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ORIGINAL ARTICLE

Into and out of the tropics: the generation of the latitudinal gradient among New World passerine birds

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ABSTRACT

Aim One prominent explanation for the latitudinal gradient in biodiversity proposes that its prime cause is the greater age and/or higher origination rates of tropical clades, and the infrequent or delayed dispersal of their component species into temperate regions. An alternative is that species' carrying capacities vary regionally, which influences rates of time-averaged diversification via ecological opportunity. We contrast these hypotheses, in order to assess potential historical influences upon the latitudinal gradient of New World passerine birds (order Passeriformes), comparing patterns among the two suborders present (oscines and suboscines), which are known to have had different routes of dispersal across the region.

Location New World.

Methods We examine diversity patterns, their abiotic and biotic correlates, and the distributions of phylogenetically old and young species.

Results Strong latitudinal gradients are present within both oscine and suboscine birds, with maximum diversity towards the equator, but their overall shapes differ. Among the oscines, older lineages are found towards the north, with progressively younger lineages present further south. Regional variation in oscine richness is statistically well explained by a combination of productivity and elevation (R^2 = 0.76). In contrast, few suboscine groups have colonized the north, so their current diversity is well correlated with temperature seasonality (R^2 = 0.74).

Main conclusions Because the oscines colonized the Americas from the north, their latitudinal gradient must reflect regional differences in time-averaged diversification rates, and not the time present within a region. The richness patterns derived from phylogenetic data and the strong predictive power of the normalized difference vegetation index (NDVI) suggest that the radiation of the oscines is consistent with the idea that entry into a new region stimulates a burst of diversification, which is higher and/or continues for longer in areas with greater carrying capacity. Conversely, the suboscine distributions potentially reflect a large historical barrier to dispersal and niche conservatism of climatic tolerances, possibly coupled with competition from the oscines. Although contemporary conditions can explain much of the passerine diversity patterns, history has had an important influence on the taxonomic composition of this gradient.

Keywords
Carrying capacity, dispersal routes, diversification rates, diversity-dependence, diversity gradient, latitudinal gradients, niche conservatism, passerine birds.

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INTRODUCTION

Across terrestrial environments, species richness among the majority of clades peaks in tropical latitudes (Hillebrand, 2004). The generation of this pattern has often been argued to reflect the history of dispersal, including the timing of colonization of different regions (Fine & Ree, 2006; Jablonski *et al.*, 2006; Wiens *et al.*, 2006; Buckley *et al.*, 2010; Kozak & Wiens, 2012), and/or differences in rates of time-averaged diversification (Cardillo *et al.*, 2005; Ricklefs, 2006a,b; Mittelbach *et al.*, 2007; Weir & Schluter, 2007; Wiens, 2007, 2011; Pyron & Wiens, 2013). However, any such explanatory model for the regional variation in species richness must account not only for time and diversification rates, but also for why dispersal has failed to homogenize richness patterns. Even poorly-dispersing species have often had millions of years to spread beyond their areas of origin, so some external constraint must restrict their ability to become established in new places (Wiens & Donoghue, 2004; Price *et al.*, 2011).

Two popular explanations for the failure of species to extend their ranges are geographical barriers and niche conservatism (Wiens & Donoghue, 2004; Wiens, 2007; Romdal *et al.*, 2012); both have been suggested to underlie the strong latitudinal gradient in New World species richness (Hawkins *et al.*, 2006; Weir *et al.*, 2009; Smith *et al.*, 2012) that is observed in many taxa (Hillebrand, 2004). First, the large historical area covered by mesic tropical habitats in South America and/or the stable climates found in several locations (Fjeldså *et al.*, 2012) should have led to the generation and accumulation of many species adapted to these conditions (Wiens & Donoghue, 2004; Romdal *et al.*, 2012). Second, geographical barriers may have restricted this diverse fauna to South America, which was an island continent for much of the past 40 Myr. In birds, for example, the closure of the Isthmus of Panama 3–4 Ma (although Montes *et al.*, 2012 suggest an earlier date) was clearly associated with the northward expansion of the ancient South American passerine groups (Weir *et al.*, 2009; Smith & Klicka, 2010). However, even in the absence of geographical barriers, tropical species may find it difficult to establish in temperate climates (the tropical niche conservatism hypothesis articulated by Wiens & Donoghue, 2004 and Wiens *et al.* 2006), especially if competitors are already present (Price *et al.*, 2011). Putative support for niche conservatism has come from phylogenetic analyses. First, in New World birds, older lineages are concentrated in the tropics, with younger lineages found in the temperate regions (Hawkins *et al.*, 2006, 2007; Fjeldså & Irestedt, 2009). Second, dispersal from temperate North America to tropical South America has been more frequent than the reverse scenario (Smith *et al.*, 2012).

The latitudinal gradient in New World birds has probably been more extensively analysed than any other continent-wide gradient (Rahbek & Graves, 2001; Hawkins *et al.*, 2003, 2006, 2007; Hurlbert & Haskell, 2003; Hurlbert, 2004; Cardillo *et al.*, 2005; Rahbek *et al.*, 2007; Weir & Schluter, 2007). Previous work has shown that climatic variables and topography can explain up to 70% of the variance in species richness on scales of hundreds of square kilometres (Rahbek & Graves, 2001; Hurlbert & Haskell, 2003; Hawkins *et al.*, 2006, 2007). This relationship may be causal, implying a higher carrying capacity in some locations than in others (e.g. Hurlbert & Jetz, 2010), but may also be correlative and reflect historical influences, because ancient and contemporary climates are generally found in similar locations (Ricklefs, 2004, 2006b; Hawkins *et al.*, 2006). More generally, both historical and current processes may influence the pattern (Rahbek & Graves, 2001). In analysing the historical mechanisms generating the New World bird gradient, Hawkins *et al.* (2006) reported that many older clades are restricted to the tropics. They interpreted this finding as suggesting that the ultimate cause of the different richness patterns was the time available for speciation to occur, i.e. a long presence in the tropics relative to other regions explains the high species richness in these localities. Diniz-Filho *et al.* (2007) then used a modelling approach to show how prolonged diversification within the tropics, plus occasional colonization of temperate regions followed by a pulse in speciation, matches this interpretation. These analyses have been framed as support for 'out of the tropics' or niche-conservatism models as the drivers of patterns of regional species richness.

