



Does the colonization of new biogeographic regions influence the diversification and accumulation of clade richness among the Corvides (Aves: Passeriformes)?

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Regional variation in clade richness can be vast, reflecting differences in the dynamics of historical dispersal and diversification among lineages. Although it has been proposed that dispersal into new biogeographic regions may facilitate diversification, to date there has been limited assessment of the importance of this process in the generation, and maintenance, of broad-scale biodiversity gradients. To address this issue, we analytically derive biogeographic regions for a global radiation of passerine birds (the Corvides, c. 790 species) that are highly variable in the geographic and taxonomic distribution of species. Subsequently, we determine rates of historical dispersal between regions, the dynamics of diversification following regional colonization, and spatial variation in the distribution of species that differ in their rates of lineage diversification. The results of these analyses reveal spatiotemporal differences in the build-up of lineages across regions. The number of regions occupied and the rate of transition between regions both predict family richness well, indicating that the accumulation of high clade richness is associated with repeated expansion into new geographic areas. However, only the largest family (the Corvidae) had significantly heightened rates of both speciation and regional transition, implying that repeated regional colonization is not a general mechanism promoting lineage diversification among the Corvides.

KEY WORDS: Biogeographic regions, centers of diversification, dispersal, passerine birds, speciation.

Global variation in the distribution and abundance of species has been recognized by biologists for centuries. Although the generation of diversity gradients across large spatial scales are acknowledged to reflect the historical dynamics of speciation, extinction and dispersal, the relative importance, and interplay between these processes remain contentious (Jablonski et al. 2006; Mittelbach et al. 2007). Given the predominance of allopatric speciation throughout the animal kingdom (Coyne and Orr 2004), dispersal and diversification are proposed to be closely linked, with range expansions into new areas a prerequisite for continued lineage diversification (Price 2008; Fritz et al. 2012). Differences in the rates at which lineages colonize (i.e., disperse to and establish

in) new areas may influence the dynamics of their diversification, and the accumulation of species diversity (Wilson 1959; Moyle et al. 2009; Ricklefs 2009; Fjeldså 2013). However, to date much of the evidence in support of these ideas has come from studies of small, isolated insular assemblages (Losos and Ricklefs 2009), with the role of colonization in the generation of diversity gradients among richer continental biotas less well established, due to their more complex geological histories and patterns of landmass connectivity.

Given that geographically congruent breakpoints in the distribution of many taxonomic groups have long been recognized (Sclater 1858; Wallace 1876), it is possible to identify distinct

biogeographic regions at large spatial scales. These regions may play an important role in the accumulation of clade richness. This is because the colonization of one biogeographic region from another may provide novel ecological opportunities (Simpson 1953), lead to a release from competitors/parasites (Ricklefs 2011) and/or expose lineages to landscapes of increased geological/topological complexity (Cracraft 1985), resulting in their increased diversification (Simpson 1953; Rabosky and Hurlbert 2015). Should these opportunities differ among regions, they could account for differences in the rate of diversification, the geographic extent over which it occurs (Ricklefs 2003; Kennedy et al. 2014; Rabosky and Hurlbert 2015), and thus the number of species that accumulate through time. Regional differences in opportunities for lineage diversification and maintenance likely reflect variation in biotic, climatic, and geological conditions across large spatial and temporal scales. Here we study how regional colonization influences the diversification dynamics and variation in clade richness among a global radiation of passerine birds.

Bird species vary greatly in their ability to disperse and establish in new areas. While some groups are able to undertake seasonal movements over large distances, others are unable to cross small water bodies (Diamond 1981; Moore et al. 2008) or gaps in forest vegetation (Claramunt et al. 2012). While low, intermediate, and high colonization abilities have all been proposed to facilitate speciation (Diamond et al. 1976; Belliure et al. 2000; Price 2008; Claramunt et al. 2012), it is possible that high colonization abilities are most conducive for diversification among global radiations, where colonization occurs over large and potentially disconnected landmasses. For example, range expansions as a result of colonizing new and remote areas have initiated radiations throughout a number of continental and insular settings (Grant 1998; Hughes and Eastwood 2006; Ohlson et al. 2008; Lerner et al. 2011; Jönsson et al. 2012; Fjeldså 2013). The rate and extent over which lineages colonize new areas could therefore be an important determinant both of their propensity to speciate, and of the way in which species diversity accumulates across space (Mayr 1947; Ricklefs 2003; Claramunt et al. 2012).

In this study, we test whether repeated dispersal and establishment promotes diversification at regional scales, and whether this acts as a key driver on the accumulation of clade richness among a diverse (c. 790 species) and globally distributed group of passerine birds, the Corvidae (sensu Cracraft 2014). This group is particularly suitable for such a study because species richness varies spatially and taxonomically, with their global distributions reflecting multiple independent events of continental and insular colonization (Jönsson et al. 2011; Aggerbeck et al. 2014). The Corvidae originated in a region of dynamic landmass connectivity at the edge of the Australasian plate (Jönsson et al. 2011), before colonizing all continental land masses (excluding Antarctica) as a result of the evolution of eco-morphological traits that

promoted range expansion out of the Indo-Pacific (Jönsson et al. 2011; Marki et al. 2015). Here, we first define biogeographic regions among the Corvidae based on turnover in the phylogenetic composition of species assemblages across large geographic areas (c. 220×220 km grid cells). Subsequently, we assess historical patterns of dispersal, diversification, and species build-up among these regions, before examining the distribution of species that differ in their rates of lineage diversification at finer spatial scales.

Methods

PHYLOGENETIC AND SPATIAL DATA

We obtained an estimate of the phylogenetic relationships among 665/789 species of the Corvidae recognized by the IOC v.2.7 (Gill and Donsker 2010) from the Maximum Clade Credibility (MCC) phylogeny of Jönsson et al. (2016). The remaining 124 species for which sequence data were unavailable at the time of the tree generation (c. 15% of the overall Corvidae) are generally well established based on current taxonomic information to be members of terminal clades (del Hoyo et al. 2005–2010). Following the methods of Marki et al. (2015), we added these species as polytomies to the phylogeny based on this taxonomic knowledge, before using a birth-death model to resolve the polytomies and assign branch lengths (Kuhn et al. 2011). The resulting MCC tree was used in all analyses described below unless otherwise stated, and can be accessed from Dryad <http://dx.doi.org/10.5061/dryad.80n42>. Distributional data for the breeding range of these species were obtained from an expert-validated database (Rahbek et al. 2012), with the ranges recorded at a resolution of $1^\circ \times 1^\circ$.

PHYLOGENETIC-BETADIVERSITY

(PHYLOBETADIVERSITY) AND BIOREGIONALIZATION

We used hierarchical clustering algorithms after quantifying the phylogenetic turnover among species assemblages to define biogeographic regions for the Corvidae (Kreft and Jetz 2010; Holt et al. 2013). This approach provides a statistically tractable definition of regional units that attempts to maximize the contribution of in situ speciation relative to dispersal in delineating the regional species assemblages. This property results because the regional boundaries reflect areas in which species turnover is exceptionally high, and where the species in adjunct assemblages belong to distinct (but paraphyletic) parts of the phylogeny. To achieve the regional delimitation, we first computed phylobetadiversity distances between all $2^\circ \times 2^\circ$ grid cell assemblages using the $\text{phylobeta}_{\text{sim}}$ metric (see Holt et al. 2013). We assessed these patterns at the 2° scale, to reduce comparisons among grid cells containing a low number of species, as suggested by Kreft and Jetz (2010). $\text{Phylobeta}_{\text{sim}}$ quantifies the differences in the amount of shared branch length among grid cells, while accounting for the variation in species richness among them (Lennon et al.

