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Cite this article: Kennedy JD, Borregaard MK, Marki PZ, Machac A, Fjeldså J, Rahbek C. 2018 Expansion in geographical and morphological space drives continued lineage diversification in a global passerine radiation. *Proc. R. Soc. B* **285**: 20182181.
<http://dx.doi.org/10.1098/rspb.2018.2181>

Received: 27 September 2018

Accepted: 19 November 2018

Subject Category:

Evolution

Subject Areas:

evolution, ecology

Keywords:

adaptive radiation, allopatric speciation, non-adaptive radiation, secondary sympatry, phenotypic evolution

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Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4324058>.

Expansion in geographical and morphological space drives continued lineage diversification in a global passerine radiation

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Why diversification rates vary so extensively across the tree of life remains an important yet unresolved issue in biology. Two prominent and potentially independent factors proposed to explain these trends reflect the capacity of lineages to expand into new areas of (i) geographical or (ii) ecological space. Here, we present the first global assessment of how diversification rates vary as a consequence of geographical and ecological expansion, studying these trends among 15 speciose passerine families (together approximately 750 species) using phylogenetic path analysis. We find that relative slow-downs in diversification rates characterize families that have accumulated large numbers of co-occurring species (at the 1° scale) within restricted geographical areas. Conversely, more constant diversification through time is prevalent among families in which species show limited range overlap. Relative co-occurrence is itself also a strong predictor of ecological divergence (here approximated by morphological divergence among species); however, once the relationship between co-occurrence and diversification rates have been accounted for, increased ecological divergence is an additional explanatory factor accounting for why some lineages continue to diversify towards the present. We conclude that opportunities for prolonged diversification are predominantly determined by continued geographical range expansion and to a lesser degree by ecological divergence among lineages.

1. Introduction

Why some clades continue to diversify towards the present, yet others have apparently exhausted their capacity to generate further species represent central questions in macroevolution [1,2]. The degree to which diversification rates decline through time has been hypothesized to reflect the capacity of lineages to undergo continued expansion into new areas of geographical and/or ecological space, as both processes can facilitate the production of genetically distinct and reproductively isolated taxa [1–10]. Although these hypotheses are well developed theoretically [2,11,12] and have received some empirical support (e.g. [7,9]), the relative influence of ecological and geographical constraints upon diversification have yet to be assessed in a global context. We address this issue by testing if geographical and eco-morphological expansion can predict variation in diversification rates among a speciose global radiation of passerine birds. We perform this analysis to understand whether geographical and ecological divergences represent significant influences upon the diversification dynamics of different passerine families.

Range expansion into new areas can result in the formation of geographically isolated populations, or lead to secondary contact among those that were

recently isolated from one another [1,4,10,13–16]. Thus, an important distinction that defines the geographical dynamics of radiation among different clades is whether range expansion (following speciation) results in the sympatric build-up of closely related species (e.g. members of the same family/genus) or not [17]. At one end of this continuum lie clades that have accumulated many co-occurring species within restricted geographical settings [18,19], while at the other are those that have radiated over much larger areas, accumulating few co-occurring species, and many more geographically separated taxa [20–24]. These two extremes reflect both ecological opportunities within the region where the diversification process unfolds, and the accessibility of other regions as a consequence of colonization and range expansion [2,18]. However, whether the accumulation of co-occurring species or ecological differences predict longer-term diversification dynamics across multiple independent radiations remains largely untested (but see Harmon *et al.* [25]).

Although a lack of available geographical or ecological opportunity may eventually inhibit diversification [5,26], these limits are likely to differ among clades as a consequence of their ability to evolve new physiological and morphological traits that facilitate their respective lineages to exploit novel resources [2,27]. Niche evolution and character displacement allow species to co-occur with one another, because this enables the exploitation of different parts of the available resource spectrum [4,28–30]. Differences in niche space occupation reflect variation in species morphology [31], i.e. locomotive abilities, resource acquisition, and modes of foraging in the case of passerine birds [28–30,32,33]. Therefore, range expansion and co-occurrence can conceivably influence, and be influenced by, the evolution of morphological traits that are representative of key ecological differences among lineages [30].