In this paper, we extend these studies by dissecting patterns within the two major subclades of passerine birds (which, together, represent around two-thirds of the total avian species diversity present in the New World) – the oscines (Passeri) and the suboscines (Tyranni). Both clades show latitudinal diversity gradients (Fig. 1). However, phylogenetic studies in a biogeographical context illustrate that they have had very different histories, which alters any interpretation of the underlying causes. Although both suborders appear to have originated in austral Gondwana (Boles, 1995; Barker *et al.*, 2004), the South American suboscines apparently became isolated when the continent separated from Antarctica, about 40 Ma (Ericson *et al.*, 2003; Barker *et al.*, 2004; Scher & Martin, 2006). Conversely, the oscines diversified extensively in the Australo-Papuan region before lineages subsequently colonized North America via the temperate regions of Eurasia (Barker *et al.*, 2004). Multiple oscine groups independently entered North America (Fig. 2), beginning perhaps 25–30 Ma (Ericson *et al.*, 2003; Barker *et al.*, 2004), and then proceeded into South America from the north, beginning at least 15 Ma, again in several independent colonization events (Ricklefs, 2002; Weir *et al.*, 2009; Smith & Klicka, 2010).

Colonization by the oscines from the north implies that their latitudinal gradient has been established as a result of regional differences in time-averaged diversification, not time per se. We evaluate the history of diversification and climatic/biotic correlates of species richness to argue that a simple explanation for both the historical pattern and the latitudinal gradient is an increased oscine carrying capacity towards the tropics. Conversely, the suboscines show a stronger imprint of history, with their distributions likely to have been influenced by the water barrier present before the

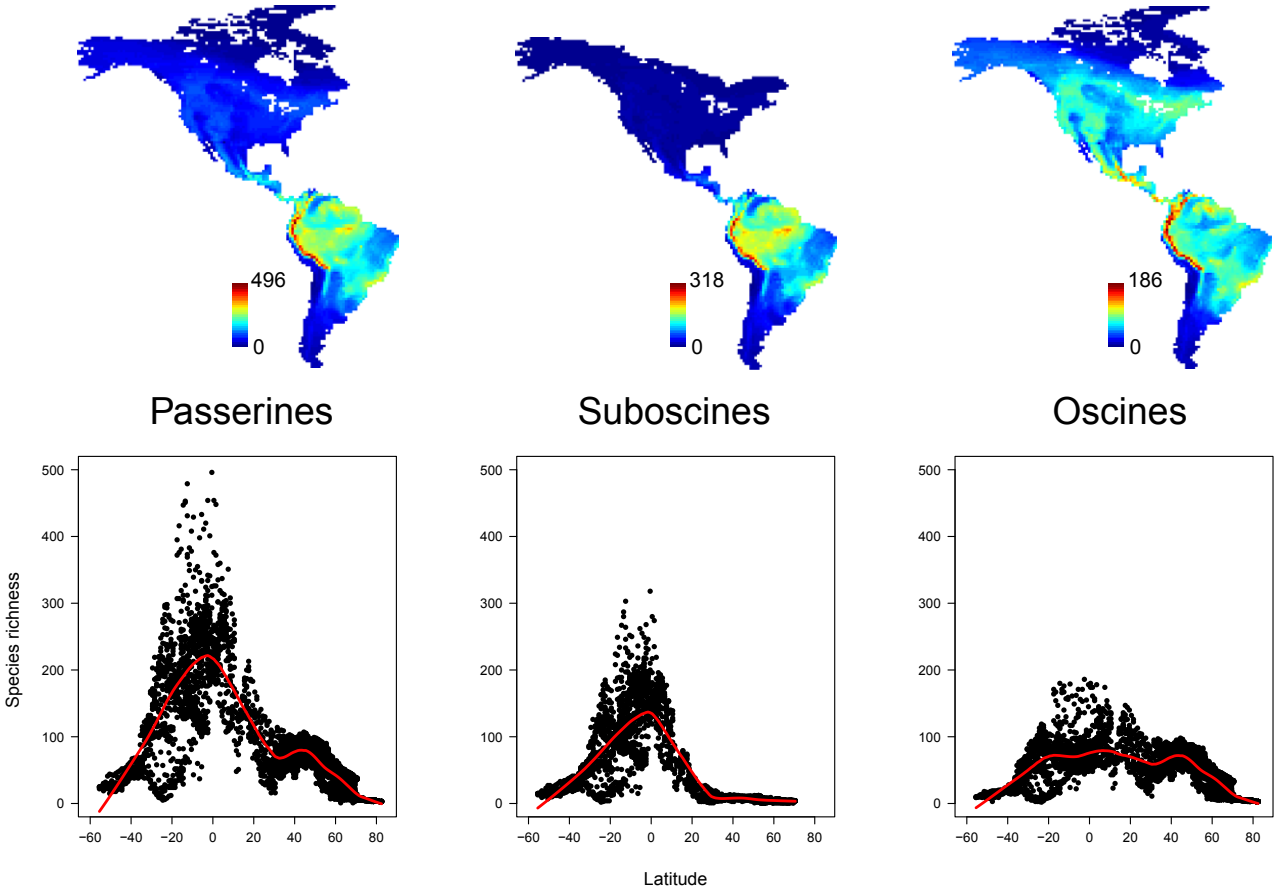

Figure 1 Maps of breeding species richness in 1° × 1° grid cells for all New World passerines (left) and passerines separated into the two suborders: suboscines (centre) and oscines (right). Below: plots of cell richness against latitude; lines are LOWESS fits.