2001). Following this computation, we performed a nonmetric multidimensional scaling (nMDS) ordination of these results, to assess the geographic structure in the turnover of phylogenetic diversity throughout the study area (Fig. S1; Kreft and Jetz 2010).

To cluster our global grid cells into discrete regions, we assessed various clustering algorithms and resulting number of clusters from the $\text{phylobeta}_{\text{sim}}$ comparisons. The clustering algorithms tested included all nine hierarchical approaches suggested by Kreft and Jetz (2010), as well as the nonhierarchical Partitioning Around Medoids (PAM) approach (Kaufman and Rousseeuw 1990). We subsequently inspected each clustering result for the presence of poorly supported clusters, using the silhouette statistic (Rousseeuw 1987), which quantifies the degree of cohesion or separation among data points (in this instance grid cells) within a cluster. A mean silhouette score of less than 0.25 was used as a measure by which the clusters were deemed poorly supported. Biogeographic regions were selected from the algorithm that returned the highest number of clusters, among the results that contained no poorly supported clusters. The resulting regions represent geographically cohesive units of phylogenetically distinct species assemblages.

REGIONAL ANCESTRAL AREA RECONSTRUCTION

We used the R package BioGeoBEARS (Matzke 2013, 2014) to compute and compare alternative models of geographic ancestral area reconstruction using Maximum Likelihood. We determined the geographic distribution of all lineages based on their presence in the regions defined from the bioregionalization analyses, before assessing six alternative models of ancestral area reconstruction (DEC, DEC+J, DIVA, DIVA+J, BayArea, and BayArea+J). These models represent Bayesian approximations of the most commonly used ancestral reconstruction software (LAGRANGE, DIVA, and BayArea). In three of these models, we included an additional parameter, which allowed for founder event speciation (indicated by +J, Matzke 2014). After computing their log likelihood scores, we used the Akaike Information Criteria (AIC) to select the best model, before subsequently calculating the probabilities of the regional states at all nodes in phylogeny.

GEOGRAPHIC PATTERNS OF DIVERSIFICATION

We computed estimates of Diversification Rate (DR; Jetz et al. 2012) and Species Age for all corvid species, before ranking them based on these values. DR reflects the number of nodes separating a species from the root of the phylogeny, weighted by how close these lineage splitting events occur toward the present. This statistic has been shown to be highly correlated with speciation rate estimates in birth-death simulations (Jetz et al. 2012), although it is limited in its representation of diversification over

historical timescales, due to its failure to account for extinction and the potential for diversification rates to vary through time (Kennedy et al. 2014). However, as species with many young and close relatives attain high values of DR, and those with few close relatives recover lower values, DR effectively allows us to score all lineages in respect of their relative phylogenetic isolation. An alternative metric, Species Age (SA), represents the length of the terminal branch subtending each species until the most recent speciation event. As the estimates of DR and SA are highly correlated with one another (Fig. S2), the spatial analyses (described below) produced extremely similar patterns regardless of the metric assessed. We therefore focus on the results using the DR values in the main text. Species that recover low values of DR should be considered those that are present on phylogenetically isolated lineages, and result from older speciation events, whereas those with high DR values are members of terminal diverse radiations, and tend to have originated from more recent speciation events.

Following the approach of Kennedy et al. (2014), we used the species ranks of DR and SA to divide our distributional database into quartiles. The first quartile contained the oldest and least diverse lineages, while the fourth quartile contained the youngest and most diverse ones. We subsequently generated maps of species richness at the $1^\circ \times 1^\circ$ scale for each quartile. As our aim was to determine areas that have accumulated a higher or lower number of species in each DR quartile than predicted, we regressed the grid cell richness of each quartile against that of the overall Corvids, using linear models, before assessing the geographic patterns of the residuals. Finally, we determined the distribution of DR values among the lineages present within each biogeographic region, and the total number of species found within each region across the four DR quartiles.

Our assessment of the geographic dynamics of diversification among the Corvids is based on the distributional and phylogenetic relationships among extant species alone, and as such the results we present come with two general caveats; (1) they do not directly consider the influence of extinction, and (2) the distribution of species are likely to have changed throughout the timescale of this radiation. However, with respect to the latter point, even given this influence, we recover a strong spatial signal in the data, such that groups of species that are similar in the extent of their phylogenetic isolation (and hence are currently diversifying at similar rates) have a tendency to be maintained in similar geographic areas. A further consideration in interpreting our results is that the phylogenetic relationships among c. 15% species were inferred based on taxonomy alone. Nonetheless, despite their precise placement in the phylogeny and the timing of their diversification remaining uncertain to some degree, we show that our results remain robust to the exclusion of these species from the analyses.

THE ACCUMULATION OF CORVOID FAMILY SPECIES RICHNESS

Using the results from the ancestral area reconstruction we assessed potential factors determining the accumulation of species numbers among corvoid families. The families we consider are broadly those classified by the IOC v.2.7 (Gill and Donsker 2010), with amendments made in a few instances where monophyly was not recovered in the MCC tree. These rare instances of paraphyly reflect the placement of a small number of taxa whose current taxonomic affinities remain uncertain.

We determined the number of regions occupied, and the number of transitions between regions that occurred within each family. Transition events reflect descendent nodes that occur either partially (in the case of states shared between two regions), or completely, in a different regional state relative to that of their ancestor. To account for the uncertainty in the reconstructions at some nodes (i.e., when the probability of presence was divided among many regional states), we drew a single state at each node based on their probabilities, before calculating the number of transitions per family, repeating this procedure 1000 times. For transitions and the number of regions occupied, we used PGLS, implemented in the R package *caper* (Orme et al. 2013), to assess their relationship with overall family richness. We controlled for the phylogenetic nonindependence of this data using the MCC tree, pruned to contain a single representative of each family. For the transitions, we computed these models for all families, and also considering only those that transitioned between regions. We also assessed whether transitioning between regions or not (irrespective of the absolute number of transitions recorded) was related to family species richness, using a phylogenetically corrected ANOVA, implemented in the R package *phytools* (Revell 2012).

We assessed the probability of transition within each family against the background rate of transition (the transition probability among nodes and terminal diversification events within all corvoid families). Transition probabilities reflected the average number of transitions (calculated after drawing the regional states 1000 times) that occurred among nodes or terminal diversification events subtending the most recent common ancestor of a family, divided by the total number of these events. We evaluated whether the transition probabilities of each family were significantly different from the background rate by first generating a binomial distribution with integers between 0 and the total number of species within a family (representing the quantiles), utilizing the background transition rate as the probability. *P*-values were generated by summing the proportion of this distribution with a higher or lower number of transitions compared to the empirical number.