In this study, we evaluate the effects of geographical and ecological constraints on diversification. We do so using phylogenetic path analyses [34], which enable us to directly test hypothesized causal associations between morphological divergence, species co-occurrence, and diversification rates. We study diversification rate variation among 15 species-rich families of corvid birds (together comprising approximately 750 species) to understand whether this can be predicted by patterns of range overlap (reflecting the capacity of families to expand into new geographical space) or morphological differentiation (reflecting the capacity of families to expand into new ecological space). Corvid passerines represent a good study system to address these questions for several reasons; (1) multiple lineages have undergone biogeographical expansion from the Australasian ancestral area, such that the overall clade has radiated across the majority of the world's insular and continental landmasses, thus encompassing a near global distribution [10,35,36], (2) corvid lineages are extremely diverse in their morphological forms, both within and among groups (e.g. body masses of all corvid species range from less than 10 g to greater than 1000 g [37]), and (3) the degree of geographical range overlap varies extensively among clades and across geographical space.

2. Material and methods

(a) Phylogenetic, spatial, and morphological data

We performed our comparative analyses on 15 families of corvid passerines (table 1), which represent a subset of those

considered in Kennedy *et al.* [41]. Together, the combined species richness of these families amounts to approximately 95% of the overall species diversity of the Corvidae (741/789 species [38]). Given our aim of assessing the relationship between patterns of co-occurrence and diversification, we excluded the 16 most species-poor corvid families from our analysis, which together represent only 48 species.

Estimates of the phylogenetic relationships among the 741 species which are members of the 15 families were obtained from the maximum clade credibility tree analysed in Kennedy *et al.* ([41]; <http://dx.doi.org/10.5061/dryad.128249>). Distributional data representing the breeding range were also collated for these same species from an expert-validated database [42], in which the ranges are recorded at a resolution of $1^\circ \times 1^\circ$ (ca 110 km \times 110 km). The range maps were determined from museum specimens, published sightings, and more than 1000 original references [42]. In addition, for 734/741 species (99% of all analysed species) PZM measured museum study skins to determine 10 different aspects of their external morphology (reflecting measurements of the wings, tail, tarsus, bill, and claws; full details of the measurement techniques can be found in electronic supplementary material, appendix A). Similar morphological measurements have been used extensively in previous comparative analyses of passerine birds (e.g. [33,43,44]), as these traits have been shown to predict important ecological differences among species [31,32,45,46]. A total of 4091 museum study skins were measured (electronic supplementary material, table S1) for a mean of 5.57 ± 1.22 specimens per species. We attempted to measure male specimens when possible, except in the relatively small number of instances where these were poorly represented in the collections, in which case we supplemented them with those from females or unsexed specimens (20/4091 measured specimens).

(b) Geographical analyses

For each of the 15 families, we determined their species richness gradients and thus the degree to which they have accumulated co-occurring forms by overlaying their range maps and summing the number of species found in each 1° grid cell. Subsequently, we computed the overall area occupied by each family (the number of unique 1° grid cells in which the family was present), the mean range size of their constituent species (the average number of 1° grid cells occupied by each species), and the mean value of species richness across all 1° grid cells. Clade area and mean range size (both log-transformed) were included in our analyses as covariates, as these variables may influence diversification rates independently from the extent to which co-occurring species accumulate [3,47].

(c) Morphological analyses

We performed a principal component analysis (PCA) on the log-transformed morphological traits. Log-transformation was necessary, because the distribution of our measured traits were all right-skewed, reflecting the evolution of large body sizes in some corvid lineages [37]. Loadings of the log-transformed traits upon the individual principal component axes (PC1–10) can be found in electronic supplementary material, table S2. We used the species scores on the 10 principal component axes to estimate the Functional Dispersion (FDis) of each family [48] which served as a measure of the relative morphological disparity among their constituent species. These analyses were implemented in the R package *metricTester* [49]. The FDis of each family reflects the unweighted mean distance to the centroid of morphological space of all species [48], here represented by the principal component scores. Although other measures of morphological disparity have been proposed (e.g. functional volume, functional divergence), simulations have

Table 1. Species diversity, diversification rates, range size, area, morphological disparity, and average grid cell richness among 15 corvid families. These families were delimited in accordance with the taxonomy of the IOC 2.7 Gill & Donsker [38].