Isthmus of Panama formed, and/or niche conservatism, possibly mediated by competition with the oscines. We highlight the geographical areas where these historical effects appear to be of importance, using residual variation in the richness–climate relationship (following e.g. Jetz & Rahbek, 2002; Hawkins *et al.*, 2003).

MATERIALS AND METHODS

Data

We obtained distributional data for the 1127 oscines and 1183 suboscines native to the New World (2310 passerine species in total) from an expert-validated database in which species' ranges were defined from museum specimens, published sightings and more than 1600 original references (Rahbek & Graves, 2001; Rahbek *et al.*, 2012). The geographical ranges of all species were recorded at a resolution of 1° × 1°, and are considered to reflect a conservative estimate of the breeding area. These maps were rasterized at the same spatial resolution using ArcGIS 10.1 (ESRI, Redlands, CA, USA) to create maps of species richness. We excluded all island-endemic species from the analyses owing to the differences in age and area between continents and islands, and its potential influence in regulating species diversity. An estimate of phylogenetic relationships among the same 2310 species was obtained from Jetz *et al.* (2012), via http://www.birdtree.org/ (accessed 28 June 2013). We used the complete species-level trees, with the backbone topology inferred from Hackett *et al.* (2008). All phylogenetic analyses were performed on 1000 tree topologies, and the ensuing statistics averaged.

Climatic and physical variables capture prominent hypotheses of how carrying capacity might be larger in tropical rather than temperate regions. First, areas of high productivity may contain more 'niches' associated with increased vegetation and hence habitat complexity (Hurlbert & Jetz, 2010). Second, environments that are more seasonal may select for increased generalism, with a few generalists able to exclude multiple specialists in any one location (Valentine *et al.*, 2008; Krug *et al.*, 2009). This principle may also operate along elevational gradients (Janzen, 1967; McCain, 2009), leading to greater turnover and smaller elevational ranges in the tropics. Although both of these processes may contribute to potential differences in regional carrying capacity, their relative contributions have previously been difficult to tease

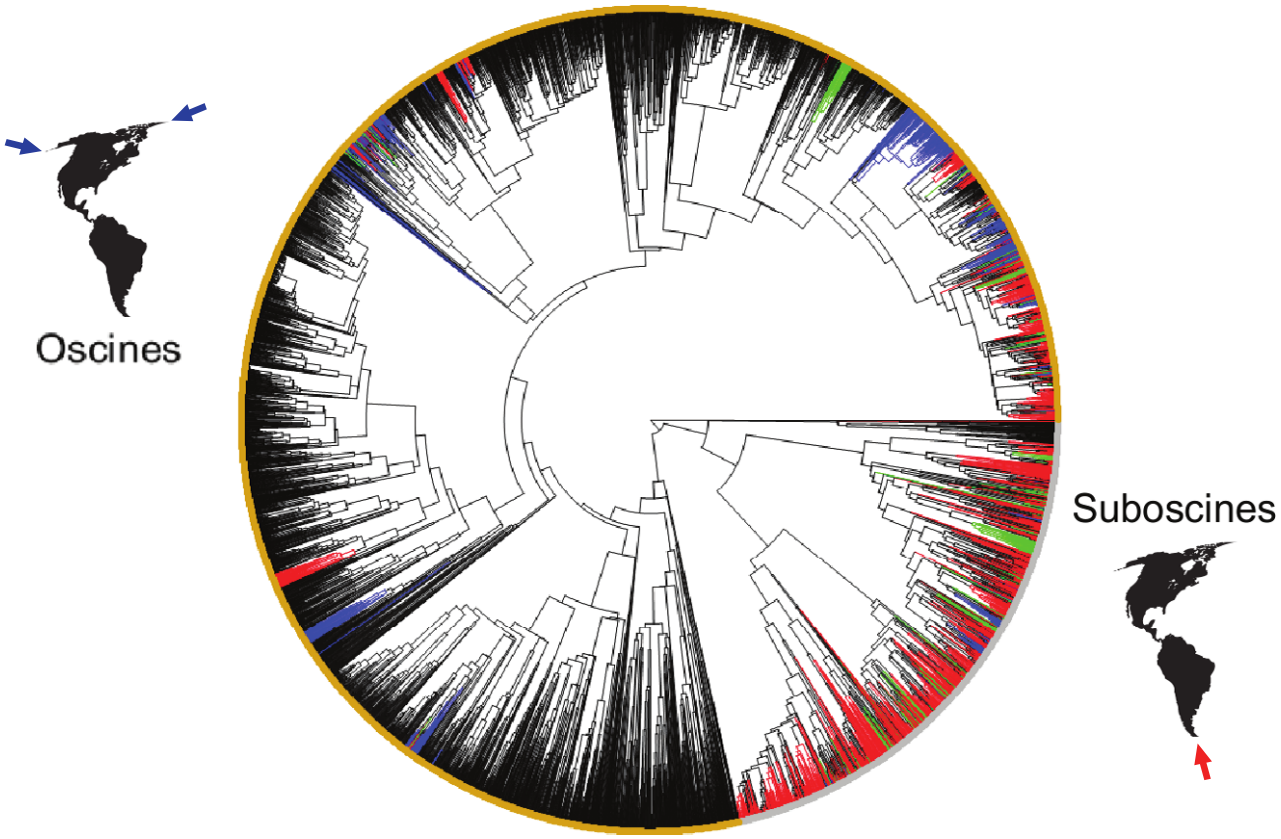

Figure 2 Phylogenetic tree of all globally extant passerines reproduced from Jetz *et al.* (2012). The outer border highlights species that belong to the suboscines (grey) and oscines (orange) respectively. Branch colours denote the distributions: black, outside the New World; blue, North America; red, South America; green, North and South America. The Isthmus of Panama differentiates North and South America, because this is likely to reflect the greatest historical barrier to dispersal between these regions. Map insets show the inferred routes of New World colonization by the suboscines and oscines, respectively.