We calculated the area occupied by each family as the number of unique 2° grid cells in which they occur, because

this scale facilitates comparison with the other results presented. We then determined the predictive power of this variable on the variation in family species richness, accounting for the influence of the regional transitions (and vice versa) using partial correlations. Finally, we assessed the relationships between the number of regions occupied and transition rates, as a function of the crown age of the families, using PGLS.

DIVERSIFICATION DYNAMICS FOLLOWING REGIONAL COLONIZATION

We assessed historical variation in speciation rates among the Corvids using the program Bayesian Analysis of Macroevolutionary Mixtures v.2.5 (BAMM; Rabosky 2014). BAMM uses a Reverse Jump Markov chain Monte Carlo (RJMCMC) algorithm to explore different models of lineage diversification that vary in their rates of speciation and extinction. This method generates a posterior distribution of speciation and extinction rate values at continuous time intervals throughout a phylogeny, such that BAMM evaluates a number of potential evolutionary rate shift scenarios, sampled in proportion to their posterior probability. Each rate shift defines a cohort of taxa (all lineages downstream of the rate shift assuming no further rate shifts) that share common rates of speciation and extinction. We determined whether our results were sensitive to different values of the prior (1, 5, 10, 50, and 100) reflecting the expected number of rate shifts, and found the number of rate shifts recovered to be highly consistent throughout these analyses (Fig. S3). The results presented in the main text were derived from an analysis where the prior reflecting the expected number of rate shifts was set to 1. We used BAMMtools (Rabosky et al. 2014) to estimate the remaining priors for the analysis, before running the RJMCMC chain for a total of 10,000,000 generations on the MCC tree of Jönsson et al. (2016), providing a global sampling fraction (0.85 of all species sampled) to account for the missing species. Following a visual confirmation of the chain mixing and convergence, we removed the first 10% of samples as a burn-in before further analysis.

To investigate whether regional colonization and transition are positively correlated with diversification, we determined the distinct rate shift configurations on all postburnin samples recovered from BAMM, before assessing the frequency of diversification rate shifts between families. For the families in which rate shifts were recovered in >25% of samples, we estimated the rates of speciation of each macroevolutionary cohort, and the average number of regional transitions for that cohort (following the methods documented above, sampling all regional states 100 times at each node), before investigating the relationships among these variables.

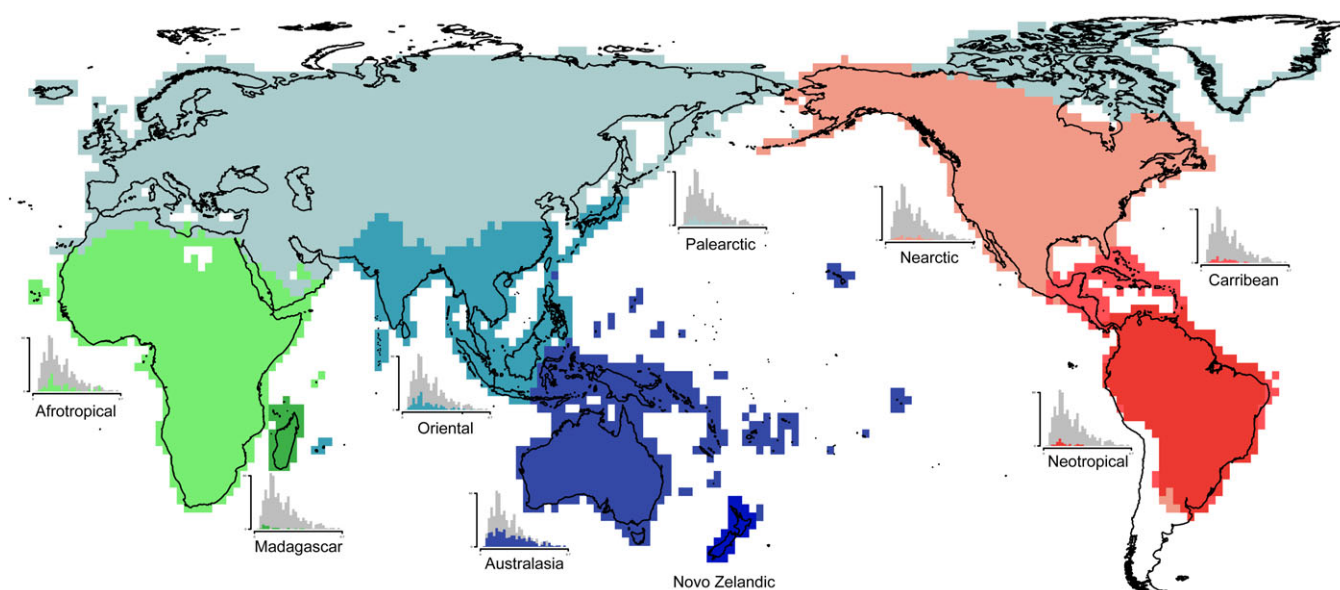


Figure 1. Map of $2^\circ \times 2^\circ$ grid cells colored to reflect the nine corvid biogeographic regions proposed by the McQuitty clustering algorithm. Similar colors represent regional assemblages that are relatively close to one another in ordination space, defined by the turnover in their $\text{phylobeta}_{\text{sim}}$ values. Conversely, divergent colors reflect regions that are distant from one another in this same space. Histograms represent the frequency distribution of DR values among all corvid species (gray), and the distribution of DR values for the species present within the respective regions. Due to the low number of species present, the histogram for the Novo Zelandic region is not shown.

Results

BIOGEOGRAPHIC REGIONALIZATION OF THE CORVIDES

A nonmetric multidimensional scaling (nMDS) ordination of the regional clustering results is shown in Figure S1. Considering only the well-supported clusters, we defined nine global regions of the Corvidae using the McQuitty algorithm (Fig. 1). The New World, excluding the most northerly areas, was divided into the “Nearctic,” “Caribbean,” and “Neotropical” regions. The “Caribbean” region amalgamated all associated islands, and a number of New World continental grid cells in Central America, bordering the “Nearctic” and “Neotropical” regions in Southern Mexico and at the Isthmus of Panama, respectively. In the Old World, the island of Madagascar (“Madagascan”), and the majority of continental Africa (“Afrotropical”) formed separate regions. The northern parts of the Sahara desert separate the Afrotropical region from the “Palearctic,” which contains most of Eurasia. However, India, and South East Asia, in addition to the Western Indo-Pacific islands (approximately until Wallace’s line) form the “Oriental” region. Further east, the “Australasian” region begins, which encompasses the remaining Indo-Pacific islands and also Australia. New Zealand was classified as its own region (“Novo Zelandic”).

ANCESTRAL AREA RECONSTRUCTIONS

The results of the ancestral area reconstruction among the nine regions implemented in BioGeoBEARS (Matzke 2013) are shown

in Figure 2. Of the models evaluated, those containing the potential for founder event speciation were consistently supported by likelihood ratio tests to have higher statistical support compared to those that did not (Table S1). The DEC+J model received the lowest AIC score, and was selected as the model from which we computed the ancestral states (Fig. 2).