family	overall species richness	proportion of missing species from Jönsson <i>et al.</i> [39]	gamma (γ) estimated from Jönsson <i>et al.</i> [39]	gamma (γ) estimated from Kennedy <i>et al.</i> [40]	log (mean range size)	log (area)	FDis	mean grid cell richness
Artamidae	23	0.17	0.48 ± 0.24	1.14	4.84	7.53	1.13	3.35
Campophagidae	92	0.18	-1.16 ± 0.27	0.61	3.75	8.26	0.76	3.07
Cinclosomatidae	10	0.1	-1.14 ± 0.32	-0.79	4.03	6.08	0.35	1.5
Corvidae	127	0.11	-1.78 ± 0.23	-1.56	4.33	9.65	0.83	3.44
Dicruridae	24	0.21	-1.3 ± 0.25	-0.9	4.41	8.1	0.45	2.19
Laniidae	34	0.12	-0.11 ± 0.35	0.05	5.48	9.18	0.47	1.77
Malaconotidae	50	0.4	-2.21 ± 0.22	-0.93	4.2	7.51	0.45	5.59
Monarchidae	94	0.07	-1.79 ± 0.29	-1.53	2.81	8.29	0.44	2.07
Oriolidae	35	0	-1.29 ± 0.26	-1.35	3.94	8.42	0.37	1.36
Pachycephalidae	51	0.1	-0.68 ± 0.3	-0.12	3.21	7.27	0.44	2.41
Paradisaeidae	41	0.02	-1.69 ± 0.26	-1.77	2.77	5.06	0.91	6.18
Platysteiridae	30	0.33	-1.21 ± 0.44	0.03	3.97	7.37	0.4	2.2
Rhipiduridae	46	0.28	-2.57 ± 0.23	-1.33	3.27	7.66	0.37	1.92
Vangidae	21	0	-3.38 ± 0.19	-3.42	3.13	4.28	1.03	8.57
Vireonidae	63	0.18	-3.02 ± 0.22	-2.28	4.07	8.22	0.41	3.13

shown that FDis is by far the least sensitive to variation in overall species richness among groups, while also reliably capturing the range and standard deviation of the original traits [50].

(d) Diversification analyses

For each family, we assessed whether rates of diversification were either constant or slowing through time by computing the γ -statistic [51]. Values of γ provide an estimate of whether the nodes within a phylogeny are disproportionately distributed towards the root or tips of the tree. The more negative the values of γ , the greater the proportion of branching events that have occurred towards the root of the tree, indicating a decline in rates of net diversification towards the present [51]. These interpretations are drawn from the expectations of γ under the pure birth model, which is known to follow a normal distribution [51]. Although multiple alternative metrics for estimating diversification rates exist [52], we chose to analyse γ because this statistic allows us to directly quantify the relative degree to which diversification is continuing towards the present among the different families, and thus test our key hypotheses.

We computed γ for each corvid family using the phylogeny of Kennedy *et al.* [41], which added 124 species to the phylogeny of Jönsson *et al.* [39] (who sampled 629/741 corvid species) as polytomies based on current taxonomic information [53]. These 124 species did not have DNA sequence data available at the time of the original tree generation. The birth–death model was used to randomly resolve these polytomies and assign branch lengths for the respective diversification events, following the methods of Kuhn *et al.* [54]. For the vast majority of the analysed families, species sampling in the phylogeny of Jönsson *et al.* [39] was greater than 80% (table 1). However, we tested the robustness of our results to the exclusion of the 124 taxonomically placed species, by repeating our analyses using the mean estimates of γ across 1000 post-burnin samples of the Jönsson *et al.* [39] trees (electronic supplementary material, appendix B).

(e) Phylogenetic comparative analyses

While causal relationships cannot be determined using standard correlative methods, path analysis enables the relative importance of alternate causal models that propose direct and indirect relationships among variables to be compared [34,55]. We determined the causal relationships among our predictor variables (clade area, mean range size, mean grid cell richness, and FDis), and how they may influence diversification rates, using phylogenetic confirmatory path analysis [34] which combines the methodologies of phylogenetic least squares (PGLS) and d-separation (herein d-sep) [55]. We evaluated the relative support of 20 path models each proposing a biologically plausible causal structure for the variation in γ . The directed acyclic graphs (DAGs) for all models are shown in electronic supplementary material, figure S1. Models were fitted by evaluating the minimal set of conditional independencies among the predictor variables necessary for each path model to be true. We controlled for the non-independence of the data points due to the shared ancestry of the taxa [34] using a family-level phylogeny of the Corvides (our species-level phylogeny pruned to contain a single member of each family). We first tested the conditional independencies of each model by performing the relevant PGLS regressions. Subsequently, we assessed whether the proposed independencies of each model are fulfilled in the empirical relationships using Fisher's C statistic. Finally, we used the C statistic information criterion (CICc) proposed by von Hardenberg & Gonzalez-Voyer [34] to assess the relative fit of all models. These analyses were performed in the R package *phylopath* [56].

