

ORIGINAL  
ARTICLE

# Historical limits on species co-occurrence determine variation in clade richness among New World passerine birds

Jonathan D. Kennedy<sup>1,\*</sup>, Trevor D. Price<sup>2</sup>, Jon Fjeldså<sup>1</sup> and Carsten Rahbek<sup>1,3</sup>

<sup>1</sup>Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark,

<sup>2</sup>Department of Ecology and Evolution, University of Chicago, Chicago, IL 60637, USA, <sup>3</sup>Imperial College London, Silwood Park, Buckhurst Road, Ascot Berkshire SL5 7PY, UK

## ABSTRACT

**Aim** Species richness is unevenly distributed among clades, reflecting differences in the extent to which species co-occur, their rates of geographical turnover and total area occupied. Here, we study richness variation among 10 large clades of New World passerine birds, assessing the dynamics of range expansion and diversification that led to the build-up of co-occurring species.

**Location** New World.

**Methods** We defined co-occurrence based on the presence in  $1^\circ \times 1^\circ$  grid cells, an area substantially smaller than the geographical scale of speciation in birds, implying that range expansion is the main mechanism by which species accumulate within grid cells. For each species, we estimated its ‘diversification rate’, a measure of the extent to which it is a member of an actively diversifying lineage. Within each group, we ranked all species by this measure, before dividing them into quartiles.

**Results** Neither clade age nor geographical area correlates with overall clade richness, but the maximum number of co-occurring species does. Within each group, locations supporting large numbers of species in actively diversifying lineages generally differ from those containing many species belonging to more ancient groups. The tropical Andes and Amazon are notable for continuously generating and maintaining species, such that the most species-rich clades have predominantly radiated in these areas. Based on the timing of their speciation events, we infer that a lack of reproductive isolation may limit the co-occurrence of species that are members of actively diversifying lineages, but not those that are generally long diverged.

**Main conclusions** Spatiotemporal differences in the rates of range expansion and diversification are likely set by the capacity of regions to generate and maintain species. This, rather than the rate at which reproductive isolation accrues, area occupied, or time for diversification, appears to be the major factor underlying the disparity in clade richness between New World passerine groups.

## Keywords

Andes, centres of diversification, dispersal, passerine birds, range expansion, reproductive isolation, secondary sympatry

\*Correspondence: Jonathan Kennedy, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark.  
E-mail: jonathan.kennedy@snm.ku.dk

## INTRODUCTION

Within a region, clades vary greatly in the number of species they contain (Ricklefs, 2006, 2009). These differences are determined by the total area the clade occupies, the rate at which species turnover geographically, and the number of

species that can co-occur. However, these three factors are themselves a consequence of the processes of range expansion and diversification (speciation minus extinction). Range expansions affect both the overall area that a clade occupies and the number of co-occurring species within a given location, although co-occurrence also requires the accumulation

of reproductive and ecological isolation (predominantly achieved in allopatry), plus dispersal into secondary sympatry (Price *et al.*, 2014; Pigot & Tobias, 2015). In this article, we show that the build-up of co-occurring species, but not area occupied, is a major contributing factor to the variation in species richness among 10 large groups of New World passerine birds. We subsequently focus on the historical build-up of co-occurring species by comparing the spatial distribution of species that belong to actively diversifying groups with those that are currently diversifying more slowly.

Considering a large region, differences in species richness across clades must ultimately reflect differences in the rates of dispersal into the region, the rates of *in situ* diversification, the time that clades have been present and/or geographical variation in the capacity for species to co-occur (Rabosky, 2009; Wiens, 2011). In passerine birds, both time and dispersal throughout the New World are thought to be of minimal importance in determining the spatial variation in species richness, implying geographical differences in historical rates of diversification to be the causal factor (Kennedy *et al.*, 2014; Rabosky *et al.*, 2015). However, given that rates of diversification have the potential to change across time (Phillimore & Price, 2008; Rabosky, 2009) and space (Jetz *et al.*, 2012; Kennedy *et al.*, 2014), a complete understanding of the historical generation of species richness variation necessitates assessment of how the process of diversification has been regulated. Here, we ask if variation in species richness across small geographical areas correlates with the current diversification rates of the species present. We show that it generally does not, which we argue results from locality-specific controls on the species which invade from a larger species pool (Webb *et al.*, 2002), with some locations able to accumulate, and maintain, a greater number of species than others.

We set  $1^\circ \times 1^\circ$  grid cells as our unit of spatial co-occurrence because cells of this size are likely to have accumulated the large majority of their species by range expansions, rather than *in situ* speciation. The reason for using this scale rather than one that is smaller or larger is twofold. First, the smallest island upon which substantial *in situ* speciation has occurred in birds is Madagascar (*c.* 600,000 km<sup>2</sup>, Coyne & Price, 2000), *c.* 50 $\times$  larger than a grid cell. Second, the  $1^\circ \times 1^\circ$  scale is large enough to encompass habitat turnover within a cell and, therefore, includes ecological diversity as a potential contributor to the accumulation of species diversity (Terborgh, 1977; Rahbek, 1995; Rahbek & Graves, 2001). Although a  $1^\circ \times 1^\circ$  grid cell defines our scale for co-occurrence, these cells are embedded within regions that generate the pool of potentially colonizing species (Lessard *et al.*, 2012; Cornell & Harrison, 2014). Here, we study the build-up of species across the Americas, a landmass containing a number of biogeographical regions (Holt *et al.*, 2013) and within which appreciable amounts of speciation and adaptive radiation have occurred (Ohlson *et al.*, 2008; Fjelds , 2013). We ask if two factors commonly thought to explain variation

in diversification rates, age and area, are strongly related to the species richness and co-occurrence patterns within clades (see Ricklefs, 2006; Cornell, 2013), or whether constituent properties of areas in terms of their propensity to generate and maintain species are more important.

