

# The association between morphological and ecological characters across a global passerine radiation

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## Abstract

1. Strong relationships between morphological and ecological characters are commonly predicted to reflect the association between form and function, with this hypothesis being well supported in restricted taxonomic and geographical contexts. Conversely, among broader sets of species, ecological variables have been shown to have limited power to explain morphological variation.
2. To understand these apparent discrepancies, for a large and globally distributed passerine radiation, we test whether (a) the character states of four ecological variables (foraging mode, diet, strata and habitat) have different morphological optima, (b) ecological variables explain substantial variance in morphology and (c) ecological character states can be accurately predicted from morphology.
3. We collected 10 linear morphological measurements for 782 species of corvid passerines, and assessed (a) the fit of models of continuous trait evolution with different morphological optima for each ecological character state, (b) variation in morphological traits among ecological character states using phylogenetically corrected regressions and (c) the accuracy of morphological traits in predicting species-level membership of ecological character states using linear discriminant analysis (LDA).
4. Models of morphological evolution with different ecological optima were well supported across numerous morphological axes, corresponding with significant differences in trait distributions among ecological character states. LDA also showed that membership of the ecological categories can be predicted with relatively high accuracy by morphology. In contrast to these findings, ecological variables explain limited amounts of variation in morphological traits.
5. For a global radiation of passerine birds, we confirm that the generation of morphological variation is generally consistent with ecological selection pressures, but that ecological characters are of limited utility in explaining morphological

differences among species. Although selection towards different optima means that membership of ecological character states tend to be well predicted by morphology, the overall morphospace of individual ecological character states tend to be broad, implying that morphology can evolve in multiple ways in response to similar selection pressures. Extensive variation in morphological adaptations among similar ecological strategies is likely to be a widespread phenomenon across the tree of life.

#### KEYWORDS

diet, ecological characters, ecological selection, feeding ecology, form–function, morphology, passerine birds, selective optima

## 1 | INTRODUCTION

Analyses of morphological data have been crucial to the advancement of comparative biology (Ricklefs & Miles, 1994), improving understanding about a multitude of ecological and evolutionary processes, including adaptations for ecological segregation (Hutchinson, 1959; Pigot & Tobias, 2013; Schoener, 1974), its underlying mechanistic basis (Bock, 1966; Fjelds , 1982), the formation and maintenance of communities (Miles & Ricklefs, 1984; Pigot, Trisos, & Tobias, 2016; Ricklefs, 1987) and variation in lineage diversification (Claramunt, Derryberry, Remsen, & Brumfield, 2012; Rabosky et al., 2013). Direct associations between morphological form and ecological function represent a key assumption underpinning comparative analyses of this nature, leading to the general conclusion that morphology can be considered a reliable surrogate for ecology across many taxa (Miles & Ricklefs, 1984; Miles, Ricklefs, & Travis, 1987; Naval n, Bright, Marug n-Lob n, & Rayfield, 2019; Pigot et al., 2016; Ricklefs, 2012; Ricklefs & Travis, 1980). Of the tests performed to date, the interrelationships between ecological and morphological characters have been supported both from experimentation and observational field studies, notably among adaptive radiations (Schluter, 2000) such as Darwin's finches (Schluter & Grant, 1984a, 1984b) and *Anolis* lizards (Losos, 1990a, 1990b; Losos & Sinervo, 1989). Further evidence for the link between morphological form and ecological function has also been shown in comparative studies within and between biological communities (Miles & Ricklefs, 1984; Pigot et al., 2016). However, these findings are seemingly in stark contrast to the results of recent analyses which suggest that ecological variables have limited power to explain morphological variation across taxonomically diverse sets of taxa (Felice, Tobias, Pigot, & Goswami, 2019; Naval n et al., 2019). To better understand these apparent discrepancies, and to improve our quantitative understanding of how well morphology reflects ecology more generally, we provide a comprehensive investigation of the relationships between ecological and morphological characters for a global avian radiation.

