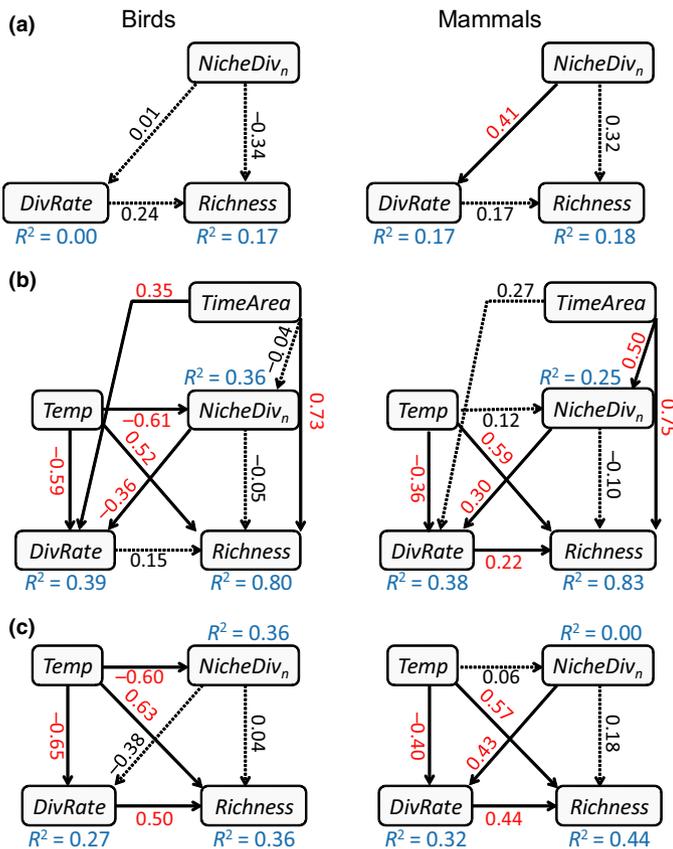
## DISCUSSION

In this study, we have directly contrasted the relative strengths of four set of processes underpinning global richness patterns. For two almost complete large taxa (excluding only marine species), we uncovered both strong similarities and unexpected discrepancies in the apparent relevance of different mechanisms. These findings benefit from an integrative phylo-spatial analysis framework that offers an effective way to identify the different processes underlying richness gradients.

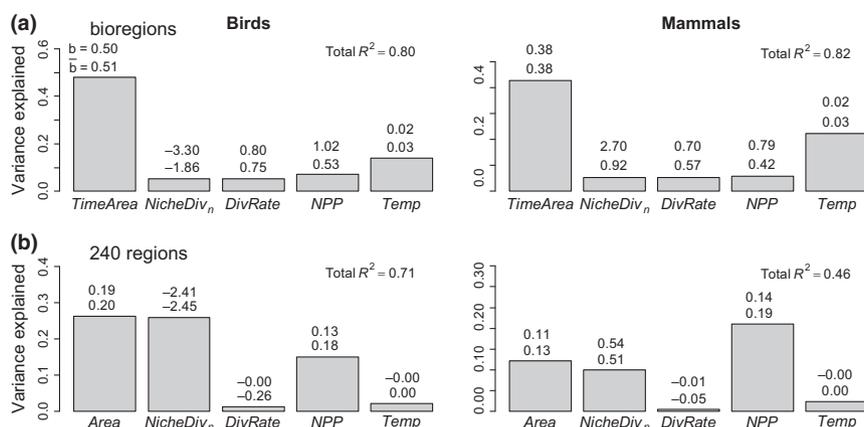
### Diversification rate

$DivRate$  explains some of the variance in  $Richness$ , but its effect is generally smaller than the influence of other predictors (Figs. 2 and 3). This result is robust to the method used to calculate  $DivRate$ , to geographical scale, and to whether *Resident* or *All* species were used. This finding falls in line with recent studies that have found low correlations between  $DivRate$  and  $Richness$  (Jetz *et al.* 2012; Soria-Carrasco & Castresana 2012). Nevertheless, the lack of a strong correlation between  $DivRate$  and richness is surprising, and suggests that either global richness is largely at equilibrium or that processes such as dispersal or region history are strong enough to mask the influence of  $DivRate$ .