To quantify historical rates of diversification among lineages, Jetz *et al.* (2012) introduced a metric [diversification rate (DR)] that determines the extent to which a species belongs to a highly diverse terminal clade or is relatively isolated on the phylogeny. Although a species DR depends on its relationship to both co-occurring and allopatric forms, the average values of all species within a grid cell have been used to indicate regions of the world that are actively diversifying, compared with others where diversification rates are currently low (Jetz *et al.*, 2012). Kennedy *et al.* (2014) extended this approach and ranked all species of New World passerines by their DR values, before dividing these ranks into quartiles. They showed that among one suborder, the oscines, assemblages with the highest number of old species lay to the north, while those with the highest number of young species lay to the south, consistent with their proposed route of colonization and dispersal throughout the Americas (Ericson *et al.*, 2003; Barker *et al.*, 2004, 2015; Winger *et al.*, 2014). Conversely, the suboscines (the other passerine suborder present in the New World) remain largely confined to their area of origin in South America. Both suborders have undergone prolonged diversification within the tropics (Kennedy *et al.*, 2014). By considering five species-rich clades within each of the oscines and suboscines, we attempt to elucidate the evolutionary processes most important in generating the spatial and taxonomic disparities in species richness. We achieve this by assessing how historical events of range expansion and diversification have led to the accumulation of species within  $1^\circ \times 1^\circ$  degree grid cells.

## MATERIALS AND METHODS

### Data

Following the International Ornithological Community (IOC) classifications v 3.3, with further taxonomic updates (notably Barker *et al.*, 2013; Ohlson *et al.*, 2013; Klicka *et al.*, 2014), we obtained breeding range maps at the  $1^\circ \times 1^\circ$  scale for 1718 species of New World passerine birds (Rahbek & Graves, 2001; Rahbek *et al.*, 2012; Kennedy *et al.*, 2014). These species represent members of five suboscine (Thamnophilidae, Furnariidae/Dendrocolaptinae, Cotingidae/Pipridae, Tyrannidae and Pipromorphidae) and five oscine (Troglodytidae, Thraupidae, Passerellidae, Icteridae and Parulidae) clades. Together, they amount to *c.* 74% of the overall passerine species present within the New World and can be fairly well characterized in terms of differences in foraging strategies and habitat preferences, based on species treatments in the *Handbook of Birds of the World* (del Hoyo *et al.*, 2003–2011) and *The Birds of North America* (Poole, 2005). We created maps of species richness for all groups by

overlaying their respective ranges and rasterizing them in R 3.1.0 (R Development Core Team, 2008), using the packages ‘raster’ (Hijmans & van Etten, 2012) and ‘rgdal’ (Bivand *et al.*, 2014). Our estimate of the phylogenetic relationships among New World passerine species was obtained from Jetz *et al.* (2012), with the backbone topology inferred from Hackett *et al.* (2008) (downloaded from [www.birdtree.org](http://www.birdtree.org) on the 28th June 2013). These are the same tree topologies considered in Kennedy *et al.* (2014).

## Statistical analyses

### *Spatial patterns of diversification*

We ranked all species of New World oscines and suboscines by their DR. These values reflect the number of nodes separating a species from the root of a phylogenetic tree, weighted by how close the respective diversification events occur towards the present (Jetz *et al.*, 2012). Although DR has been shown to be highly correlated with speciation rate estimates in birth–death simulations (Jetz *et al.*, 2012), we acknowledge that it is limited in terms of its representation of historical diversification. This is because DR fails to account for temporal variation in speciation and extinction (Kennedy *et al.*, 2014), and as a result, it is suggested to be a more appropriate estimate of speciation rates closer to the present (Jetz *et al.*, 2012; Belmaker & Jetz, 2015). We calculated the DR for each of the 1718 species as the mean across 1000 phylogenetic trees containing all New World passerines [the global Jetz *et al.* (2012) phylogenies pruned to contain only the New World species]. We selected this approach so as to only consider diversification events resulting in the accumulation of lineages that currently occur within the New World, limiting the potential bias in DR values that may result from the inclusion of extra-limital speciation events.

There remains some uncertainty in the time-scale of diversification and taxonomic relationships proposed by Jetz *et al.* (2012) (e.g. Mayr, 2013; Price *et al.*, 2014), particularly as many of the New World passerine species were sampled without genetic data (282/991 suboscines and 129/727 oscines considered in this study; see Table 1 for further information). Although the species sampled without genetic data are primarily distributed within the tropics, given the relatively even distribution of DR values among these species (i.e. they represent both phylogenetically isolated and derived lineages; see Table 1), this issue is unlikely to strongly bias the spatial patterns presented. Furthermore, whereas it is possible that the addition of further genetic data may change the taxonomic relationships, time-scale of diversification and the number of recognized species in the Jetz *et al.* (2012) tree, as our aim is primarily to rank species in respect of their phylogenetic isolation (using DR), our results should be robust to future refinements of this phylogeny.

As a complement to DR, we also determined the age of the speciation events (species age) that resulted in the species we consider. These values represent the average length of the terminal branch subtending the placement of each species, assessed over 1000 tree topologies. We subsequently ranked all species based on these ages. The values of log DR and log species age were highly correlated with one another (minimum  $r = -0.76$ , maximum  $r = -0.92$ ; Fig. S1) and the resulting richness patterns based on their ranks were also very similar (Fig. S2–11). Therefore, we only refer to the results from the DR analyses in the main text. Species that record low values of DR should be considered to be phylogenetically isolated and the result of older speciation events. Conversely, species that recover high DR scores are members of terminally diverse clades and tend to be young.

For each group, we divided its species database into quartiles based on the ranks of DR, before computing the species richness of each quartile at the  $1^\circ \times 1^\circ$  scale using R 3.1.0

**Table 1** The total number of species present within the 10 New World passerine groups, in addition to the number and proportion of species included without DNA sequence data in the phylogeny of Jetz *et al.* (2012), and the distribution of these species among the DR quartiles.