Among families of the Corvidae, three predominant patterns of geographic dispersal and diversification emerge from this reconstruction: (1) diversification constrained mainly to the Australasian region, in some cases shared with the Oriental region, (2) diversification constrained to the Afrotropical region, and (3) cosmopolitan patterns of dispersal and diversification throughout multiple regions, generally including the Australasian, Oriental, and Afrotropical regions (Fig. 2). Several small clades are restricted to the Australasian region, and this is also the case for a few major families, namely Cinclosomatidae, Paradisaeidae, and Pachycephalidae (the latter marginally entering the Oriental region). Extensive radiation in the Afrotropical region was observed for a single large clade that contains the families Malaconotidae, Platysteiridae, Prionopidae, and Tephrodornitidae. Among this group, a small number of old and relictual taxa have remained restricted to the Oriental region (e.g., *Pityriasis*), while others appear to have back colonized from the Afrotropics (e.g., *Tephrodornis*, *Hemipus*). The Vangidae represent the only corvid family to have diversified exclusively within Madagascar. The remaining large families: Artamidae, Campephagidae, Corvidae, Dicruridae,

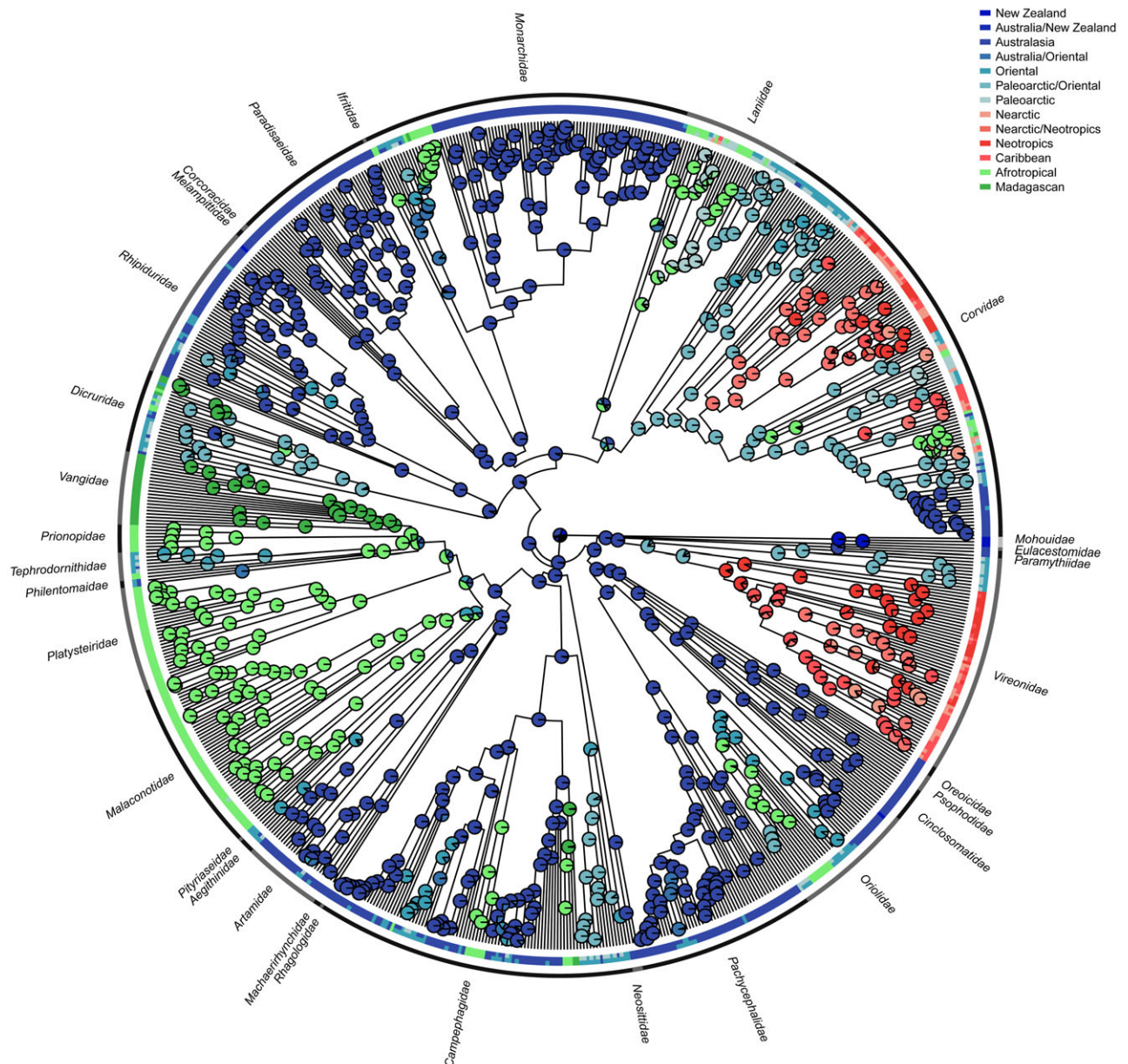


Figure 2. Reconstructed ancestral regional states, as computed from the DEC + J model in BioGeoBEARS. Pie charts at the nodes represent the probability of regional occurrence using the same color scheme as in Figure 1 to denote the regions. States that are shared between two regions are represented by an intermediate color. Thirteen states (or potential combination of states) explain >95% of all areas sampled in the analysis, and are highlighted in the figure legend. The remaining sampled states are colored white. The regional distributions of all species are represented by segments at the tips, whereas the outer gray and black border denotes the family delimitations.

Laniidae, Monarchidae, Oriolidae, Rhipiduridae, and Vireonidae, are much more widespread in their distributions, given that all have extant species and ancestral nodes in at least three regions (Fig. 2). However, the number of regions occupied by these families is variable (Fig. S4). These general trends remain highly consistent on a reconstruction in which the 124 species not sampled with DNA sequences in the phylogeny of Jönsson et al. (2016) were excluded (Fig. S5).

SPECIES RICHNESS PATTERNS AND SPATIAL VARIATION IN DIVERSIFICATION RATES

At the $1^\circ \times 1^\circ$ scale, species diversity among the Corvidae is highest in the Australasian region, specifically in New Guinea (Figs. S6 and S7). Here, up to 93 species can be found in a single $1^\circ \times 1^\circ$ grid cell. Other areas that have also accumulated a relatively high number of species include (1) Borneo and Java (Oriental), (2) The Sino-Himalayan mountain range (Oriental/Palearctic boundary),