3. Results

(a) The distribution of γ and FDis among corvid families

The estimated values of γ for the 15 corvid families are shown in table 1. Eleven out of 15 families recovered negative

values of γ , implying that the nodes within the respective phylogenies tend to be distributed towards the roots of the trees. Although γ is known to become negatively biased when estimated on phylogenies with incomplete species-level sampling [51], we found no evidence for a significant correlation between γ and the proportion of unsampled species per family within the Jönsson *et al.* [39] tree. This was the case either when γ was computed on the phylogeny of Jönsson *et al.* [39] (PGLS slope = 0.38, $R^2 = 0.01$, $p = 0.88$; electronic supplementary material, figure S2a), or Kennedy *et al.* [41] (PGLS slope = 4.2, $R^2 = 0.17$, $p = 0.13$; electronic supplementary material, figure S2b). There was also no significant relationships between γ and overall family richness (γ estimated on Jönsson *et al.* [39]; PGLS slope = -0.006 , $R^2 = 0.04$, $p = 0.46$, electronic supplementary material, figure S2c. γ estimated on Kennedy *et al.* [41]; PGLS slope = -0.002 , $R^2 = 0.01$, $p = 0.81$, electronic supplementary material, figure S2d). Given these findings, we present the results from phylogenetic path analysis of the complete species-level tree (Kennedy *et al.* [41]) in the main text, and those from Jönsson *et al.* [39] in electronic supplementary material, appendix B. Our results remained consistent in both analyses.

Estimates of FDis were also highly variable among corvid families (table 1). Families that consist of morphologically disparate species (e.g. Artamidae, Paradisaeidae, and Vangidae) scored high values of FDis. Conversely, families containing species that possess similar morphologies (e.g. Laniidae, Oriolidae, Rhipiduridae, and Vireonidae) recovered low values of FDis. As with γ , the values of FDis were unrelated to the overall family species richness (PGLS slope = 0.001 , $R^2 = 0.006$, $p = 0.78$; electronic supplementary material, figure S3).

(b) Phylogenetic comparative analyses

The results from the d-sep test for the models proposed in electronic supplementary material, figure S1 are shown in electronic supplementary material, table S3. The ΔCICc values of these models imply that model 13 was our best fitting model (relative weighting 0.50, electronic supplementary material, table S3). Two other models, model 11 and model 1 received the majority of the remaining model weighting (0.36 and 0.11, respectively). p -values from the d-sep test imply that these three models represent plausible sets of causal relationships among the variables. Despite receiving less overall weight, the ΔCICc value for model 11 (0.68) suggests that this cannot be considered a significantly poorer fit than model 13; however, the ΔCICc for model 1 (3.07) suggests that model 13 provides a significantly better explanation of the causal relationships among our variables. We present the standardized path coefficients (SPC) for the average of models 11 and 13 in figure 1, and electronic supplementary material, table S4, following the approach of von Hardenberg & Gonzalez-Voyer [34]. The SPC for the individual models is shown in electronic supplementary material, figure S4. The averaged model results show that grid cell richness is a significant negative predictor of γ (SPC = -0.71 , figure 1, and electronic supplementary material, figure S5a) while FDis is a significantly positive predictor (SPC = 0.73, figure 1, and electronic supplementary material, figure S5b,c), albeit with this relationship only being proposed in model 11.

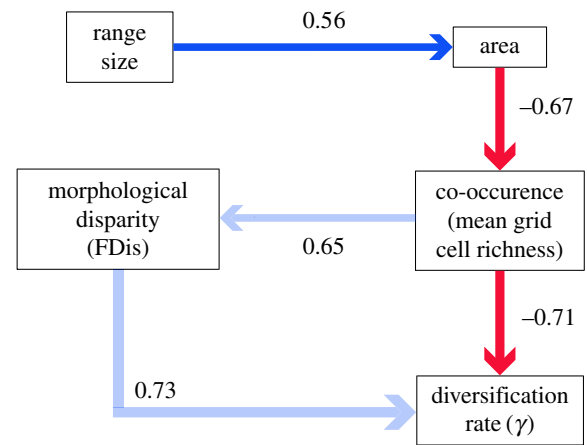


Figure 1. Directed acyclic graph showing the standardized path coefficients averaged among the best fitting phylogenetic path models (with ΔCICc less than 2) presented in electronic supplementary material, table S3. Bold lines indicate paths supported in both of the best fitting models, whereas faded lines illustrate paths supported only in single models. Positive path coefficients are shown in blue, while negative correlations are shown in red. All models predicted variation in gamma (γ) among 15 corvid passerines as a consequence of the relationships between mean range size, area, morphological disparity (FDis), and mean grid cell richness.