|                                  | Total no. species | No. species without DNA sequence | Proportion of overall species without DNA sequence | No. species without DNA sequence (1st DR quartile) | No. species without DNA sequence (2nd DR quartile) | No. species without DNA sequence (3rd DR quartile) | No. species without DNA sequence (4th DR quartile) |
|----------------------------------|-------------------|----------------------------------|----------------------------------------------------|----------------------------------------------------|----------------------------------------------------|----------------------------------------------------|----------------------------------------------------|
| Troglodytidae                    | 75                | 18                               | 0.24                                               | (4/18)                                             | (6/19)                                             | (5/19)                                             | (3/19)                                             |
| Thraupidae                       | 347               | 74                               | 0.21                                               | (18/86)                                            | (20/87)                                            | (19/87)                                            | (17/87)                                            |
| Passerellidae                    | 116               | 28                               | 0.24                                               | (7/29)                                             | (7/29)                                             | (7/29)                                             | (7/29)                                             |
| Icteridae                        | 90                | 6                                | 0.07                                               | (1/22)                                             | (1/22)                                             | (4/23)                                             | (0/23)                                             |
| Parulidae                        | 99                | 3                                | 0.03                                               | (0/24)                                             | (2/25)                                             | (1/25)                                             | (0/25)                                             |
| Thamnophilidae                   | 218               | 53                               | 0.24                                               | (13/54)                                            | (13/54)                                            | (16/55)                                            | (11/55)                                            |
| Furnariidae/<br>Dendrocolaptinae | 276               | 84                               | 0.30                                               | (21/69)                                            | (21/69)                                            | (21/69)                                            | (21/69)                                            |
| Cotingidae/Pipridae              | 117               | 37                               | 0.32                                               | (9/29)                                             | (9/29)                                             | (9/29)                                             | (10/30)                                            |
| Tyrannidae                       | 280               | 62                               | 0.22                                               | (16/70)                                            | (16/70)                                            | (13/70)                                            | (17/70)                                            |
| Pipromorphidae                   | 100               | 46                               | 0.46                                               | (12/25)                                            | (12/25)                                            | (9/25)                                             | (13/25)                                            |

(R core development team). Areas containing cells with many species in the 4th quartile (high DR scores) are considered to contain actively diversifying groups, whereas those with high richness in the 1st quartile contain lineages whose current rate of diversification is low (Kennedy *et al.*, 2014). Although the distribution of these species is likely to have been impacted by climatic and geological change over the time-scales since their origination (Zachos *et al.*, 2001; Hoorn & Wesselingh, 2010), we show that a strong spatial signal is present in the richness patterns assessed in the light of the phylogenetic ranks.

#### *Within grid cell accumulation*

We compared the maximum grid cell richness values of each quartile to ask if species with few close relatives (low DR values) were more likely to co-occur (i.e. be present in the same grid cell) compared with those with many (high DR values). A lack of reproductive isolation may be an important limit on the accumulation of species within grid cells (Weir & Price, 2011; Price *et al.*, 2014). To assess this influence, we estimated the average species age for each DR quartile; taxa < 2 Myr in age are unlikely to be completely reproductively isolated from their closest relatives (Weir & Price, 2011). In order to account for the influence of species sampled without genetic data, we repeated these analyses after pruning them from the trees, but the results remained quantitatively similar (Figs S12 and S13).

#### *Regional movement*

We compare species richness among areas that contain members of terminally diverse clades (high numbers of 4th quartile species in the grid cells) to those that are more phylogenetically isolated (high numbers of 1st quartile species in the grid cells). We consider that, if a region represents both a historical and ongoing area of diversification, it should contain species in all quartiles. The alternative is that diversification rates have varied temporally among lineages (Phillimore & Price, 2008; Rabosky, 2009) and/or among regions (Ricklefs, 2003; Cardillo *et al.*, 2005; Jetz *et al.*, 2012). We quantified these alternatives by comparing the geographical positions of the grid cells that have the maximum species richness value for each DR quartile. In order to do this, we computed the geographical distance (in km) between the most species-rich grid cell in the 1st quartile to the most species-rich grid cell in the 2nd quartile, between the 2nd and 3rd quartiles, and between the 3rd and 4th quartiles (Fig. S14). In some instances, multiple grid cells may contain the maximum value of species richness, and in these cases, we averaged the distances among all such cells. We assessed the robustness of these findings by including the 2nd, 3rd and 4th highest species richness values for each quartile, but as the distances remained highly congruent, the results are not shown. Subsequently, we summed the three mean distances between the quartiles and asked whether the

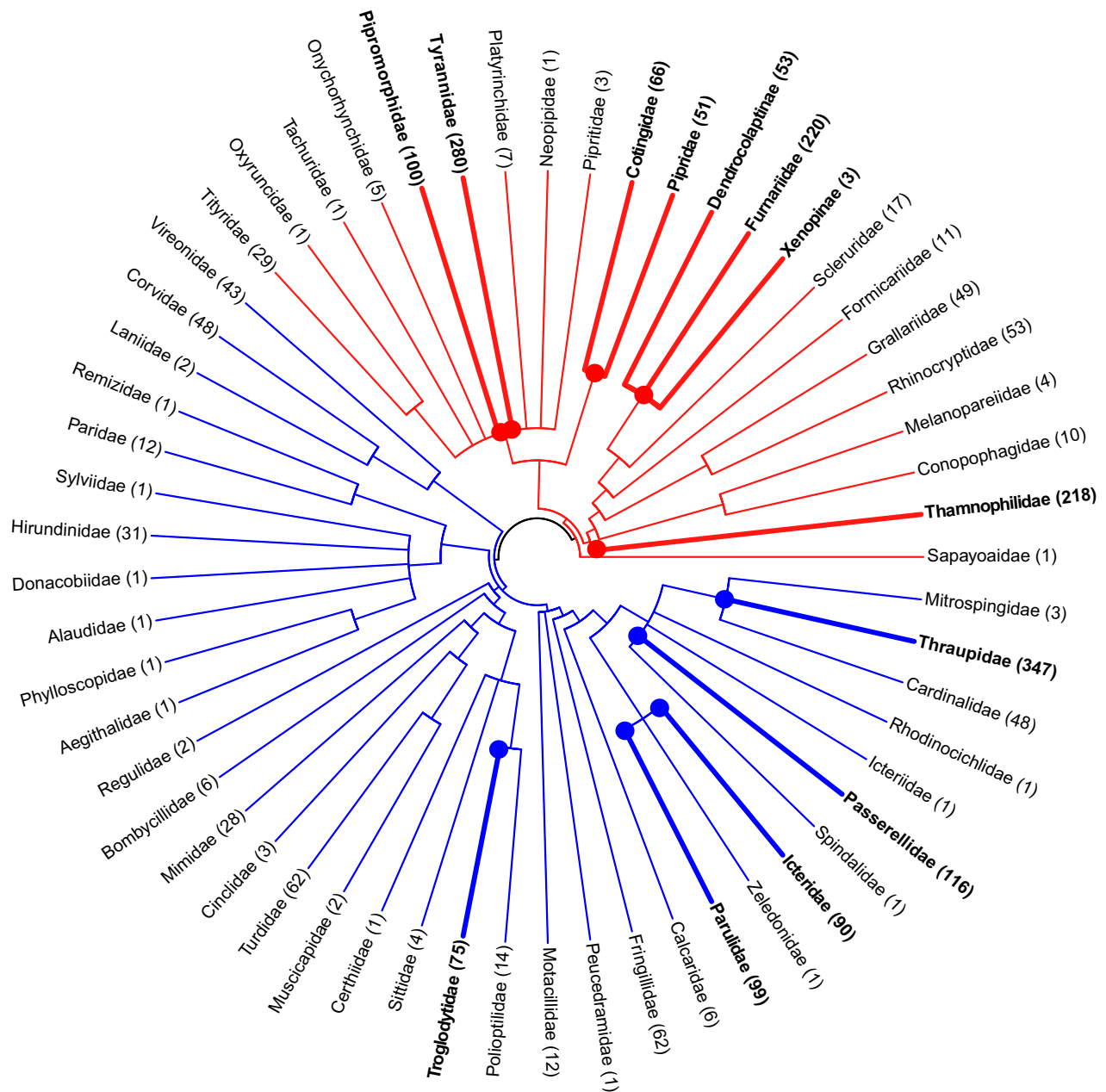
overall values were significantly different among the oscines and suboscines using a phylogenetically corrected *t*-test, with the groups as replicates. To do this, following Wheatcroft & Price (2014), we estimated confidence limits on phylogenetically weighted ancestral values for these distances among each suborder (after pruning the phylogenies to contain a single lineage of each of the 10 groups), using the ACE function in the R package 'ape' (Paradis *et al.*, 2004).