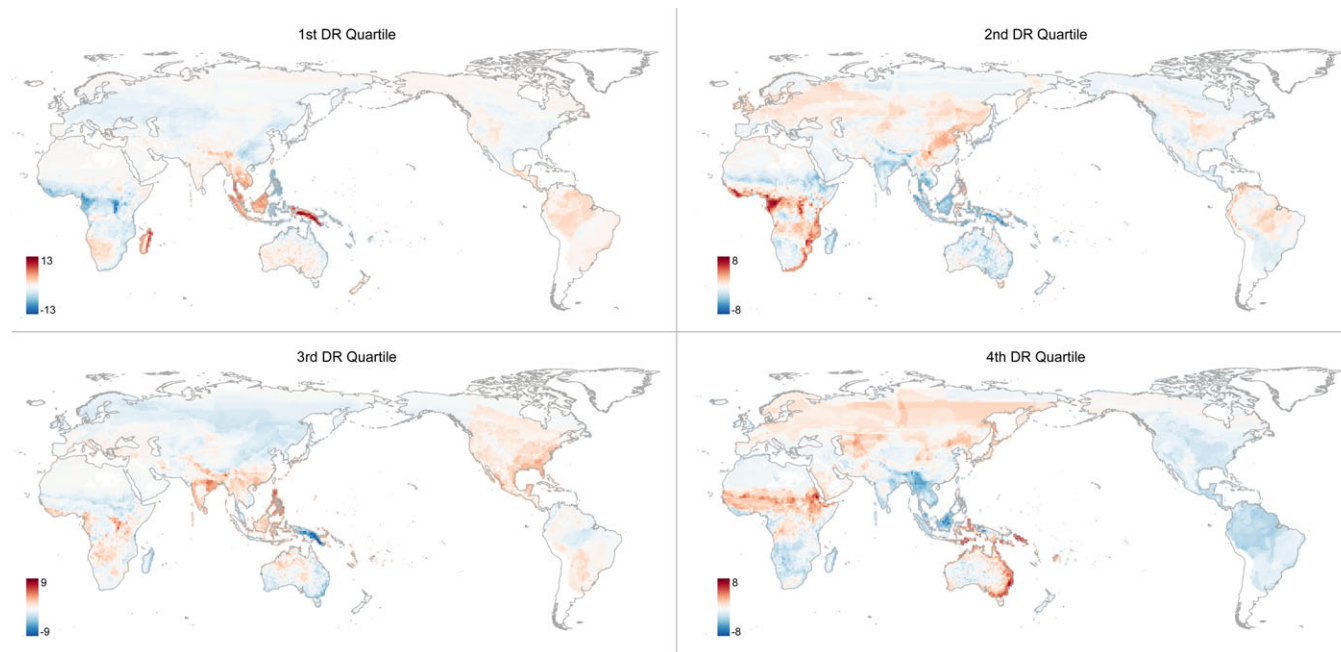


Figure 3. Plot of studentized residuals from linear models evaluating the relationship between $1^\circ \times 1^\circ$ grid cell richness for each DR quartile ~ the overall corvid richness. Red colors highlight grid cells with a greater number of species within the respective DR quartile than predicted under the expectation of a linear relationship with overall richness, whereas blue colors indicate grid cells with fewer species than predicted. DR values represent the number and timing of diversification events along a lineage, such that species in the 1st DR quartile have few close relatives, whereas species in the 4th quartile have many young and close relatives (see Methods for further information on this metric).

(3) The East African habitat mosaic (Afrotropical) and (4) Eastern Australia (Australasian). However, other than in these areas, species numbers never reach >30 species per $1^\circ \times 1^\circ$ cell.

The patterns of species richness among the $1^\circ \times 1^\circ$ grid cells from the quartiles defined by values of DR and SA, suggest geographic variation in lineage accumulation (Figs. S6 and S7); a trend that remains consistent upon the exclusion of species placed in the phylogeny based on taxonomic information alone (Figs. S8 and S9). The residuals from regressing quartile richness against overall species richness show clear spatial patterns, in that some grid cells contain a higher or lower number of species in specific quartiles than predicted given a linear relationship (Fig. 3). The total number of species accumulated in each region among the DR quartiles, are shown in Figure 4. These results highlight Australasia as the region that has generated, and maintained, the largest number of lineages having both high and low values of DR. This pattern appears to predominantly reflect the accumulation and maintenance of species diversity in New Guinea (Fig. 3, Figs. S6 and S7). Aside from New Guinea, species with the fewest close relatives (those in the 1st DR quartile) are also maintained in high numbers throughout the Oriental region (e.g., Borneo, Java, and the Sino-Himalayas), and additionally on Madagascar (Fig. 3, Figs. S6 and S7). The distribution of 2nd quartile species supports a hypothesis of early dispersal and diversification events

throughout the Afrotropical region. The East African habitat mosaic is notable for its high species numbers in this, and the 3rd quartile, with the Nearctic (Central America) and Oriental (Sino-Himalayas) regions also diverse (Fig. 3, Figs. S6 and S7). Finally, among the youngest and most diverse lineages (4th quartile species), the highest number of species have accumulated in the Australasian region, with New Guinea, the surrounding archipelagoes of the Indo-Pacific, and the eastern coastal regions of Australia, highlighted to be a source of recent diversification events (Fig. 3, Figs. S6 and S7). The distributions of DR values among the species found in each region are presented in Figure 1. These results suggest temporal variation in the rate of regional lineage accumulation through time (see Discussion).

THE ACCUMULATION OF FAMILY SPECIES RICHNESS

The overall number of biogeographic regions occupied by families of the Corvids and the number of transitions between these regions are shown in Figure S4 and Figure 5, respectively. We assessed the linear relationship between the number of species per family and these two variables, and recovered significant positive relationships in both cases (number of regions; slope = 13.7, $R^2 = 0.61$, $P < 0.001$; mean number of regional transitions; slope = 4.7, $R^2 = 0.59$, $P < 0.001$). With respect to the transitions, a similar result was recovered considering only those groups that transitioned