Mean grid cell richness was also supported to positively determine FDis (SPC = 0.65, figure 1 and electronic supplementary material, figure S5d), meaning that families with a higher average number of co-occurring species tend to comprise groups of species that are more morphologically divergent from one another. In addition, we found significant support for a positive relationship between range size and area (SPC = 0.56, figure 1 and electronic supplementary material, figure S5e), and a negative relationship between area and mean grid cell richness (SPC = -0.67 ; figure 1 and electronic supplementary material, figure S5f).

The results of these analyses indicate that corvid families with wide-ranging species generally occur over larger areas, and that groups occurring over larger areas tend to have low average co-occurrence within 1° grid cells. Corvid families that have more co-occurring species, or those that are relatively conserved in their morphology, are more likely to have slowed down in their rates of diversification towards the present (figure 1). In addition, higher levels of co-occurrence lead to the evolution of greater morphological disparity within families (figure 1). These trends can be evidenced by contrasting the different diversification trajectories, species richness gradients, and morphological variability of the individual corvid families (figure 2 and electronic supplementary material, figure S6). Furthermore, these findings are generally consistent when removing species placed in the phylogeny by taxonomy alone, or when pruning taxa that have formed within the last 1 million years (electronic supplementary material, appendix B).

4. Discussion

Opportunities for speciation by ecological and geographical expansion have long been considered important in determining rates of lineage diversification [1,4,7,25,57]. Here, we provide the first comparative quantification of these