Finally, we asked whether the summed path lengths among the DR quartiles, the overall area occupied (the total number of grid cells occupied by a group), the maximum number of co-occurring species within a grid cell, or the time a group has been present in the New World (crown clade age) was correlated with its total species richness, using the PGLS framework to correct for the phylogenetic non-independence of the data. We implemented these analyses, and a phylogenetically corrected ANOVA of all predictor variables, in the R package 'caper' (Orme *et al.*, 2013). In addition, given that the maximum species richness value within any grid cell is limited by the overall richness of a clade, it is possible that larger clades may have higher maximal grid cell richness as a result of a random configuration of ranges alone. We assessed this potential relationship using a null model approach, contrasting the results with our empirical relationships (Appendix S2).

## RESULTS

### **Predictors of clade richness**

Across the New World, species richness is unevenly distributed among passerine groups (Fig. 1), and different groups reach their maximal diversity in different places (Fig. 2). Neither the total number of one degree grid cells occupied by clades ( $b = -0.01$ ,  $R^2 = 0.02$ ,  $P = 0.71$ ; Fig. 3, left) nor their crown age ( $b = -1.09$ ,  $R^2 < 0.001$ ,  $P = 0.88$ ; Fig. 3, centre) was associated with species richness; both relationships being slightly negative. In contrast, groups with greater overall species richness have a larger maximum number of species that co-occur at the  $1^\circ \times 1^\circ$  scale, compared with smaller groups (Fig. 4). The maximum number of co-occurring species scales to the total number of species in the group with a slope of  $b = 3.2$ . This implies that groups that differ by 100 species in their overall numbers differ by 32 species in their maximum grid cell diversity (Fig. 4). Although clades that contain higher species richness are expected to have a greater number of co-occurring species given a random distribution of ranges, many of our studied groups significantly deviate from this null expectation (Appendix S2). In general, groups that have radiated predominantly in the tropics tend to accumulate a greater number of species (Fig. 2). Given the importance of co-occurrence as a predictor of overall clade richness, as evidenced by the results of our phylogenetically corrected ANOVA (Table S1), we now focus on the history of co-occurrence for the 10 groups.



**Figure 1** Proposed relationships among all New World passerine families following Dickinson & Christidis (2014). Extant species diversity of each family within the New World is in parentheses. The 10 groups considered in this study are highlighted in bold and with circles at the base of the subtending branch or branches. *Blue branches*: oscine groups, *Red branches*: suboscine groups.

### The history of co-occurrence

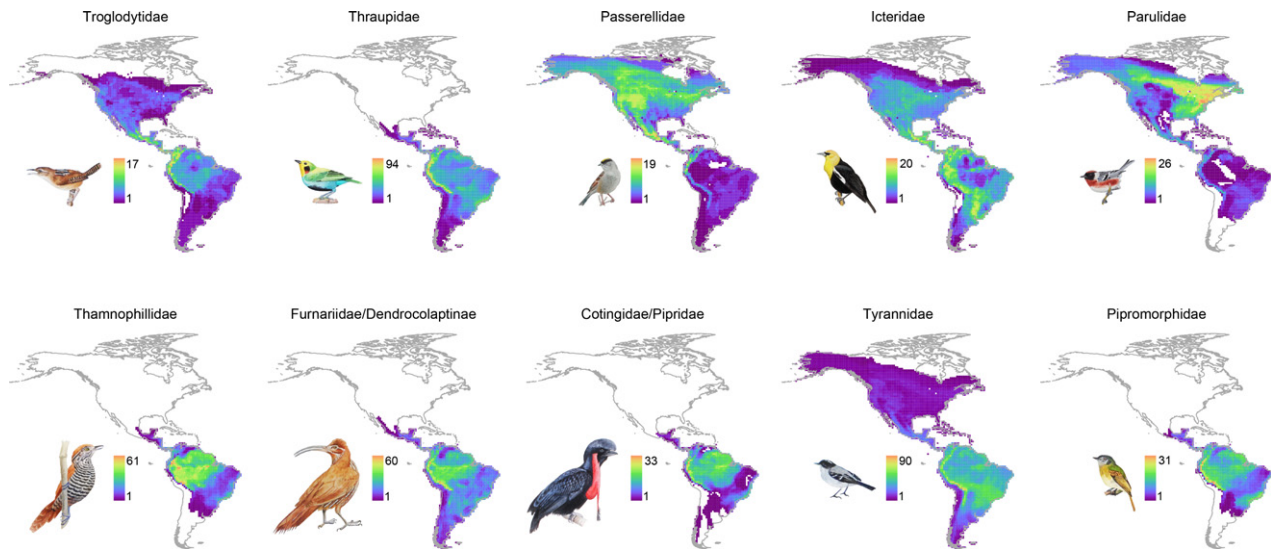
When we consider maximal richness among the DR quartiles, the 1st quartile, that is the one that comprises the oldest and least diverse lineages, generally reaches higher maximal grid cell richness than those containing the younger and more diverse lineages. However, this pattern is only prominent in the four groups that contain > 200 species (Fig. 5). The average species age in the 1st quartile among all groups is 6.4 Myr (oscines: 6.2 Myr, suboscines: 6.7 Myr), which contrasts with the average age in the 4th quartile of 1.6 Myr (oscines: 1.5 Myr, suboscines: 1.7 Myr; Fig. 4).