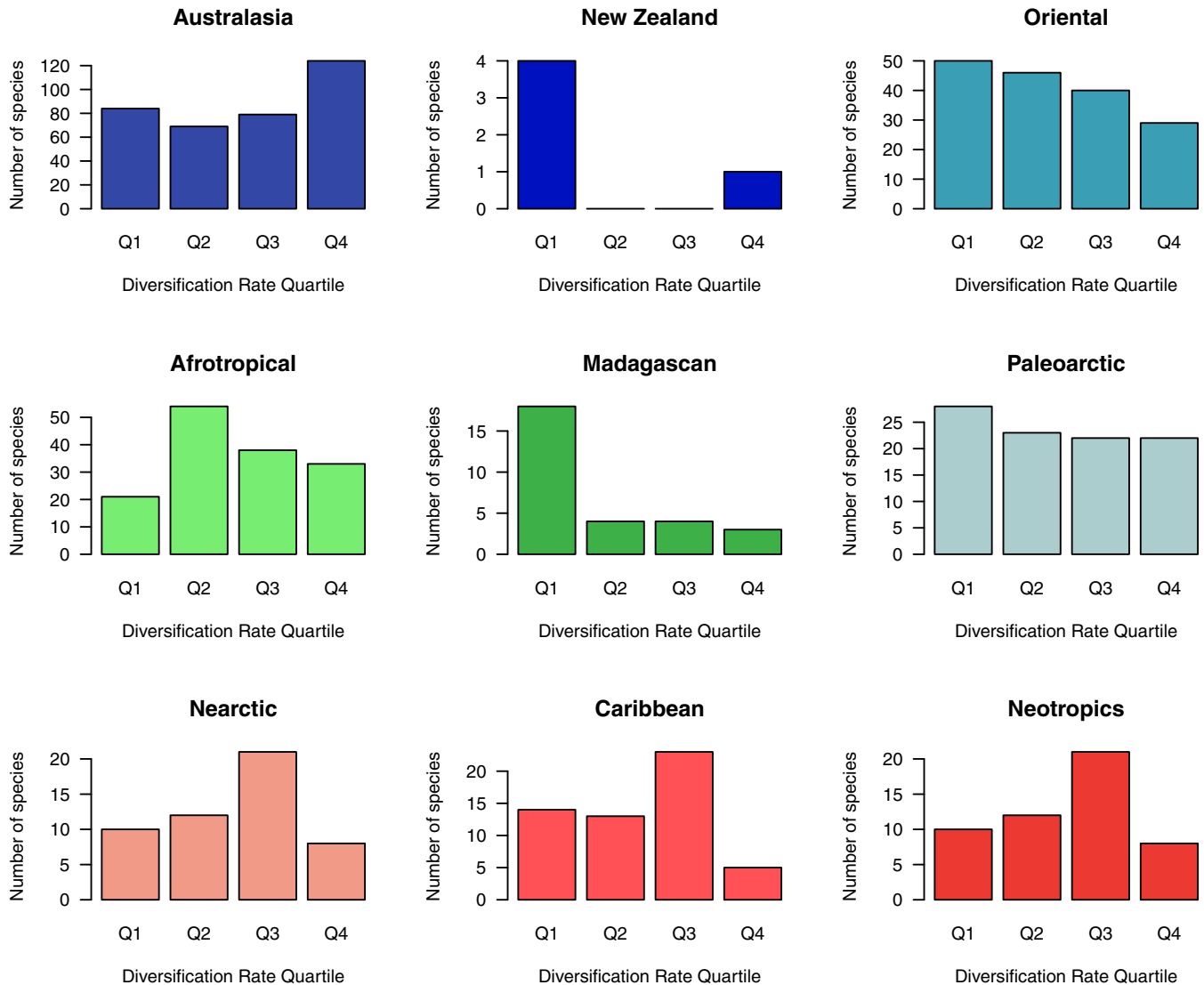


Figure 4. Bar plots of species numbers within each DR quartile among the nine regions proposed in Figure 1.

between regions (slope = 3.6, $R^2 = 0.49$, $P = 0.02$). The effect of transitioning between regions alone (irrespective of the number of transitions) was also related to significantly higher family species diversity, as inferred using a phylogenetically corrected ANOVA ($F = 26.8$, $t = 5.17$, $P = 0.001$). Three of the 31 families showed a higher rate of transitions between regions than expected given the binomial distribution (Corvidae, Laniidae, and Dicruridae, Table S2), and five of the families showed a lower rate than expected (Malaconotidae, Monarchidae, Pachycephalidae, Paradisaeidae, and Platysteiridae Table S2). These results were generally consistent upon the exclusion of the taxonomically placed species (Figs. S10).

Area occupied (the number of unique 2° grid cells) significantly predicts family species richness (slope = 13.8, $R^2 = 0.5$, $P = 0.001$), but our partial correlation analysis shows that the

number of regional transitions explained a greater amount of variance in family species richness, and was comparably a significantly better predictor (Table S3). Neither the number of regions occupied, nor the number of transitions between regions were significantly related to the crown age of the families (number of regions; slope = 0.09, $R^2 = 0.04$, $P = 0.10$; mean number of transitions; slope = 0.23, $R^2 = 0.07$, $P = 0.14$; Fig. S11).

DIVERSIFICATION DYNAMICS FOLLOWING REGIONAL COLONIZATION

The results of our BAMM analyses reveal that four families (Campephagidae, Corvidae, Monarchidae, and Pachycephalidae) were consistently found to have had increased rates of speciation throughout their histories, in comparison to all other corvid lineages (Figs. S12 and S13). After estimating the rates of regional

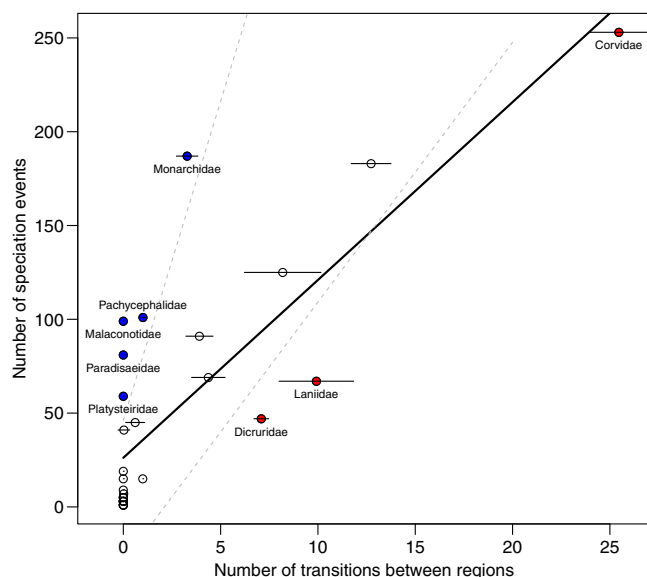


Figure 5. Plot of the number of diversification events within each corvid family as a factor of the number of inferred transitions between regional states. Transitions are considered as descendent nodes, partially (in the case of shared states) or completely in a different regional state compared to their ancestral node. The solid line represents the least squares regression. Dashed lines represent the 95% confidence intervals for the expected number of transitions given the binomial distribution. Blue points highlight families with a significantly lower rate of transition given this expectation, whereas red points illustrate families with a significantly higher rate of transition (see Methods for further information about this model). Error bars represent the standard deviation of the average regional transition rates, computed from 1000 draws of the regional states across all nodes.

transition and speciation for each distinct macroevolutionary cohort within these families, we found that the Monarchidae and Pachycephalidae have lower rates of regional transition in comparison to the background rate, while the Campephagidae have similar transition rates, albeit with a broad confidence interval (Fig. 6). These differences in estimated parameter values reflect uncertainties both in the location of the diversification rate shifts, and in the ancestral regional states. Finally, among the Corvidae, increased rates of speciation were associated with high rates of regional transition (Fig. 6).

Discussion

Among a global radiation of passerine birds, we show that repeated colonization and establishment in new biogeographic regions is associated with the accumulation of high clade richness (Fig. 5), and in one family (the Corvidae), increased rates of speciation (Fig. 6). This finding is based on a regionalization approach delimiting nine global regions among the Corvidae that reflect

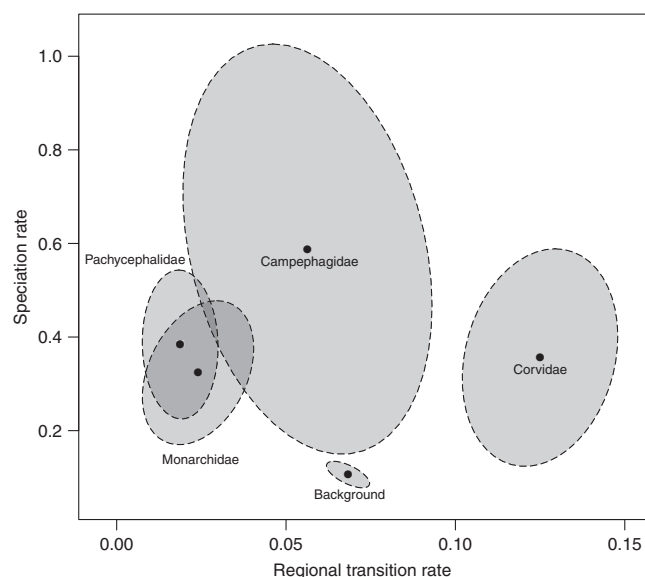


Figure 6. The relationship between rates of speciation (estimated from our BAMM analysis) and regional transition, among five groups of corvid birds. Four of these groupings represent families (Campephagidae, Corvidae, Monarchidae, and Pachycephalidae) that were consistently recovered to have increased rates of speciation, whereas the final group represents the remaining lineages that are diversifying at the background rate. For each macroevolutionary cohort within these groupings, we estimated rates of regional transition rates (computed from 100 draws of the regional states across all nodes) downstream of the rate shift events. Points reflect the mean estimates of speciation and regional transition from the 4500 post burn-in samples generated by BAMM. Ellipses represent the 50% confidence interval of the mean.