The discrepancy between our results of a weak influence of  $DivRate$  on  $Richness$  and other recent analyses (e.g. Rolland *et al.* 2014) is puzzling and may stem from methodology and scale. Methodologically, our estimate of diversification rates do not account well for processes such as extinction or rate variation (see 'Limitations' below). More complex methods such as geographical state speciation and extinction (GeoSEE, Goldberg *et al.* 2011) attempt to simultaneously account for speciation, extinction, and dispersal, but have now been shown to potentially suffer significant Type I error rates (Rabosky & Goldberg 2015). Furthermore, such methods are limited in the number of regions that can be tested and hence latitudinal gradients are treated as binary tropical-temperate comparison that may conceal patterns such as the East–West gradient uncovered in this study. Scale differences may further complicate comparisons as many studies have focused on specific clades while our analyses address extant mammals and birds in their entirety and compare the average characteristics of large regions. While the regions analysed show substantial variation in predictors and response (and the strong effects of  $TimeArea$  and consistency of  $DivRate$  results among the two scales analysed reassure of the power of the analysis), the effect of single constituent clades (and their above- or below-region average  $DivRate$ ) necessarily decreases with regional assemblage size. Thus, while specific clades may experience reduced extinction or elevated speciation at low latitude, such results may not necessarily generalise and scale up to explain latitudinal gradients of large clades.



**Figure 2** Path models depicting the relationships among the putative predictors of bioregion *Resident* species richness (see Fig. 1a), for the bioregion scale ( $N = 32$  bioregions). Panels a–c correspond to alternative formulation of the path models. (a) Using only  $NicheDiv_n$  and  $DivRate$ ; (b) Full model; (c) Full model, but excluding  $TimeArea$ . Solid path arrows represent significant (at  $P < 0.05$ ) associations. Numbers adjacent to arrows represent standardised regression coefficients (red: significant at  $P < 0.05$ ).  $R^2$  value associated with each exogenous variable are presented in blue. We rarified  $NicheDiv_n$  to  $n = 10$  species.



**Figure 3** Relative importance (% of total variance explained) of mammal and bird species richness predictors. (a) Bioregion scale ( $N = 32$  bioregions) and *Resident* species only. We rarified *NicheDiv<sub>n</sub>* to  $n = 10$  species. (b) 240 regions based on maximum taxonomic dissimilarity and all species. We rarified *NicheDiv<sub>n</sub>* to  $n = 40$  species. Upper numbers are regression coefficients as single predictors, lower numbers are average coefficient value across all models. Relative importance was assessed as the average contribution of each predictor to the variance in species richness over all possible models.

### Ecological niche diversity and constraints

We characterises the density of ecological niches within assemblages using *NicheDiv<sub>n</sub>*, i.e. *NicheDiv* rarified to  $n$  species, and find that *NicheDiv<sub>n</sub>* does not underlie global richness gradients. This result differs from the view that the global richness variation reflects gradients in available niche size, and implies that the increase in richness towards low latitudes is not necessarily a direct consequence of more ‘ecological opportunities’ in tropical regions.

While a direct relationship between *NicheDiv<sub>n</sub>* and richness is not strongly supported, we find important differences between taxa in the relationship between *NicheDiv<sub>n</sub>* and *DivRate*. Under ecologically constrained diversification an increase in *NicheDiv<sub>n</sub>* would be expected to increase *DivRate*. In mammals, a signal of ecology on diversification is seen in the positive correlation between *NicheDiv<sub>n</sub>* and *DivRate* (Fig. 2). Thus, in mammals *DivRate* is higher in regions whose assemblages also exhibit greater ecological differentiation. In contrast, in birds we find a negative effect of *NicheDiv<sub>n</sub>* on *DivRate*. This suggests that, on the scale of regional evolutionary arenas, diversification in birds is decoupled from the ecological constraints that shape trait diversity. For example, the species-rich Furnariidae (and also Tyrannidae) radiated extensively in the Amazon region despite their great similarity in foraging height, body size and diet (Ohlson *et al.* 2008). This means that birds are either more prone to diversify without additional ecological divergence (Ricklefs 2012), that the examined traits are not the ones over which ecological divergence takes place, or that the ecological axes over which birds partition space or time are found on scales much finer than those examined here.