Ninety-eight per cent of all species in the 1st quartile have an age > 2 Myr, but this was true for only 28% of species in the 4th quartile. These differences suggest that part of the limit on grid cell co-occurrence in the younger quartiles is a result of incomplete reproductive isolation among the respective lineages (see Discussion).

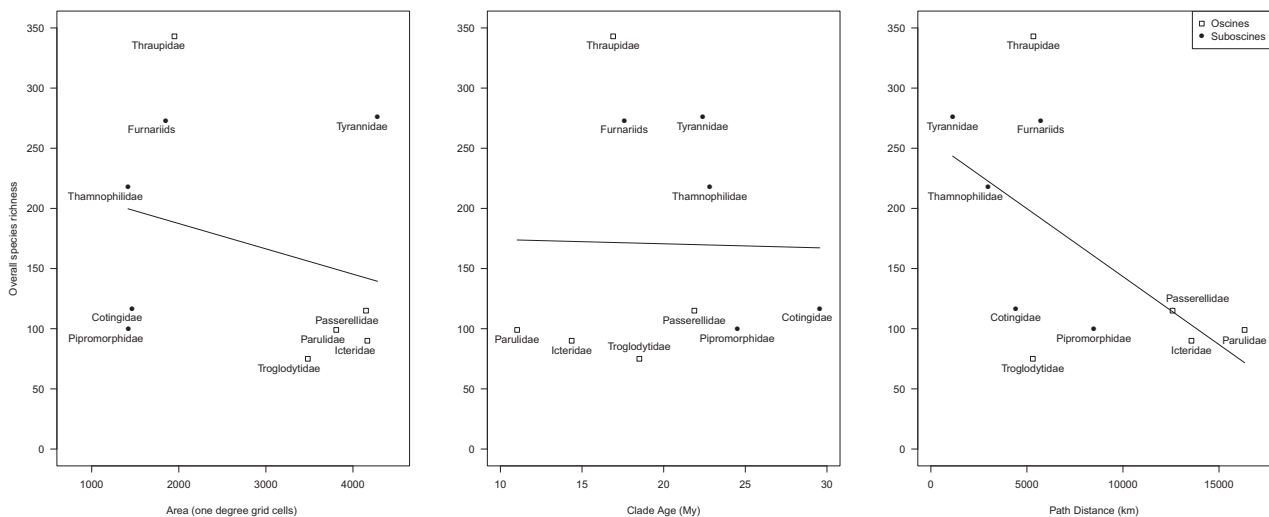
### Geographical patterns of diversification

The distribution of species richness across the DR quartiles are illustrated in Figs 6 and S3 for the tanagers (oscines: Thraupidae) and in Fig. S2–11 for the other nine groups.





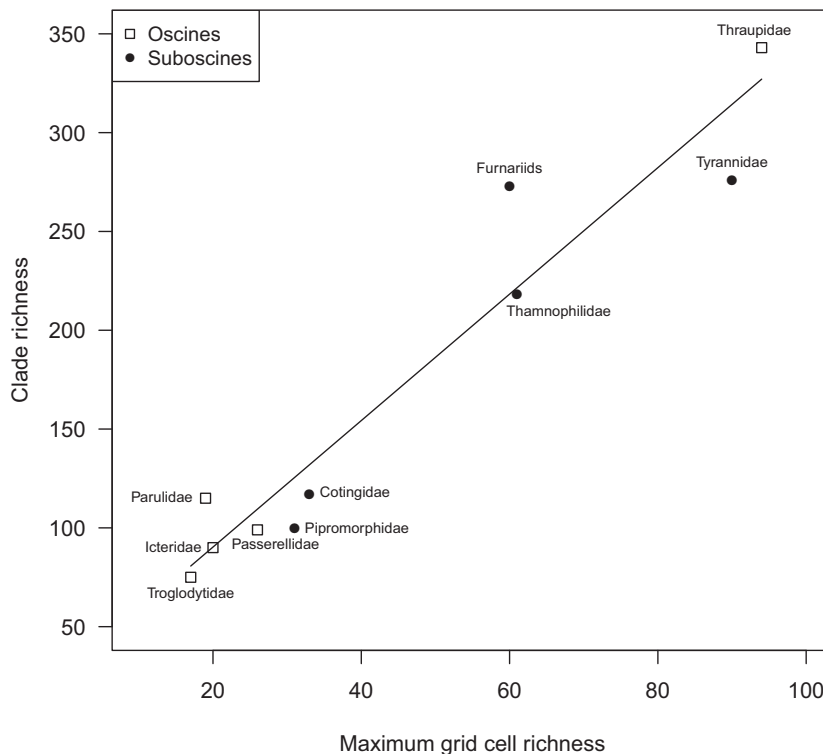
**Figure 2** Maps of species richness at the scale of  $1^\circ \times 1^\circ$  for 10 groups of New World passerines. *Above*: the five oscine groups, *below*: the five suboscine groups. The illustrations by JF represent members of the respective groups; Troglodytidae – *Cistothorus platensis*, Thraupidae – *Chlorochrysa nitidissima*, Icteridae – *Xanthocephalus xanthocephalus*, Passerellidae – *Zonotrichia atricapilla*, Parulidae – *Setophaga castanea*, Thamnophilidae – *Thamnophilus multistriatus*, Furnariidae/Dendrocolaptinae – *Drymornis bridgesii*, Cotingidae/Pipridae – *Cephalopterus glabricollis*, Tyrannidae – *Serpophaga cinerea* and Pipromorphidae – *Leptopogon taczanowskii*.