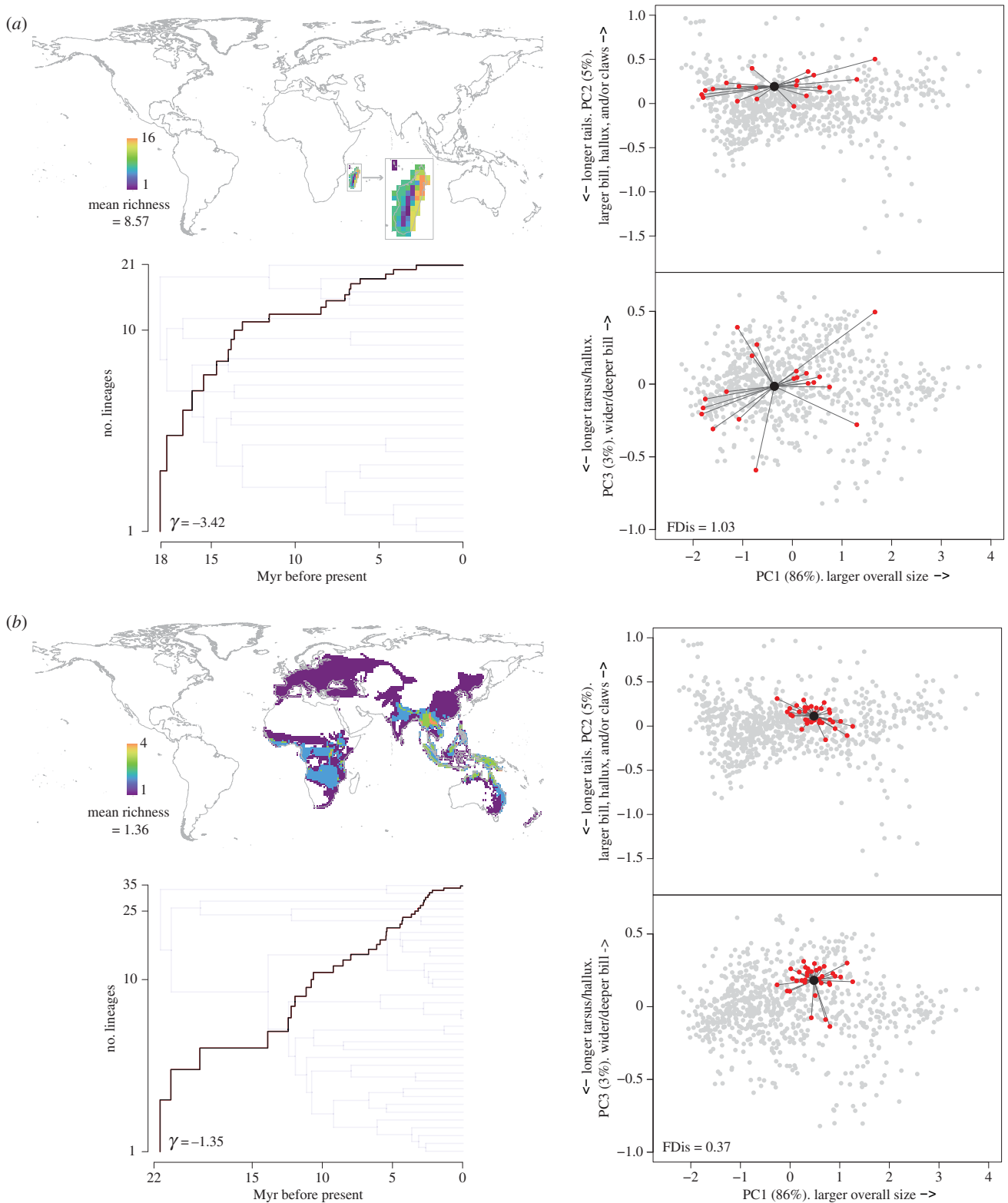


Figure 2. Lineage through time plots, maps of species richness and species scores on PC axes 1–3 for two corvid families; Vangidae ((a), $N = 21$) and Oriolidae ((b), $N = 35$). These families highlight different associations between lineage diversification, co-occurrence, and morphological disparity. In the case of the Vangidae, a strong slowdown in diversification is associated with extensive morphological differentiation and high numbers of co-occurring species that are only distributed within Madagascar. Conversely, among the Oriolidae, more continual diversification is associated with limited variability in their morphology and low numbers of co-occurring species that are distributed across an extensive geographical area. For the plots representing morphological disparity, red points show the species within the respective families and their divergence from the centroid of the families' morphospace. Grey points represent the morphospace occupation of the remaining corvid species.

relationships for a global radiation of birds. Our results reveal that diversification rates tend to decline both as relative range overlap increases within families [9,40], and as a result of a limited evolutionary change in eco-morphological traits

(figure 1). Furthermore, we find that heightened species co-occurrence is itself a determinant of increased morphological differentiation (figure 1). Families that have expanded over large geographical areas and consist of mainly allopatric

species continue to diversify at constant rates towards the present (figure 2 and electronic supplementary material, figure S5). Conversely, clades confined to restricted geographical areas and that have high levels of grid cell co-occurrence tend to exhibit diversification that is more consistent with a slowdown in rates towards the present (figure 1). These same groups also tend to show extensive morphological differentiation (figure 2 and electronic supplementary material, figure S6). However, once the influence of species co-occurrence has been accounted for, in one of our two best supported path models (electronic supplementary material, figure S5), we find evidence suggesting that the evolution of morphological variability also promotes continued diversification (figure 1 and electronic supplementary material, figure S5). Overall, our results imply that geographical opportunity and allopatric differentiation is the primary axis that enables continued radiation, while eco-morphological divergence generally evolves extensively among families that do not expand further geographically.

The accumulation of species within a clade can reflect the generation of both co-occurring and geographically isolated forms, however, in the majority of families geographical and morphological expansion have occurred largely independently among the Corvidae. In other words, clades with high numbers of allopatric species tend not to be those that have diverged extensively in their morphology (electronic supplementary material, figure S6). Radiation as a consequence of predominantly ecological or geographical speciation might therefore represent extremes along a continuum of diversification trajectories for different groups. Specifically, the different diversification dynamics among corvid clades reflect the degree to which species co-occur with one another (and thus potentially compete for the same resources), as heightened co-occurrence can lead to divergent natural selection pressures, and ultimately ecological speciation [4,17]. Intermediate scenarios (diversification that has involved both ecological and geographical speciation) are also prevalent, given that some corvid families which occur over relatively large areas have morphologically disparate species, while also maintaining relatively high numbers of co-occurring species within certain parts of their range (electronic supplementary material, figure S6). The most obvious example of the combined influences of these different processes is the family Artamidae (electronic supplementary material, figure S6a). Here, geographical expansion and many of the most recent allopatric speciation events (located in the dark purple areas of the maps in electronic supplementary material, figure S6a) occurred among morphologically conserved *Artamus* woodswallows in Southeast Asia and the Pacific. Conversely, the Australian grid cells, which maintain much higher species richness, support many larger bodied species (e.g. currawongs and butcherbirds) in addition to the woodswallows, which themselves are represented by more distinct eco-morphs in this area. Thus comparatively, the Australian assemblages (and to a lesser degree those in New Guinea) have diverged more extensively from one another in their ecologies, particularly in terms of the occupation of different strata and foraging strategies, reflecting their morphological differences. Although the coupling of morphological divergence, geographical expansion, and continued diversification may also be evidenced in the families Corvidae and Campephagidae (electronic supplementary material, figure S6b,d), a more general pattern