Divergent natural selection pressures can cause evolutionary differentiation in morphology, when environmental conditions present distinct and underutilized sets of resources whose optimal use

is determined by morphological traits (Pigot & Tobias, 2013; Price, 2008; Schluter, 2000; Van Buskirk, McCollum, & Werner, 1997). Initial approaches that documented the outcome of these processes were based on detailed mechanistic analyses of functional systems (Bock, 1966; Fjelds , 1982), but such analyses are of limited feasibility for more than a few species, and thus unable to provide general conclusions about the association between morphological and ecological features in a wider context. Fortunately, the development of phylogenetic comparative methods has enabled assessment of the correlations between ecological and morphological characters among much larger samples of species (Felice et al., 2019; Naval n et al., 2019; Ricklefs, 2005). These methods now facilitate testing for the presence of morphological optima among different ecological strategies that can be considered consistent with alternate selection pressures through time (Beaulieu & O'Meara, 2016; Butler & King, 2004; Clavel, Escarguel, & Merceron, 2015; Lapiedra, Sol, Carranza, & Beaulieu, 2013; Mahler, Ingram, Revell, & Losos, 2013). Assuming ecological selection is a significant influence upon morphological evolution, statistical differences in the distribution of trait values should be expected among sets of species that differ in their ecological strategies (e.g. Marki, Kennedy, Cooney, Rahbek, & Fjelds , 2019; White, 2016). However, even if ecological selection pressures influence morphological evolution, statistical models with low predictive ability may result (e.g. Felice et al., 2019; Naval n et al., 2019). This is because of the possibility that distinct morphological solutions can be found to meet similar ecological challenges (Alfaro, Bolnick, & Wainwright, 2005; Bock, 1959; Bock & von Wahlert, 1965; Ricklefs & Miles, 1994), and therefore that there are multiple ways for morphology to evolve in response to shared selection pressures (i.e. many-to-one mapping in which different morphologies can produce the same/similar ecological functions; Alfaro et al., 2005; Ricklefs & Miles 1994; Wainwright, Alfaro, Bolnick, & Hulsey, 2005).

Birds have proven an important taxonomic group for providing examples of the tight congruence between morphology, ecology and environmental conditions (Schluter, 2000). Through observations of birds, Lack (1947) and Hutchinson (1959) were some of the first biologists to propose that niche space occupation may reflect morphology, specifically that overall body size was strongly associated with the size

of consumed resources. Considering passerine birds (ca. 2/3 of all extant bird species), subsequent morphological analyses have suggested that different morphological traits (or trait combinations) directly influence locomotion (Leisler, Ley, & Winkler, 1989; Norberg, 1979), flight performance (Claramunt et al., 2012; Leisler & Winkler, 2003), diet (Benkman, 1993; Miles & Ricklefs, 1984; Schluter & Grant, 1984a), foraging mode (Leisler et al., 1989; Marchetti, Price, & Richman, 1995; Miles & Ricklefs, 1984; Partridge, 1976; Pigot et al., 2016; Suhonen, Alatalo, & Gustafsson, 1994) and habitat preferences (Kennedy et al., 2016; Robinson & Holmes, 1982; White, 2016). However, clarifying the morphological features most strongly associated with different aspects of passerine ecology represents an outstanding question that we aim to address here at a large geographical and phylogenetic scale.