**Figure 3** Correlation of the total species richness among the 10 New World passerine groups as a factor of the total number of  $1^\circ \times 1^\circ$  grid cells occupied (*left*), crown clade age (*centre*) and the summed path lengths between the maximum species richness cells across the DR quartiles (*right*). Squares represent the 5 oscine groups, whereas circles represent the 5 suboscine groups. Lines are the least squares regression.

For each group, in the figure legend, we qualitatively describe their ecological characteristics and geographical patterns of diversification. In the case of the tanagers, their radiation occurred extensively throughout the Andes in all but the youngest groups, as illustrated by the high Andean species richness in the first three quartiles. Subsequently, younger lineages expanded and diversified in the Amazon basin (notably those in the 3rd quartile), with the terminal radiations occurring predominantly in the Atlantic forests and savanna grasslands of south-eastern Brazil (4th quartile). Some

groups show similar patterns in terms of radiating out of the Andean region (Cotingidae/Pipridae and Pipromorphidae; Figs S9 and 11), whereas others apparently radiated into this area, as evidenced by the high species diversity in the younger but not older quartiles (Passerellidae, Parulidae, Furnariidae/Dendrocolaptinae, Tyrannidae; Figs S4, 6, 8 and 10). The remaining groups show less affinity for the Andes, such as the Thamnophilidae, which radiated extensively throughout the Amazon basin (Fig. S7). Continual shifts in the geographical areas harbouring lineages that differ in their



**Figure 4** Correlation of the maximum species richness value recorded in any  $1^\circ \times 1^\circ$  degree grid cell with total species richness among the 10 New World passerine groups. Squares represent the five oscine groups, whereas circles represent the five suboscine groups. Line is the least squares regression.

diversification rates appear to be a defining property of New World passerine radiations.

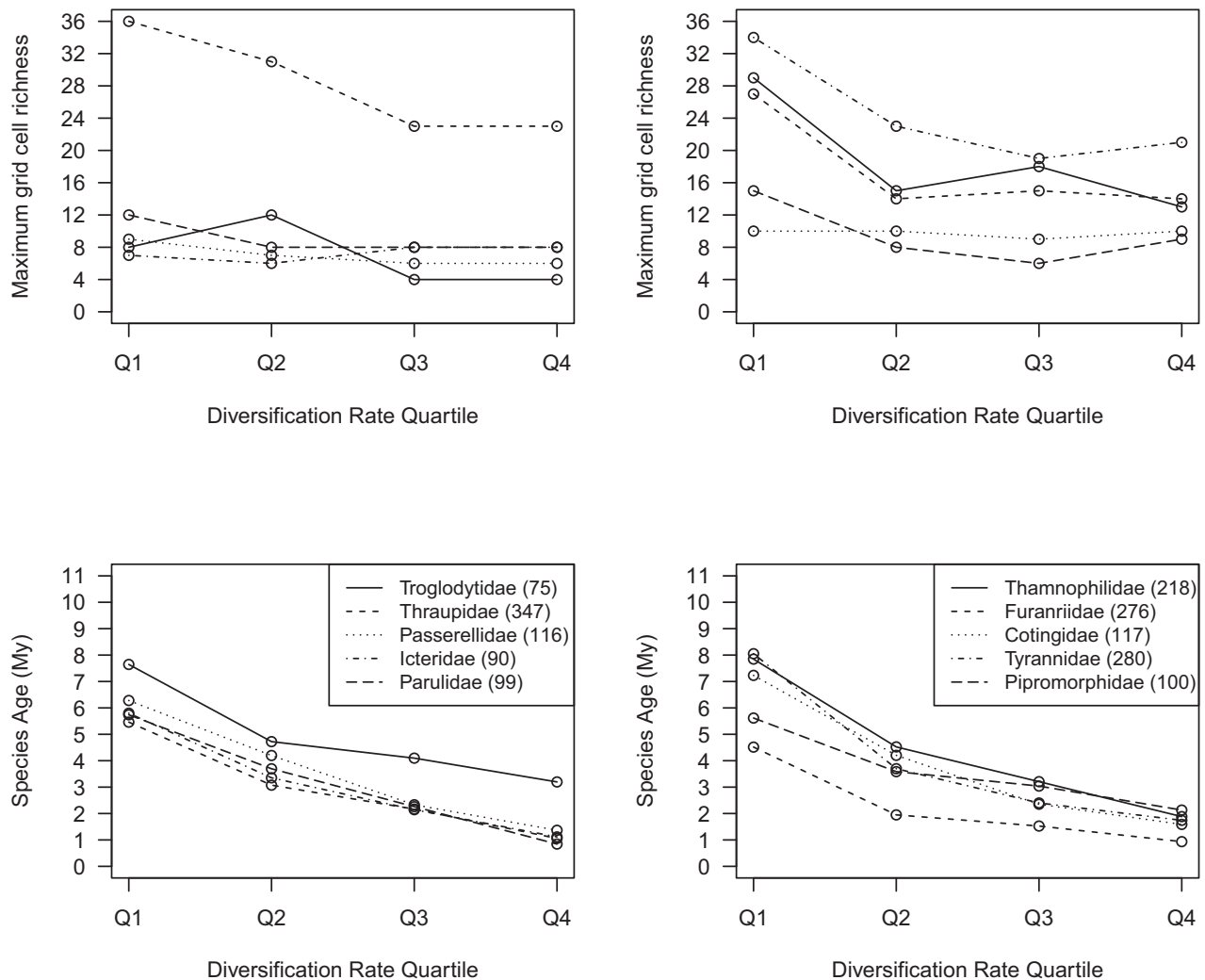
For each group, we computed the geographical distances between the maximum diversity cells for each DR quartile and summed the distances for the three paths (Fig. S14). Three oscine groups (Passerellidae, Icteridae and Parulidae) show particularly large distances, as a result of having lineages that diversified in both South America and North America. Overall, the oscines have significantly greater distances among their maximum diversity cells than the suboscines (phylogenetically corrected  $t_8 = 26.2$ ,  $P < 0.001$ ). The summed distances between the maximum diversity quartile cells showed a significantly negative correlation with total richness ( $b = -0.01$ ,  $R^2 = 0.41$ ,  $P = 0.04$ ; Fig. 3, right), implying that groups which disperse over larger distances have fewer species. This result appears to be driven by the large differences in species richness and associated path lengths between the Thraupidae and the three oscine groups listed above (Fig. 3, right), which are all quite closely related (Barker *et al.*, 2015).