patterns of spatial turnover in the phylogenetic composition of species assemblages (Fig. 1). Considering the historical events of dispersal between regions (Fig. 2), and the geographic distribution of lineages with high and low DR values (Figs. 3 and 4), we find that rates of lineage diversification have varied through time and space, and this has generated the observed differences in regional and clade diversity. Although the causal factors determining spatiotemporal variation in diversification rates and the accumulation of species richness remain contentious (Ricklefs 2003; Mittlebach et al. 2007; Rabosky 2009), our results suggest that one important variable is the extent to which lineages repeatedly disperse into new geographic regions, and diversify there (Ricklefs 2009).

REGIONAL PATTERNS OF DIVERSIFICATION

Although the Corvidae only represent c. 12% of overall passerine species diversity, they encompass an almost global distribution, resulting from several pulses of expansion to continental and insular regions from their origins in the Indo-Pacific (Jönsson et al. 2011; Aggerbeck et al. 2014). The results of our ancestral

area reconstruction corroborate these findings, highlighting the Australasian region as playing the most prominent role in the early diversification of the group, given that many old nodes are well supported to have occurred there (Fig. 2). Following dispersal out of this area, the subsequent colonization of new regions has in some cases occurred with limited, or a complete lack, of subsequent dispersal to other regions. This pattern is particularly prevalent among families currently distributed in the Afrotropical and Madagascan regions for example Malaconotidae, Platysteiridae, and Vangidae (Fig. 2). In other cases, families with low numbers of species (those which are present in the 1st DR quartile that is the older and more isolated lineages) tend to be restricted to Australasia, notably in New Guinea (likely their area of origin, as exemplified by the strictly endemic small clades Eulacestomidae, Ifritidae, Melampittidae, and Rhagologidae), suggesting this area may have had a high rate of lineage maintenance (Fig. 3).

The results of the ancestral area reconstructions, and the distribution of lineages with high and low DR values, imply spatiotemporal variation in the accumulation of species diversity at regional, and also finer spatial scales (Figs. 1 and 3). Transitioning between regions (i.e., the colonization of one region from another) appears to promote diversification, given that the frequency of transition is correlated with the total number of species within corvid families (Fig. 5). Furthermore, the relative explanatory power of transitioning between regions as a predictor of species richness remains strong, even after accounting for the differences in the amount of area occupied by each family (Table S3). These results illustrate that the propensity to colonize new areas is an important component in the continued build-up of both clade and regional diversity (Grant 1998; Ricklefs 2003; Hughes and Eastwood 2006; Ohlson et al. 2008; Fjeldså 2013). However, as some families transition at a lower rate than expected given their diversity, and many conform to our null expectation (Table S2), it is apparent that the colonization of new areas, at least at the regional scale, cannot fully account for differences in species diversity among families of the Corvides.

FACTORS DETERMINING SPATIAL/TEMPORAL VARIATION IN LINEAGE DIVERSIFICATION AND ACCUMULATION

Temporal variation in diversification rates are observed across different spatial scales among the Corvides (Figs. 1 and 3). These differences must, at least in part, reflect the biogeographic history of the group, and the timing of regional colonization from their ancestral areas in the Indo-Pacific (Fig. 2; Jönsson et al. 2011). Spatiotemporal differences in the accumulation of species diversity imply the limited importance of time in predicting regional diversity. This is further supported by the lack of a relationship between the crown age of the families, and either the number of regions occupied, or the number of transitions between regions

(Fig. S11). Instead, we propose that the spatiotemporal variation in lineage accumulation reflects regional differences in historical climatic (Zachos et al. 2001) and/or geological change (Hall et al. 2011), in addition to the diversity and distribution of other avian lineages throughout these areas.

Range expansion into new geographic areas is proposed to be a key stage in the process of allopatric speciation (Coyne and Orr 2004; Price 2008), and has been suggested in many instances to initiate extensive radiation (Grant 1998; Moyle et al. 2009; Lerner et al. 2011). Although the biogeographic dynamics of such radiations have historically proven difficult to study at large continental scales, our analyses illustrate differences among corvid families in their capacity to colonize and diversify in new regions (Figs. 2 and 5). Despite the proposed regions appearing to be continuously connected landmasses throughout many areas (Fig. 1), physical (e.g., large areas of open ocean, mountains) and ecological (unfavorable climatic conditions or habitats) barriers have limited the exchange of lineages between them (Fig. 2). Yet, although regional colonization events are generally rare among the Corvides, extensive regional colonization is not generally associated with increased rates of speciation among corvid families (Fig. 6). This may reflect that major factors promoting increased diversification rates (e.g., exposure to increased topographic complexity or land-mass connectivity) are not necessarily related to the colonization of new biogeographic regions. Reconciling this finding with the one that families which transition between regions tend to be more speciose (Fig. 5) may result from a decoupling between the processes of species production and maintenance at regional scales.

The Corvidae (crows and allies) represent the only family that stands out as having exceptionally high rates of both regional transition and speciation (Fig. 6 and Table S2). This family is extraordinary for being the most speciose of the overall Corvides, having an almost global distribution and containing some of the most intelligent species of nonprimates known (Emery and Clayton 2004). The association of increased rates of regional transition with increased rates of speciation within this family may reflect several facets of its radiation: (1) the evolution of long-distance dispersal capabilities within the family may have aided lineages to reach new and potentially remote areas (Marki et al. 2015), (2) their tolerance to a broad range of climatic conditions, and (3) high rates of behavioral innovation reflecting the evolution of large brains increase rates of range expansion into new areas (Sol et al. 2005a). Together these factors are likely to result in increased colonization capacities compared to other corvid clades, leading to heightened rates of geographic isolation and subsequent diversification (Sol et al. 2005b).

The ability to colonize new regions does not represent a general explanation for differences in the species diversity of Corvides, given that some families distributed in single regions are also fairly species rich (e.g., Malaconotidae, Paradisaeidae,

Platysteiridae, and Vangidae). Several factors may contribute to these findings. First, variation in opportunities for diversification and coexistence may result in the accumulation of high species numbers in some regions, but not others (Cracraft 1985). These opportunities are likely influenced by factors relating to topographic/geological complexity, levels of landmass connectivity and the extent of habitat/climatic turnover, such that areas in which this is extensive (e.g., tropical mountain regions in the case of habitat/climatic turnover, and island archipelagoes in the respect of landmass connectivity), generate and/or maintain large numbers of species. In this respect, it is notable that 3/4 families for which we recovered increased rates of speciation (Campephagidae, Monarchidae, and Pachycephalidae; Fig. S13), have all diversified extensively throughout island settings, implying levels of landmass connectivity within regions (specifically in the Oriental and Australasian regions) strongly influence the diversification dynamics. Second, the modes of diversification among some groups may not necessarily promote repeated events of range expansion among the resulting species. This is evidenced by radiations that have occurred within restricted geographic areas, but display extensive divergence in ecological (Vangidae; Jönsson et al. 2012), or sexually selected traits (Paradisaeidae; Irestedt et al. 2009, Fritz et al. 2012) that are decoupled from dispersal ability. Finally, lineage variation in the ability to adapt to novel habitats, climates, and compete with those that are already established all seem likely to influence the propensity for families to accumulate diversity within a given geographic setting.