apart. We estimated seasonality as the standard deviation of monthly mean temperatures (BIO4 in WorldClim), and elevational range as the difference between maximum and minimum elevation, at a scale of approximately 0.17° × 0.17°, from the WorldClim database (Hijmans *et al.*, 2005). Then, using the zonal overlay function in ArcGIS 10.1, we calculated the mean values of these measures in each of the 1° × 1° cells for which we computed species richness. We obtained a monthly average of the NDVI (normalized difference vegetation index, a measure of plant growth) over the period 1982–2000 (http://edit.csic.es/Soil-Vegetation-Land-Cover.html) at a scale of 0.1° × 0.1°, before calculating mean annual values at the same 1° × 1° spatial resolution. The NDVI has previously been shown to correlate strongly with productivity (see Hurlbert & Haskell, 2003, for a detailed discussion of this metric).

Under both the carrying-capacity and the non-equilibrium models, intrinsic or extrinsic factors have the potential to increase diversification rates within the tropics (Mittelbach *et al.*, 2007). In order to assess this, we computed a metric of diversification rate (see below), which we assigned to each 1° × 1° cell.

Statistical analyses

Distributional information and species-richness patterns

We defined a species' presence in either North America, South America, or in both regions, based on its breeding distribution. We used the Isthmus of Panama to separate North and South America, because the water gap present prior to its formation is likely to represent a major historical barrier to dispersal between the two regions (Weir *et al.*, 2009; Smith & Klicka, 2010). We then examined the placement of these species in the context of global passerine phylogenetic relationships, using the topologies of Jetz *et al.* (2012). Our results are illustrated using a single topology (Fig. 2), but the patterns remain similar across all trees.

We separately ranked all lineages of suboscines and oscines along a continuum from phylogenetically old and species-poor to young and species-rich, using the individual lineage diversification rate (DR) statistic proposed by Jetz *et al.* (2012). This statistic infers a species' 'diversification rate' to reflect the number of diversification events that have occurred throughout the history of its lineage, weighted by

the relative timing of these events (see the supplementary information of Jetz *et al.*, 2012, for further information). We computed this statistic on the tree topologies pruned to contain only the New World passerine species. In this respect, these values reflect a measure of diversification only in terms of the lineage splitting events that have subsequently lead to a New World species, and thus any diversification events in which at least one of descendants is found outside the region are ignored. We selected this approach in order to consider only diversification events that were relevant for the accumulation of New World diversity, but also to limit potential bias in the DR values of New World species computed on the global tree, as a consequence of the differences in the diversity and distribution of extralimital groups. Values of the DR statistic computed on the global trees are, however, so highly correlated with those from the pruned New World trees (suboscines, $r = 0.99$; oscines, $r = 0.96$) that our results are unlikely to be affected.

Despite considering information on branch lengths, and the strong predictive ability of speciation rates in homogenous birth–death simulations (Jetz *et al.*, 2012), the DR statistic is limited in two respects: (1) its failure to account for the influence of extinction; and (2) the failure to consider density-dependent mechanisms of diversification and therefore the potential for diversification rates to vary through time. By measuring the relative isolation of a lineage on a phylogeny of extant species, the DR statistic differentiates species based on their age and the diversity arising from the connected older nodes. Hence, the statistic largely reflects recent diversification rates, which may or may not differ from historical rates, and which may or may not differ in terms of the relative contributions of speciation and extinction. For example, a lineage undergoing high rates of both speciation and extinction would recover a high DR because many of its nodes are close to the present, when its true rate of net diversification may well be lower, as many of these newly arising species are likely to become extinct. Conversely, lineages undergoing density-dependent diversification show a slow-down in speciation events towards the present, making their DR low, although their historical rate of net diversification would have been much higher (Rabosky, 2009). To the degree that the DR reflects a lineage's recent diversification rate, however, it is useful in allowing us to rank species in terms of their phylogenetic position.

With these ranks, we divided our species database into quartiles. The first quartile contained the oldest and least diverse lineages (herein termed 'ancient'), and the fourth quartile contained the youngest and most species-rich ones (herein termed 'recent'). Using ArcGIS, we computed the species richness of all quartiles at a resolution of 1° × 1°, and the median value of these statistics across all species in each cell.

Because previous studies have used node number to study spatial variation in diversification through time (Hawkins *et al.*, 2006, 2007; Fjeldså & Irestedt, 2009), we repeated these analyses, ranking species by the number of nodes connecting them to the root of the phylogeny ('node number'). Although the node-depth measure captures the relative levels of diversification among lineages, it does not account for potential differences in the timing of these events (reflecting the relative level of a lineage's isolation within the tree), which the incorporation of branch-length information allows. We therefore further investigated the spatial distribution of old and young species directly, ranking the lineages using two further metrics: (1) the time to the most recent common ancestor (TMRCA); and (2) the relative timing of the distribution of all nodes within a lineage. For this second metric, we first computed the number of nodes occurring within each 25% slice of time (e.g. for a tree with a root of 100 Ma, this would be the number of nodes in each 25-Myr time interval) and then, depending on the age of the time slice, we multiplied the proportions by an integer (one for the youngest time slice, and four for the oldest time slice), and used these values to rank the species. When the richness patterns derived from these four alternative metrics were assessed, the results remain qualitatively similar (see Figs S1–S3 and Table S1 in Appendices S1 & S2 of the Supporting Information), and only those for DR are presented in the main text.