across corvid families, is that the repeated formation of predominantly allopatric species has resulted in the proliferation of morphologically conserved forms (e.g. Dicuridae, Laniidae, Oriolidae, Pachycephalidae, Rhipiduridae, and Vireonidae; electronic supplementary material, figure S6e, f, i, j, l, and o). Conversely, lineages that diversified in more restricted geographical areas, such as the large tropical islands of New Guinea or Madagascar, underwent more extensive eco-morphological differentiation that seems to have facilitated species build-up and stable co-occurrence [58] (e.g. Paradisaeidae and Vangidae; figure 1 and electronic supplementary material, figure S6 k).

Although the hypothesis that eco-morphological divergence promotes diversification is supported in one of our best path models (electronic supplementary material, figure S5), it is also possible that morphological variability is itself determined by the degree to which co-occurring forms build-up within an area (figure 1 and electronic supplementary material, figure S5). Grid cells supporting an average higher number of species contain more morphologically differentiated forms, likely due to the increased ecological diversity of these assemblages (figure 2 and electronic supplementary material, figure S6). These trends have been generated by repeated cycles of allopatric speciation and eco-morphological divergence following secondary contact (character displacement) [59], or because ecological divergence in allopatry has enabled stable co-occurrence (ecological filtering). Despite our path models favouring the hypothesis that co-occurrence drives ecological divergence rather than the reverse scenario (evidenced by model 13 being a significantly better fit than model 1, figure 1 and electronic supplementary material, table S3), we note that we may have insufficient statistical power to differentiate between these scenarios. It is also possible that both character displacement and ecological filtering are involved in generating eco-morphological divergence and function in a synergistic manner; however, the path analysis framework is unable to test for such feedback loops [60].

The finding that geographical expansion is a major driver of continued diversification among corvid families is in line with previous studies of the overall group, supporting the idea that dispersal and diversification throughout geographically fragmented landscapes promote lineage diversification [10,36,61]. Specifically, the heightened formation of allopatric populations on Indo-Pacific islands increases speciation rates [10,61] with the results of this analysis suggesting that these same conclusions likely apply to radiations that have taken place across more extensive continental settings. More broadly, the extent of range overlaps was shown to be an important predictor of diversification rate slowdowns among mammals [9], implying that geographical expansion and the accumulation of co-occurring forms may represent a general control upon the diversification process in vertebrates. Our other main finding that the evolution of morphological disparity can lead to faster diversification (figure 1) is also consistent with previous findings [62]. However, as with furnariid passerines [63] and plethodontid salamanders [64], we note that the capacity to explain variation in diversification rates based on morphological divergence alone is relatively low (electronic supplementary material, figure S5b).

Overall, our findings suggest the potential for a general explanation of diversification rate variation among corvid

passerine families. However, our interpretations partly rest on the assumption that our analysed traits represent a good approximation of the ecological variability among clades. While this has generally been shown to be the case for passerines [31,32,45,46], it is also notable that in some instances morphological variation could be driven by other selective forces, for example, sexual selection in the case of several species of the birds-of-paradise (Paradisaeidae; notably the genera *Astrapia*, *Epimachus*, and *Parotia*). Furthermore, our conclusions only apply to clades containing more than 10 species. We did not attempt to explain the diversification dynamics of the most species-poor corvid families, for the reason that they have accumulated relatively few co-occurring forms due to their low overall species richness. Combined, these 16 families represent only 5% of the species diversity of the Corvides and are those with the lowest overall rates of diversification. These clades tend to be restricted to limited geographical areas, mostly located within the presumed Australasian ancestral area of the group [35], and particularly the central highlands of New Guinea [41]. It remains plausible that trends of eco-morphological diversification have been an important influence on their diversification dynamics. Specifically, small passerine clades have been proposed to be peripheral in ecological and morphological space compared to more speciose groups, such that the niches they occupy have provided limited opportunities for continued lineage diversification ([43], but see [65]). Alternatively, stable environmental and climatic conditions in the areas within which these taxa currently occur may enable the maintenance and preservation of these lineages over longer timescales [66,67].