## DISCUSSION

The build-up of species richness within clades reflects both geographical turnover and the accumulation of species in sympatry. Here, we found that larger clades contain higher numbers of co-occurring species, implying that limits on co-occurrence represent an important control on clade richness (Fig. 4 and Appendix S2). The geographical locations of diversification events that generate these co-occurrence

patterns vary through time among all groups, and often areas that support large numbers of young actively diversifying groups are not those that harbour the highest overall number of species (Figs 6 and S2–11). Neither the time present within the New World, current diversification rates or geographical area predicts extant species diversity well (Kennedy *et al.*, 2014; Rabosky *et al.*, 2015; Fig. 3). Instead, these findings suggest that prolonged diversification within the tropics results from the greater availability of ecological niche space, and this is responsible for the high diversity of many clades that have radiated there. We first consider limits on the build-up of co-occurring species and then spatial variation in the patterns of lineage diversification.

One factor that may limit the co-occurrence of recently formed species is that they are incompletely reproductively isolated (Barton & Hewitt, 1989; Weir & Price, 2011). This issue is likely to be particularly relevant among actively diversifying lineages, which contain many young forms. Although the species age estimates come with many uncertainties, the average age in the 1st quartile ranges from 4 to 8 Myr within groups, whereas that for the 4th quartile is between 1 and 3.5 Myr (Fig. 5). Given that hybrid zones can form between species estimated to be as old as 4 Myr (Weir & Price, 2011; Weir *et al.*, 2015), this implies that many species, especially in the younger quartiles, may be unable to achieve sympatry as they are not completely reproductively isolated. However, even given the attainment of reproductive isolation, insufficient ecological differentiation is another potential limit on the capacity of these species to co-occur (e.g. Garcia-Moreno & Fjeldså, 1999). Furthermore, given



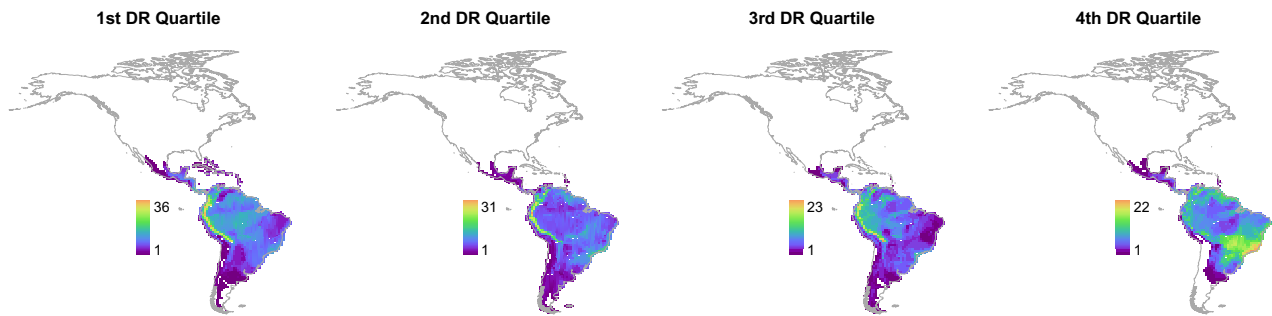
**Figure 5** Above: Maximum species richness value recorded in  $1^\circ \times 1^\circ$  grid cells for each DR quartile. Below: Average species age (the length of the branch subtending an extant species) for all species within each DR quartile. These values were first assessed over 1000 topologies of the Jetz *et al.* (2012) phylogeny (pruned to contain only the New World passerine species), with the mean values presented. Left panels: Oscines, Right panels: Suboscines. The legends include the total number of species each group has present in the New World.

that recently formed species are likely to be geographically isolated from one another, they may also have had insufficient time to expand their ranges into secondary sympatry (Weir & Price, 2011; Pigot & Tobias, 2015), even if they are ecologically and reproductively isolated.

A further explanation for limits on the number of co-occurring species in a grid cell is variation in total niche space, and we suggest this is an important contributor. Some grid cells may be able to support more species than others. Areas that maintain high levels of diversity vary between clades (Fig. 2) and can be related to their particular ecologies (Figs 6 and S2–11). This may depend on differences among groups both in their foraging behaviour and in the complexity of their principal habitats, in respect of vegetation volume and the availability of microhabitats or food types (see Lavers & Field (2006)). For example, New World blackbirds

(Icteridae) are particularly diverse on tropical floodplains (Fig. S5), which comprise mosaics of swampy habitat and tall forest that contain complex vegetation in which species exploit a broad range of food types. In contrast, although their sister group (the wood warblers; Parulidae) also colonized the tropics, they have remained restricted to more scrubby montane and riparian vegetation, where they mainly feed on small insects (Fig. S6). The variability in habitat affinities within groups represents another important factor influencing the co-occurrence patterns. Such affinities reflect the evolutionary lability of traits that underlie species ecology (e.g. foraging modes, dietary preferences; see legends of Figs 6 and S2–11) and thus determine their potential to co-exist in sympatry with both close and distant relatives (Love- tte & Hochachka, 2006). As the results from our null models imply that half of the studied clades co-occur at higher or