We consider that these quartile diversity patterns reflect the spatial structure of the phylogenetic data, although this needs to be assessed against a possible influence of the overall pattern of species richness. In order to do this, we regressed the species richness of each individual quartile against the

Table 1 R^2 values and standardized coefficients extracted from linear models examining the logarithm of species richness (for three bird groups in the New World: all passerines, oscine passerines and suboscine passerines) as a function of annual values of the following variables: normalized difference vegetation index (NDVI), NDVI + [temperature seasonality (°C) × elevational range (m)], temperature seasonality (°C) and median diversification rate (DR). For models in which there is more than one predictor variable, the standardized coefficients are listed as ordered within parentheses.

	All passerines		Suboscines		Oscines	
Variables	R^2	Coefficients	R^2	Coefficients	R^2	Coefficients
NDVI	0.82	0.91	0.49	0.7	0.71	0.84
NDVI + (temperature seasonality × elevational range)	0.83	(0.94, 0.11)	0.51	(0.62, −0.16)	0.76	(0.92, 0.24)
Temperature seasonality	0.55	−0.74	0.74	−0.86	0.28	−0.53
Median DR	0.43	0.65	0.53	−0.72	0.39	0.63

total species richness. The spatial structure of the residuals implied that substantial variation was explained by the phylogenetic ranks, beyond that explained by total richness.

Environmental predictors

We used linear models to examine the richness of breeding species as a factor of climatic, topographical and historical variables. For the climatic variables and NDVI, we analysed both the yearly values and a 'composite measure', in which cells in the tropics (23° N to 23° S) were given total yearly values, cells south of 23° S were given values for the period from October to March, and cells north of 23° N were given values for the period from April to September. We computed this composite measure for two reasons. First, breeding at high latitudes takes place at different times of the year in the two hemispheres and is composed of many migrants, whereas tropical breeding species are largely resident. Second, Hurlbert & Haskell (2003) and Hawkins (2004) found that North American bird distributions were better explained by summer productivity than annual productivity. We found that R^2 values from the linear models were, however, generally higher using the annual variables rather than the composite measure (see Table S2 in Appendix S2), and we present these in the text (Table 1).

The models and their respective R^2 values and standardized coefficients were computed for all passerines, and for the two suborders separately, for all combinations of variables related to different hypotheses for the latitudinal gradient (median cell DR, temperature seasonality, elevational range, the temperature seasonality × elevational range interaction and NDVI), as set out above, using R 2.15.0 (R Development Core Team, 2009). Models were evaluated by comparison of their parameter estimates, and by visually inspecting the linearity of the data and the variance of their residuals. The inclusion of quadratic terms added little to the models, whereas log-transformation of the dependent variable always improved the fit. The models presented in Table 1 contain predictor variables that reflect a priori hypotheses for the latitudinal gradient, but were generally also those in which the R^2 and standardized coefficients were maximized relative to the number of parameters included (results from all models are presented in Tables S2 & S3 in Appendix S2). Strong spatial autocorrelation is present in the data (confirmed by calculating Moran's I statistic in the R package SPDEP; Bivand *et al.*, 2011). We therefore re-analysed the data using spatially explicit models in addition to the linear models. On computing the z statistic from the linear slopes of these models, however, all remained highly statistically significant regardless of the spatial distance used to define the correlation matrix (results not shown).

RESULTS

Richness patterns

At a resolution of 1° × 1°, a strong latitudinal gradient is present among all passerines and also within both suborders (Fig. 1). Although both the suboscines and the oscines reach their maximum diversity in the tropical regions of the Andes,