The interpretation of our results comes with a number of caveats with respect to our phylogenetic hypothesis. We assessed the extent of diversification rate slowdowns among corvid families using the γ statistic [51] which has been shown to become negatively biased when assessed on phylogenies that do not sample all known species within a clade [51,68]. We attempted to assess this issue, by repeating our analyses using estimates of γ on a phylogeny that sampled *ca* 85% of all species using DNA sequence alone and not taxonomic inference [39]. However, regardless of the phylogeny used to estimate γ our main results remained consistent (electronic supplementary material, appendix B). Furthermore, we could not find any evidence of a systematically negative bias in γ in the respective family phylogenies as a result of the proportion of missing species (electronic supplementary material, figure S2a,b). This latter finding may reflect that the proportion of species sampled with DNA sequence was generally high (above 80%) for most families (table 1). As our phylogeny only contained DNA sequences from extant species, we consider our values of γ are most likely to reflect the influence of recent speciation events, as opposed to extinction, or diversification over deeper timescales. However, extinction may have had a significant and variable influence upon the diversification trajectories and geographical distributions of different corvid clades (e.g. the comparatively faster turnover of lineages that diversified throughout island archipelagos [61]). Yet, as the fossil record of the Corvides (and passerines more broadly) is extremely poor and the validity of estimating extinction from molecular phylogenies remains questionable [69], the relative impact of extinction upon our results is difficult to assess at the current time.

It is also important to consider the potential influence of the species-level taxonomy used upon our results, due to the potential for (i) currently unrecognized corvid species to exist, and (ii) because some recognized species at the tips of the tree may not represent good species. For the most part, these issues reflect different preferred species concepts among taxonomists, and the fact that the historical population structure of many corvid species is poorly known; a common issue among global radiations in which many taxa occur in tropical and/or remote locations. To assess the potential influence of over-splitting, we performed sensitivity analyses, collapsing corvid lineages that diverged within the last 1 Myr before repeating the path analyses. These analyses also continue to support our main findings (electronic supplementary material, appendix B). While the potential biases associated with unrecognized species are difficult to assess analytically, in almost all cases, these are highly likely to be young allopatric splits within already known species complexes. The existence of such taxa is thus likely to increase the number of morphologically similar and geographically separated species, strengthening the main conclusions of this study.

In summary, our findings highlight how simultaneous consideration of geographical and eco-morphological differentiation can explain variation in lineage diversification among comparable radiations. Differences in diversification rates predominantly reflect historical opportunities for geographical expansion, and the interplay between the colonization of new areas, eco-morphological divergence, and the build-up of closely related species at small spatial scales (figure 2). Importantly, eco-morphological divergence appears driven by the accumulation of co-occurring species. These findings apply to a species-rich and globally distributed radiation of passerine birds and provide insight into the processes that underlie the vast taxonomic and geographical differences in the distribution of species diversity. We conclude that the capacity for geographical expansion and the accumulation of co-occurring species is likely to be an important control upon diversification rates across the tree of life.

Data accessibility. The morphological data are provided in electronic supplementary material, table S1 and the species-level phylogeny is available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.80n42> [70].

Authors' contributions. J.D.K. conceived the study, P.Z.M. collected the morphological data, J.D.K. performed the analyses and J.D.K., M.K.B., P.Z.M., A.M., J.F., and C.R. interpreted the analyses and wrote the manuscript.

Competing interests. We declare we have no competing interests.

Funding. J.D.K. was supported by an Internationalisation Fellowship (CF17-0239) from the Carlsberg Foundation, and M.K.B. by an Individual Fellowship from Marie Skłodowska-Curie actions (IDEA-707968). All authors wish to thank the Danish National Research Foundation for its support of the Center for Macroecology, Evolution and Climate (DNRF96).

Acknowledgements. We thank Louis Hansen for help in compiling the distributional datasets, and the museum collections and associated staff that made possible collection of the morphological data. In this regard, we would particularly like to thank Mark Adams, Hein van Grouw, and Robert Prys-Jones at the British Museum of Natural History, Lydia Garetano, Joel Cracraft, and Paul Sweet at the American Museum of Natural History, and Pepijn Kamminga and Steven van der Mije at the Naturalis Biodiversity Center (Netherlands). Wouter van der Bijl provided valuable advice on the phylogenetic path analyses.

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