**Figure 6** Maps of species richness in  $1^\circ \times 1^\circ$  grid cells for the tanagers (Thraupidae), among quartiles defined by ranking all species based on their values of the DR statistic. The 1st quartile contains the oldest and most species poor lineages, whereas the 4th quartile represents the youngest and most diverse. *Notes:* The tanagers are the only oscine group considered here to have originated in South America. Their early diversification events were centred in the northern Andes, with subsequent expansion and diversification across the Amazon and Guianas. Terminal radiations occurred in the southern Brazilian Atlantic forests, grasslands and highlands. The group contains mostly small birds with moderately strong, conical bills. Many species feed on fruit pulp; however, throughout this radiation there have been a number of evolutionary shifts in feeding specialization, including the insertion of bills into newly ripened fruit or flowers, and feeding on grain or harder-husked seeds. Although the range of habitats occupied by this group are vast, suggesting lineages to be climatically tolerant and ecologically labile, no species have expanded north beyond Middle America.

lower levels than expected by chance (Appendix S2), this is consistent with the hypothesis of geographical variation in carrying capacity across clades. Even in instances where this is not the case, the balance between interactions increasing allopatry (competition, incomplete reproductive isolation) and promoting co-occurrence (ecological differentiation) are likely to remain important.

The exceptionally high diversity in some areas among the 1st quartiles (the most phylogenetically isolated species; Fig. 5) also requires further consideration. One potential explanation is that regions which have been climatically stable, providing refuges, are also those that have a capacity to accommodate a large number of species, as has been suggested for the Andes and Amazon (Hoorn & Wesselingh, 2010; Fjeldsø *et al.*, 2012). Many species present in these areas are also evolutionarily distinct (Jetz *et al.*, 2014), implying that they facilitate persistence over long time-scales, and thus experienced low rates of extinction (Fjeldsø & Rahbek, 2006; Fjeldsø *et al.*, 2012). However, as the interface between these two areas has amassed the highest levels of passerine species richness in the world (Fjeldsø *et al.*, 2012), heightened rates of geographical species turnover represent a further non-mutually exclusive explanation that can also account for the extremely high species richness of these grid cells.

If the time to accumulate reproductive isolation alone was limiting the build-up of co-occurring species, old stable areas should continuously accumulate species following the colonization/origination of a clade. Consequently, diversity in the quartiles containing the youngest lineages should be high in these areas, as well as in those that have been more recently colonized. While this is observed for a few groups, such as the transitional area between the central Andes and Amazon in the Furnariidae/Dendrocolaptinae (see Fig. S8, a clade which appears to have had a constant rate of lineage accumulation; Derryberry *et al.*, 2011), in the vast majority it is

not (Figs 6, S2–6, 9 and 11). In the case of the tanagers, the grid cells with the largest number of species belonging to the most actively diversifying lineages are in south-eastern Brazil, despite the highest overall species diversity being found in the Andes (Fig. 6). Furthermore, as we recovered no relationship between clade age and overall diversity (Fig. 3, centre), time, with respect to origination within the New World, appears to be of limited importance in determining overall species numbers. These latter results are inconsistent with those of a recent study that found a positive correlation between age and species diversity among 27 Neotropical lineages (Smith *et al.*, 2014). Potentially, these different results reflect the alternative temporal, taxonomic and spatial scales of the respective studies, such that processes occurring at the phylogeographical/population level (the focus of the Smith *et al.*, 2014 study) may not apply to higher taxa over longer time-scales. Finally, although we acknowledge that the addition of further genetic data could potentially alter the time-scale of diversification proposed by Jetz *et al.* (2012), as the majority of studied species are sampled with sequence data [with the remaining species evenly distributed among the DR quartiles (Table 1)], it is unlikely that subsequent updates will significantly change either the spatial patterns or relative age estimates presented here.

Temporal shifts in the areas of diversification among New World passerine groups are common (Figs 6 and S2–11), but the distances between areas supporting lineages that are diversifying at different rates vary between groups. As previously shown for the oscines and suboscines as a whole (Kennedy *et al.*, 2014), oscine groups tend to shift their areas of diversification over greater distances than do the suboscines (Fig. S14). This may reflect the widespread occurrence of migratory behaviours in many oscine lineages and their frequent settlement in the non-breeding range (Winger *et al.*, 2014). However, shifts in the areas of diversification over larger distances do not lead to the

accumulation of higher clade richness. Instead, we recover the opposite relationship. Groups that undergo range expansion and diversify over more restricted geographical settings contain the most species (Fig. 3, right). Given that the ability of lineages to expand their ranges is necessary for the continued diversification of a clade (Price, 2008; Fritz *et al.*, 2012; Price *et al.*, 2014), the invasion of new regions could increase diversification rates. However, it appears that the ability of the region to accommodate more species, and hence prolong diversification, is most important in generating high clade richness. Although different regions appear to have varied in their historical opportunities for diversification and persistence, it is the Amazonian and Andean areas that have been most able to generate, and maintain, large numbers of species. In general, repeated movements in the geographical areas of diversification among a heterogeneous set of passerine groups suggest that the historical availability of ecological opportunity has been a major factor determining temporal and spatial variation in the rates of lineage diversification.

A lack of constancy in diversification rates through time (Phillimore & Price, 2008; Rabosky, 2009) and space (Jetz *et al.*, 2012) is now widely appreciated, including among some of the groups studied here (Rabosky & Lovette, 2008; Barker *et al.*, 2013; Burns *et al.*, 2014). Given that climatic and geological change has varied temporally among regions (Hoorn *et al.*, 2010), this must have influenced opportunities for geographical isolation, ecological divergence and rates of lineage diversification/persistence. Overall, our results show that variation in regional opportunities for species accumulation, and possibly limits on the rate at which reproductive isolation is generated, to be contributing factors explaining the variation in clade richness among New World passerine birds. These results apply specifically to large clades. Smaller clades may show different patterns, if they are far from equilibrium or alternatively are on the decline from a larger size. However, many small clades occupy restricted ecological and geographical space (Ricklefs, 2005), implying limits on the numbers of species they contain.

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## SUPPORTING INFORMATION

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

**Appendix S1** Supplementary table and figures.

**Appendix S2** Null models assessing grid cell richness – clade richness.

## BIOSKETCH

**Jonathan Kennedy** is a postdoctoral researcher at the Center for Macroecology, Evolution and Climate, at the University of Copenhagen. His research interests primarily relate to the historical biogeography and macroevolution of passerine birds.

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

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