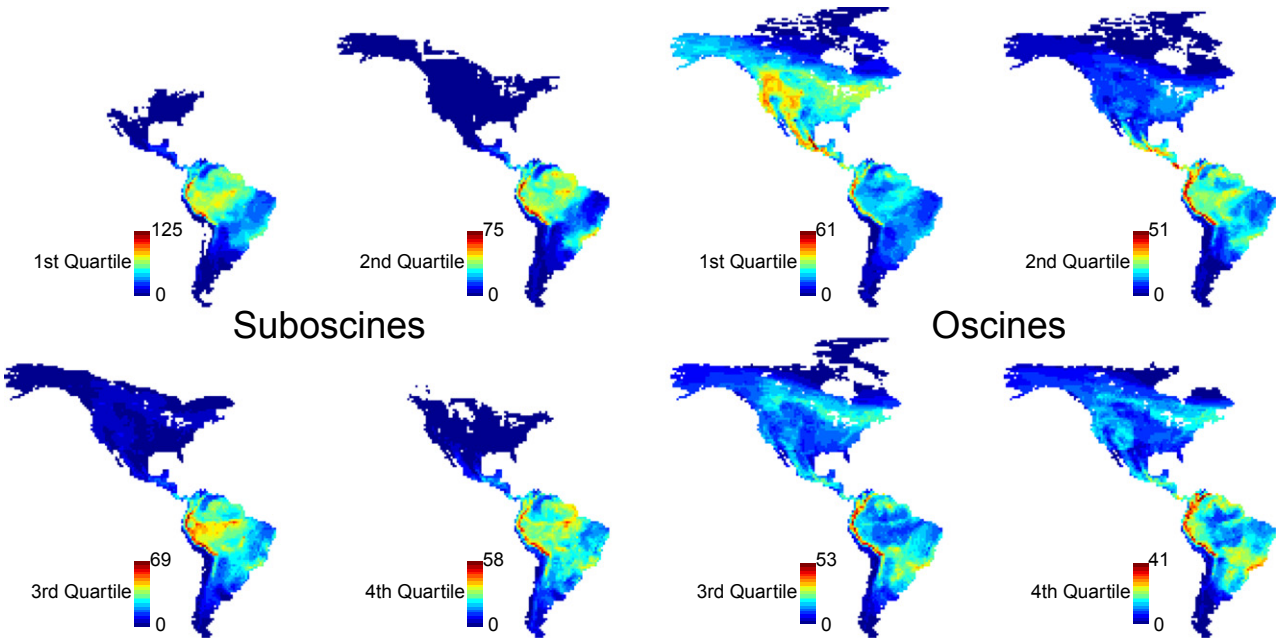

Figure 3 Maps of quartile species richness in 1° × 1° grid cells for New World suboscines (left four panels) and oscines (right four panels). The quartiles were defined by assessing species as phylogenetically ancient or recent via the diversification rate (DR) statistic. Species' values were assessed over 1000 topologies of the Jetz *et al.* (2012) phylogeny (pruned to contain only the New World passerine species), and the mean values were then used to define the quartiles. The first quartile contains the oldest and most species-poor lineages, and the fourth quartile represents the youngest and most diverse.

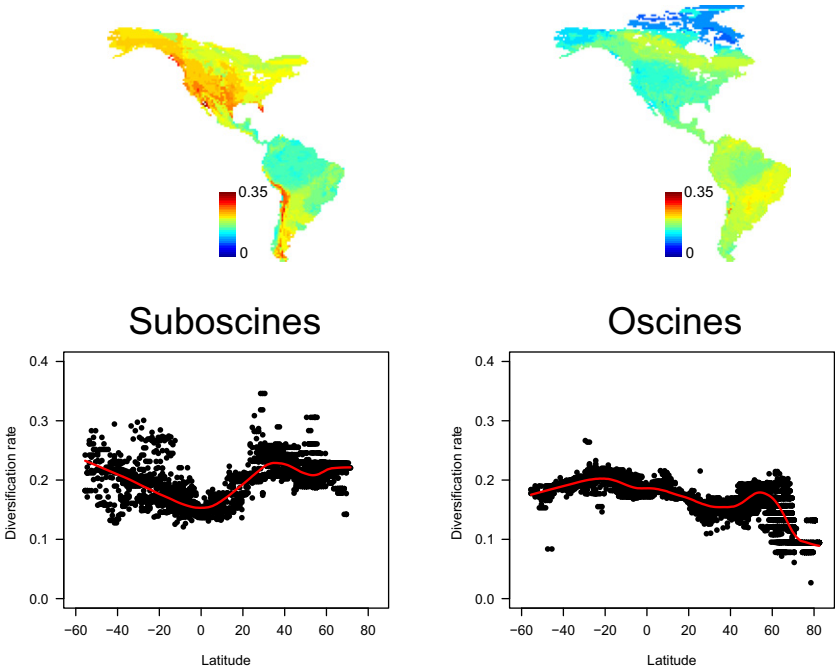

Figure 4 Maps of median values of the diversification rate (DR) statistic in each 1° × 1° grid cell, for New World suboscines (upper left) and oscines (upper right). Below: plots of median lineage diversification rate per cell against latitude, lines are LOWESS fits.

the shapes of their overall distributions in species richness differ (Fig. 1). Suboscine richness is asymmetrical around the equator, with few species in North America. In contrast, oscines occur at an average density of *c.* 60 species per cell in the Northern Hemisphere, right up to 50° N. These contrasting richness patterns result in the total passerine richness being about the same at 40° N and 40° S (Fig. 1).

Diversification

We ranked species in each of the two clades according to their DR (Jetz *et al.*, 2012) (see Fig. 3 for the spatial patterns of species richness across the four quartiles defined by these ranks). Within the suboscines, the maximum richness of all quartiles is centred in the tropical Andes and the Amazon, with the youngest species diversifying into the more temperate areas to the north and south (Fig. 3, left). Within the oscines (Fig. 3, right), the younger groups lie progressively further to the south of each other. The most ancient species are predominantly North and Central American, whereas the next two quartiles reach their maximum richness in the tropical Andes. This pattern remains similar within the fourth quartile, but here, species also reach high densities further south, in the southern Brazilian highlands and Atlantic forests. Residuals from the linear models of quartile richness against overall species richness show a very similar spatial pattern (see Fig. S4 in Appendix S1), implying that our results are not biased by the underlying richness patterns. These findings are consistent with the hypothesis that the colonization of new areas stimulates diversification, as opposed to any intrinsic influence of the tropics per se.

The suboscines show their lowest DRs within the tropical latitudes, driven by the predominance of ancient species within these areas (see Fig. 4 for median cell values of DR). DRs progressively increase in more temperate areas in North and South America. This reflects the presence of many young species, both in the southern Andes and in central and western North America. Among the oscines, DRs are very similar from 60° S to 20° N, showing a slight downward trend towards the north. These rates then increase sharply between 50° N and 70° N, before declining in the extreme latitudes further north. These analyses illustrate that younger species in both suborders are located in temperate regions, with a combination of young and old species found in the tropics.

The DR value of each species contributes to multiple cells, thus producing a smoothed relationship, because nearby cells tend to share many species, and are therefore not independent (Graves, 1985, 1988; Rohde *et al.*, 1993). In order to assess the influence of this on the patterns presented, we regressed the DR of each individual species against a randomly sampled latitudinal value from within its range, repeating the process 100 times (see Fig. S5 in Appendix S1); the results were consistent with the patterns shown in Fig. 4.