Conclusions

In this study, we have demonstrated how spatiotemporal variation in historical dispersal and diversification has shaped the contemporary distribution, and diversity, of a large radiation of passerine birds. Species diversity among families is strongly correlated with the number of regions occupied, and the rate of transition between these areas, implying that the repeated colonization of new geographic and ecological areas contributes to the accumulation of high clade richness. Determining the factors that explain why some groups disperse and diversify, yet others are more limited in their diversity and geographic extent of occurrence remains an outstanding issue. While this seems at least in part to reflect regional opportunities for diversification, the ecological properties of lineages, and their intrinsic dispersal abilities, future work should aim to directly quantify these influences across large geographic and phylogenetic scales.

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DATA ARCHIVING

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. *Left panel:* Map of $2^\circ \times 2^\circ$ grid cells coloured based on ordination values of the $\text{phylobeta}_{\text{sim}}$ grid cell values. The colour of each grid cell reflects its relative regional affinity, in terms of the composition of its assemblage in ordination space. Similar coloured grid cells represent those which share a large amount of evolutionary history. Regional affinities are reflected in the similarity of the grid cells colour to those used in Figure 1. *Right panel:* Plot highlighting the relationship between the species composition of the nine regions on the first 2 axes of the nDMS ordination generated from comparison of the $\text{phylobeta}_{\text{sim}}$ values.

Figure S2. Plot of DR and species age estimates for the 789 species of the Corvidae recognized by the IOC v.2.7 (Gill and Donsker 2010). Line is the lowess fit.

Figure S3. The number of inferred rate shifts recovered by BAMM analyses on the phylogeny of Jönsson et al. (2016), which samples 665/789 species of the Corvidae as recognized by the IOC v.2.7 (Gill and Donsker 2010). In these analyses we varied the “expected number of rate shifts” prior to values of 1, 5, 10, 50 and 100 (shown in the plots from left to right), while the values of all other priors were fixed to be constant. The results illustrate that the number of rate shifts inferred from these analyses are highly consistent regardless of the value of the “expected number of rate shifts” prior provided.

Figure S4. Bar plot highlighting the number of regions occupied by the 31 corvid families, broadly recognized by the IOC classifications v 2.7 (Gill & Donsker 2011). Coloured segments highlight the regional occurrence of each family. The regional colour scheme follows that of Figure 1. The bars representing each family are ordered by their total species richness, which is listed in parentheses.

Figure S5. Reconstructed ancestral regional states, computed from the DEC+J model in BioGeoBEARS using the phylogeny of Jönsson et al. (2016), which samples 665/789 species of the Corvidae as recognized by the IOC v.2.7 (Gill and Donsker 2010). Pie charts at the nodes represent the probability of regional occurrence using the same colour scheme as in Figure 1 to denote the regions. States that are shared between two regions are represented by an intermediate colour. 13 states (or potential combination of states) explain >95% of all areas sampled in the analysis, and are highlighted in the figure legend. The remaining sampled states are coloured white. The regional distributions of all species are represented by segments at the tips, whereas the outer grey and black borders denote the family delimitations.

Figure S6. Maps of species richness in $1^\circ \times 1^\circ$ grid cells among four quartiles defined by the relative ranks of species based on values of the DR statistic. DR values represent the number and timing of diversification events along a lineage, such that species in the 1st DR quartile have few close relatives, whereas species in the 4th quartile have many young and close relatives (see methods for further information).

Figure S7. Maps of species richness in $1^\circ \times 1^\circ$ grid cells among four quartiles defined by the relative ranks of species age values, which were estimated as the length of the terminal branch subtending each species. Age boundaries for each quartile are displayed in millions of years before the present.

Figure S8. Maps of species richness in $1^\circ \times 1^\circ$ grid cells among four quartiles defined by the relative ranks of species based on values of the DR statistic. Here, the species values were computed, and are presented, only among the 665 species sampled with DNA sequences in the phylogeny of Jönsson et al. (2016). DR values represent the number and timing of diversification events along a lineage, such that species in the 1st DR quartile have few close relatives, whereas species in the 4th quartile have many young and close relatives (see methods for further information).

Figure S9. Maps of species richness in $1^\circ \times 1^\circ$ grid cells among four quartiles defined by the relative ranks of species age values, which were estimated as the length of the terminal branch subtending each species. Here, the species values were computed, and are presented, only among the 665 species sampled with DNA sequences in the phylogeny of Jönsson et al. (2016). Age boundaries for each quartile are displayed in millions of years before the present.

Figure S10. Plot showing the average number of regional transitions per family estimated among the 665 species of Corvidae sampled with DNA sequence in the phylogeny of Jönsson et al. (2016). Transitions are considered as descendent nodes, partially (in the case of shared states) or completely in a different regional state compared to their ancestral node. These values were calculated from drawing the regional states 1,000 times from reconstructions using the DEC+J model (Matzke, 2014) on the phylogeny of Jönsson et al. (2016).

Figure S11. Plots showing the relationships between the number of regions occupied (*left panel*) and the number of regional transitions (*right panel*) ~ crown clade age (My) among the 31 corvid families broadly recognized by the IOC v 2.7. Lines are the least squared regression.

Figure S12. The number of diversification rate shifts recovered for each of the 31 corvid families across 4,500 post-burnin samples from our BAMM analysis. Note, in some runs multiple rate shifts were recovered within the same family.

Figure S13. Mean rates of speciation estimated among five groups of corvid birds. Four of these groupings represent families (Campephagidae, Corvidae, Monarchidae and Pachycephalidae) that were consistently recovered to have increased rates of speciation by BAMM, whereas the final group represents the remaining lineages that are diversifying at the background rate. Error bars represent the standard deviation from the mean of the speciation rates estimated across 4,500 post-burnin samples from BAMM.

Table S1. Number of parameters, AIC and log likelihood values of the six models of ancestral area reconstruction evaluated from the BioGeoBEARS analyses.

Table S2. Species richness and the mean number of regional transitions (among nodes and terminal diversification events) estimated among families, after the node states were sampled independently 1,000 times from their marginal probabilities generated by the ancestral area reconstruction. Empirical transition rate estimates were evaluated against the binomial distribution (see methods for further information), with families whose transition rates significantly deviate from the null expectation highlighted with *, and in bold for those that remained significant following the sequential bonferroni P-value correction. **H** indicates families that transition between regions at a significantly higher rate, whereas **L** indicates those that transition at a significantly lower rate.

Table S3. Partial correlation coefficients and associated p values assessing the relationship between corvid family richness as a factor of (1) area occupied (number of unique 2° grid cells), or (2) the number of transitions between regions. These analyses estimate the partial correlation between two variables, while controlling for the influence of a third.