### Area and Age

We use region size integrated over geological time (*TimeArea*) as a compound measure of the opportunities for within-region diversification and as a measure of the scope of species to evade sympatry. We consider the processes associated with region area intertwined over time, as lineages remain consis-

tently associated with bioclimatically distinct regions (Fine & Ree 2006; Jetz & Fine 2012). Nevertheless, we acknowledge the difficulty of separating diversification and within-region coexistence components of *TimeArea* effects on *Richness* (see ‘Limitations’ for further discussion).

Both *TimeArea* and *Area* alone explain a high percentage of variance in species richness for birds and mammals (Figs. 3, S8), emphasising the prime contribution of available bioclimatically similar area and its past dynamics to contemporary richness gradients (Rosenzweig 1995; Fine & Ree 2006; Kisel *et al.* 2011; Jetz & Fine 2012). A similar prime effect of *TimeArea* on *Richness*, appears to underlie the strong congruence in species richness between birds and mammals, despite important differences in apparent ecological constraints.

Under non-equilibrium dynamics, the strong direct effect of *TimeArea* on *Richness* suggests that older regions may have had longer time to accumulate species and larger regions a higher probability of accumulating lineages that have originated *ex-situ*, hence supporting mechanisms that focus on heterogeneity in dispersal rates among regions (Wiens *et al.* 2010). Alternatively, older and larger regions may have attained high equilibrium *Richness* as a balance of higher speciation and lower extinction (Rosenzweig 1995). If equilibrium *Richness* is reached rapidly, this will result in a diminished direct signal of *DivRate* on *Richness*.

### Temperature and productivity

Given the effect of temperature on biotic interactions (Allen *et al.* 2007) and the potential of cold temperatures to act as a constraint on species distributions, we expected a positive effect of temperature on *Richness* and, potentially, on diversification rate. While we find that average annual temperature (*Temp*) had a positive direct effect on *Richness*, the putative indirect effect promoting elevated *DivRate* or *NicheDiv<sub>n</sub>* remains unsubstantiated.

The non-significant association between *Temp* and *DivRate* is particularly surprising and rejects a straightforward application of metabolic theory (Brown *et al.* 2004) for these endotherm groups. It will be interesting to compare these

results with those for ectothermic taxa, for which a more direct temperature effect is predicted. Our findings here suggest that for endotherms high temperature promotes high *Richness* directly. Such a direct influence may be mostly related to climate placing a fundamental, e.g. eco-physiological, constraint on species distributions (Wiens *et al.* 2010; Simova *et al.* 2011).

For net primary productivity (*NPP*), a positive effect on the range of ecological opportunities and niche space has been postulated (Evans *et al.* 2005; Allen *et al.* 2007; Hurlbert & Jetz 2010). The direct effects of *NPP* on *Richness* and indirect association *via NicheDiv<sub>n</sub>* were not well supported (Fig. S7). This implies that *NPP* does not increase regional richness by elevating equilibrium richness, e.g. by providing more niches or by providing larger population sizes and hence reducing extinctions rates. Moreover, we do not find a positive association between *NPP* and *DivRate* (and thus indirectly on *Richness*) for both birds and mammals. Thus, at the scale of bioregions we find little support for hypotheses that suggest a strong role of resource availability for diversity patterns.

### Comparing spatial grains, evolutionary and ecological mechanisms

The choice of scale in macroecological analyses is often arbitrary and mostly related to operational considerations of data availability. In this study, we explicitly focus on bioregions that define evolutionary arenas for which relative independence among sampling units is ensured by focusing on *Resident* species and thus avoiding 'double counting' of wide-ranging species.

We repeat our analyses with spatially more fine-grained units (240 zoogeographically delineated regions). We predict that energy availability, by influencing resource availability, will positively affect the immigration and coexistence (range overlap) of species, and thus have a elevated effect at this scale (see also Jetz & Fine 2012). As expected, we find a much stronger effect of *NPP* at this grain (Fig. 3). We additionally find that for mammals *NicheDiv<sub>n</sub>*, which fails to directly explain gradients in *Richness* at the bioregion scale, has a direct positive association with *Richness* for more finely resolved regions (Fig. S10). Together, these finding strengthens the current paradigm that states that ecological constraints on richness, quantified by energy availability or niche diversity, are more likely to operate over fine spatial scales.