Biotic and abiotic predictors of species richness

The relationships of species richness to climatic and physical variables were non-linear, with the highest NDVI cells within the Andes and Amazon (particularly those reflecting the turnover between the lowland and highland faunas) having exceptional numbers of species. Because of this, models with log-transformed richness performed substantially better than those using the raw richness values and are presented here (Table 1). NDVI alone explained 82% of the variance in log-transformed species richness for the passerines as a whole and 71% for the oscines, being clearly the most important

predictor. Although there was little increase in R^2 with the addition of further variables for the passerines overall, a model that also contained an interaction between temperature seasonality and elevation improved the fit among the oscines ($R^2 = 0.76$) (Table 1). Compared with the oscines, however, suboscine distributions are only weakly predicted by NDVI alone ($R^2 = 0.49$), with temperature seasonality the most important explanatory variable ($R^2 = 0.74$). The median cell DR values also explain some additional variance ($R^2 = 0.53$).

In general, even after elevation is included in the model, among all three groups, the Andes contain more species than predicted (see Rahbek, 2005; Rahbek *et al.*, 2007) (see Fig. S6 in Appendix S1 for spatial patterns of the outliers from the four models presented in Table 1). The suboscines show the greatest deviations from model predictions, with North America under-represented and South America correspondingly over-represented. The Florida peninsula and Baja California are particularly poor in suboscines once climate is accounted for. In addition, when considering NDVI alone, the passerines overall and the oscines specifically show an over-representation of species over western North America; this over-representation becomes more evenly dispersed over North America when the interaction between temperature seasonality and elevation is included.

DISCUSSION

The latitudinal gradient among New World birds has previously been interpreted as reflecting an 'out of the tropics' pattern, with limits on dispersal and establishment as its prime cause (Hawkins *et al.*, 2006, 2007; Diniz-Filho *et al.*, 2007). In this study, by considering the history of dispersal within the two major suborders of passerine birds, we have shown that this explanation is incomplete, and that the underlying drivers of the two gradients differ. The oscine latitudinal gradient must reflect regional differences in time-averaged diversification rates and not the time the clade has been present in the tropics, given that the oscines entered the New World from the north. A southward progression in the timing of oscine diversification (Fig. 3) is consistent with radiations that result from entry into new geographical and ecological space. By contrast, the suboscines show a pattern concordant with a prolonged history of diversification in northern South America, and recent range expansions among lineages to both the north and south. Thus, the patterns in diversification accord with the inferred history of the two groups.

Smith *et al.* (2012) found that the majority of oscine families present in North America (14/24) contained species south of 30° S, implying multiple invasions into the tropics and southern temperate regions (see also Fig. 2). One group of particular influence in this diversity gradient are the nine-primaried oscines (Passerellidae, Parulidae, Icteridae, Cardinalidae, Thraupidae and a few other small family groups; Barker *et al.*, 2013), which, although only present in the New World, represent *c.* 8% of total global avian diversity and occur in all terrestrial environments (Barker *et al.*, 2013). Analyses of several of these invasions have demonstrated increased diversification rates after entering South America (Weir, 2006; Price, 2008, Chapter 6; Weir *et al.*, 2009). For example, entry into the Neotropics stimulated a rapid radiation among the Thraupidae, with the production of more than 400 species over the last 13 Myr (Barker *et al.*, 2013). Back-colonizations of oscines into northern temperate regions have also occurred (Weir *et al.*, 2009), but have not stimulated similar radiations (Smith *et al.*, 2012). It is notable that species of the two suborders tend to occupy different parts of the vegetation structure in areas in which they co-occur, with the oscines predominately found in the outer/exterior canopy and the suboscines within the forest interior (Ricklefs, 2002). Thus, one possible reason for the rapid oscine diversification in the south, particularly at low latitudes, is that they differ in several life-history traits from the suboscines (long-distance dispersal capabilities, habitat preference/flexibility, modes of foraging, and adaptations for consuming grain).

The New World suboscines originated in South America, and their patterns of colonization are very different from those of the oscines. Only one of the nine suboscine families studied by Smith *et al.* (2012) is present in both temperate North America and the Neotropics. This asymmetry in dispersal and establishment between temperate North America and the Neotropics has also been reported across six major vertebrate groups (Smith *et al.*, 2012). Potential causes include tropical niche conservatism (Smith *et al.*, 2012), coupled with the influence of the water gap prior to the formation of the Isthmus of Panama at 3–4 Ma. Most suboscines of tropical South America are restricted to rain forest interiors, have short, rounded wings, and appear to be unable to cross even small water gaps (Moore *et al.*, 2008; Weir *et al.*, 2009; Smith & Klicka, 2010). Hence, many groups appear to be tightly restricted both in terms of their tolerance for extreme climatic conditions and dispersal abilities. Indeed, the single suboscine family that has colonized > 30° N, Tyrannidae, shares closer morphological adaptations and habitat preferences with the oscines than with other suboscine groups (Ricklefs, 2002; Ohlson *et al.*, 2008). We suggest that these differences in key life-history traits (Ricklefs, 2002; Weir *et al.*, 2009; Smith *et al.*, 2012), may have been the major influences in determining the present-day distributions of the two suborders.

Although we have used historical information to dissect the influences of diversification rate and time in generating contemporary richness patterns, an unanswered – and difficult – question is whether diversification and dispersal are themselves the causal drivers of regional diversity patterns, or if they instead reflect responses to differences in the number of species a region can accommodate (Ricklefs, 2004, 2006b; Pyron & Wiens, 2013). On the one hand, increased speciation rates and decreased extinction rates may be associated with ecological opportunity and adaptive radiation, such that the colonization of new areas with underutilized

resources elevates diversification (Schluter, 2000; Yoder *et al.*, 2010), with resource diversity (and hence carrying capacity) highest within the tropics (MacArthur, 1965; Price, 2008; Chapter 6). Conversely, these effects could simply be intrinsic, such that tropical species are more diverse because of the predominance of clade origination and persistence in these areas, and/or generally higher diversification rates (Wiens & Donoghue, 2004; Wiens, 2007; Wiens, 2011). A general difficulty in separating the alternatives is that highly productive environments in South America are both old and large, and age and area both promote high numbers of species in the non-equilibrium models (Hawkins *et al.*, 2006), thus both carrying-capacity hypotheses and time/rate hypotheses predict similar patterns. The lineages that currently have the highest diversification rates are, however, largely extratropical, occurring within the southern and central Andes (Figs 3 & 4) and in the extreme north and south of the Americas (Fig. 4; Weir & Schluter, 2007). Among the suboscines, DRs are negatively correlated with species richness ($r = -0.72$), i.e. higher time-averaged diversification rates are negatively correlated with species numbers, suggesting that the difference in regional net diversification rates may not be the causal driver of the patterns. In the case of the oscines, diversification rates must historically have been greater in northern South America (Sedano & Burns, 2008) to produce the higher species richness observed (given their historical route of regional colonization), but as lineages with the highest rates currently lie elsewhere, variation in these rates through time would also seem necessary to explain the patterns. Thus, we suggest that a simple explanation for the observed gradients in diversification rates is that lineages invade new locations and radiate to exploit new ecological opportunities (Schluter, 2000; Yoder *et al.*, 2010).

Our conclusions regarding the differential rates of lineage and latitudinal diversification come with three caveats. First, the current distribution of species is likely to have been altered by range shifts, expansions or contractions due to historical landscape and climatic changes (Zachos *et al.*, 2001; Hoorn *et al.*, 2010), leading to uncertainty in the absolute location of the speciation events themselves. This would seem to be a minor problem, given the strong spatial signal we recover in the phylogenetic data (Fig. 3). Second, as stated in the methods section, the DR statistic is limited if diversification rates vary through time or extinction is present. Recent bursts of diversification are, however, effectively captured by this statistic. Third, the results presented here are dependent on the accuracy of the phylogenetic framework of Jetz *et al.* (2012), which is likely to be subject to taxonomic and temporal changes (Mayr, 2013), particularly as many species are currently sampled without genetic data (351 suboscines and 197 oscines studied).

Strong associations of current climate with species richness (Table 1, Fig. S6) do not necessarily imply that current rather than historical processes are the drivers of spatial richness patterns, given the correlations between past and present climate (Ricklefs, 2004; Hawkins *et al.*, 2006). Outliers in the climate–richness association may, however, reflect historical imprints over and above the patterns set by current conditions (Jetz & Rahbek, 2002; Hawkins *et al.*, 2003). These are most obvious for the suboscines, which are extremely underrepresented in North America (Fig. 1, Fig. S6; Smith & Klicka, 2010), which is attributed to low dispersal capabilities (apart from the Tyrannidae), the relatively recent closure of the Isthmus of Panama, and the possible effects of niche conservatism (Weir *et al.*, 2009; Smith & Klicka, 2010; Smith *et al.*, 2012). Niche conservatism seems particularly reasonable if we assume that competition (e.g. from the oscines) represents a significant biotic factor amplifying the effects of climate (Price *et al.*, 2011). Outliers are less obvious within the oscines, but this may partly be because we log-transformed richness; on a linear scale, richness is a strong positive outlier in tropical South America.

We suggest that the trajectory of a southward trend in diversification within the oscines is consistent with increased ecological opportunity, rather than direct climate-driven effects on speciation rates and niche conservatism. Both in marine bivalves (Jablonski *et al.*, 2006, 2013) and in the terrestrial environment more generally (Smith *et al.*, 2012; Jansson *et al.*, 2013), movements out of the tropics have been frequent, which seems to argue against a crucial role for niche conservatism in limiting dispersal (Jablonski *et al.*, 2013). However, an 'out of the tropics' dynamic (irrespective of clade origination) cannot by itself set the latitudinal gradient, because if diversification rates were similar across regions, given enough time this dynamic would result in a disproportionate accumulation of species in temperate regions and therefore a reversed gradient. Instead, in the marine bivalve system, Valentine *et al.* (2008) and Krug *et al.* (2009) suggest that carrying capacity varies latitudinally, with a lower capacity in more seasonal and climatically unstable environments in the north. In this argument, the observed pattern of higher origination rates in the tropics is important in driving the taxonomic composition of the gradient, but does not determine the gradient itself. We conclude that a similar process may also operate among New World passerines, and that a complete understanding of this and other latitudinal gradients must consider not only the history of dispersal among clades, but also the interactions that limit establishment, diversity-dependent mechanisms, and the potential for rates of diversification to vary across both time and space.

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SUPPORTING INFORMATION

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

Appendix S1 Supplementary figures.
Appendix S2 Supplementary tables.

BIOSKETCH

Jonathan Kennedy is a PhD student at the Center for Macroecology, Evolution and Climate, at the University of Copenhagen. His interests include macroevolution and historical biogeography, with a specific focus on passerine birds.

Author contributions: J.D.K. and T.D.P. designed the study; J.D.K. performed the analysis; J.D.K., Z-H.W., J.T.W., J.F., C.R. and T.D.P. contributed to interpreting the analyses and writing the manuscript.

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