### Limitations

The joint assessment of macroevolutionary and ecological mechanisms in geographical space remains constrained by available data and, as recent concerns highlight (Maddison & FitzJohn 2015; Rabosky & Goldberg 2015), by remaining methodological limitations about how to appropriately relate heterogeneity in diversification rates to character states (such as regional occurrence). The *DivRate* and *NicheDiv<sub>n</sub>* metrics used in our study are transparent, straightforward, and allow the characterisation of regional assemblages essential for testing all hypotheses in conjunction. Nevertheless, several obvious limitations exist: First, our estimate of *DivRate* may be imprecise. Sources of possible error include: (1) The reliance

on extant species only. Thus, *DivRate* estimates are more strongly associated with net diversification rates, (2) The difficulty of estimating within-region diversification. Diversification rates estimated using the entire tree necessarily conflated *in situ* diversification with diversification occurring in other regions. Internal branches with descendants in different bioregion results in shared diversification histories, and diversification may thus harbour internal signals that are not fully unique to a region, (3) Our estimate of *DivRate* does not account for possible variation through time. All these issues may cause an underestimation of the potential influence of *DivRate* on *Richness*. However, we find that strongly different ways of calculating *DivRate*, which all vary in the relevance of these issues (Appendix 1), did not affect the uncovered interdependencies among the putative drivers of *Richness* and hence our results are unlikely to hinge on precise *DivRate* estimates.

Second, *NicheDiv<sub>n</sub>* is quantified with the same set of ecological traits in all regions. Uncertainties regarding some ecological delineations remain (see Wilman *et al.* 2014), and additionally the level of detail may be more appropriate for some regions or guilds than others. Tropical insectivore birds in particular may be more finely differentiated by a combination of beak forms and foraging behaviours than the available body size and foraging height information suggest. Nevertheless, recent more detailed phenotypic work on e.g. the highly diverse insectivorous ovenbirds (Tobias *et al.* 2014) reaches the same conclusions and supports our findings that niche similarity does not prevent coexistence. Morphological attributes may offer a finer separation of species, but may not always have functional significance (e.g. due to sexual selection). Estimates of niche diversity are also likely to depend on level of species inclusion. For example, *NicheDiv<sub>n</sub>* may be underestimated when using *Resident* species because the contribution of the species from other regions may be reduced. However, we find that the sign and strength of *NicheDiv<sub>n</sub>* are very similar regardless of whether *All* or only species *Resident* species are included in the analyses (compare Fig. 2 with S9). A perfect characterisation of ecological divergence that includes all potential characters and also addresses variation among individuals and populations remains outside the scope of macroevolutionary and biogeographical work.

Finally, dispersal among bioregions might obscure the influences of region-specific diversification rates or trait diversity on richness patterns. The strong phylogenetic conservatism of lineages' association with realms and, within continents, with core biomes supports their treatment as parsimonious evolutionary arenas (Jetz & Fine 2012). While due to strong historical connections no two regions in the world are fully independent, statistically addressing all potential past migration events is difficult and the bioclimatic delineation provided by bioregions helps mitigate this issue.

### CONCLUSIONS

Our global analyses, for a total of 15,191 species in two ecologically diverse major taxa and at two spatial grains, reject the notion that differences in ecological divergence is a dominant contributor to among-regional variation in species

richness. In addition, diversification rates appear to have a relatively minor influence on broad-scale richness gradients. This implies that regional richness is likely to be either governed by equilibrium processes produced by the balance of extinction and speciation or that factors such as heterogeneity in dispersal or region age determine richness via non-equilibrium processes independent of diversification rates. Instead, we find previous suggestions about the extent of climatically similar geographical space over time as key explanatory factor for current-day biodiversity re-affirmed (Jetz & Fine 2012), together with a role for temperature. We show the direct effect these predictors have on richness without noticeable influence on diversification rates. The approach taken here which focuses on patterns among regions differs from, and complements, clade-specific analyses that address differences in the diversification rates of single taxa (Phillimore & Price 2008; Rabosky 2009; Rolland *et al.* 2014). Here, the assemblage perspective helped identify a surprisingly minor role of ecological constraints on biogeographical richness gradients.

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#### AUTHORSHIP

JB and WJ planned the research, JB conducted the analyses, JB and WJ wrote the manuscript.

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