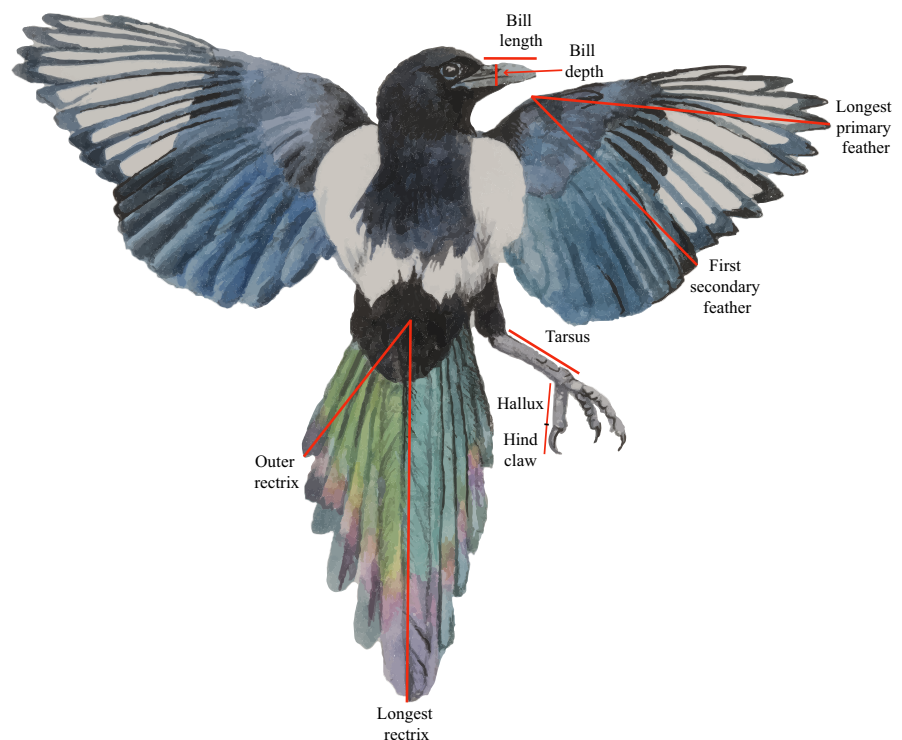
Taking advantage of the extensive range of passerine specimens available for measurement throughout the world's museum collections, and combining this with detailed natural history knowledge, we generate a comprehensive ecological and morphological dataset for the global radiation of corvid passerines (ca. 790 species). The Corvides represent an excellent study system to establish broad scale relationships between ecology and morphology for three main reasons. First, due to the relatively conserved nature of the passerine body plan, there are a wide variety of homologous anatomical structures that can be quantified among corvid species (e.g. wings, bills, feet, tarsi; Figure 1). Second, the Corvides are globally distributed, being found throughout the world's major continental landmasses and many island archipelagos (Jönsson et al., 2016, 2017; Kennedy et al., 2016). Third, species of the Corvides together encompass the vast majority of passerine morphological space (Jönsson et al., 2012; Kennedy et al., 2012), with their extensive morphological and behavioural

variation commonly inferred to correspond with extensive ecological diversity. In this analysis, we explore the relationships between ecological and morphological characters among corvid passerines to answer three main questions: (a) Is the generation of morphological variability consistent with ecological selection pressures? (b) Can ecological variables explain significant amounts of morphological variation, and how does the variance and explanatory power differ depending upon the ecological/morphological traits analysed? (c) Can species-level membership of different ecological character states be accurately predicted by morphological traits?

## 2 | MATERIALS AND METHODS

### 2.1 | Morphological, ecological and phylogenetic data

For 782 corvid species, P.Z.M. measured museum specimens to quantify 10 linear measurements of external morphology that are commonly used in comparative analyses of passerine birds (Claramunt et al., 2012; Pigot & Tobias, 2013; Ricklefs, 2005, 2012). These measurements reflect different aspects of the bills, tarsi, wings, tails and feet, and are illustrated in Figure 1. A detailed description of the measurement procedures is provided in Kennedy et al. (2018). In total, 4,092 museum specimens were measured for a mean of  $5.56 \pm 1.22$  specimens per species. We measured male specimens when possible, although in the minor number of instances when these were poorly represented in the respective collections, we supplemented them with measurements from females. Using ANOVA, we found that 97%–99%



**FIGURE 1** Illustration of the Eurasian magpie (*Pica pica*) upon which all of the morphological measurements analysed in this study, with the exception of bill width, are shown. A full description of the measurement procedures can be found in Kennedy et al. (2018)

of the variance in the individual morphological trait values was between rather than within species (Table S1), and therefore we used the mean trait values for each species in subsequent analyses. The mean values of the morphological measurements for all species are shown in Table S2, while the morphological data for all measured individuals can be downloaded from Dryad (Kennedy, 2019, <https://doi.org/10.5061/dryad.fbg79cnnr6>).

By consulting expert textbooks, field guides and original research publications (Appendix S1A), discrete classifications of the 782 species were generated for four important components of the avian niche: (a) foraging mode, (b) diet, (c) strata and (d) habitat preferences. These classifications approximate our current knowledge about the major differences in the species-level ecology of corvid passerines. It should be noted, however, that given the global distribution of this radiation and the numerous remote locations in which taxa occur (e.g. throughout Indo-Pacific island archipelagoes), many species have received limited direct observational study in this respect. For these reasons, we suggest a discrete classification system is the most appropriate representation of our present ecological knowledge about this radiation, in comparison to classifications of proportional resource usage (e.g. Wilman et al., 2014) and/or fine scale behavioural adaptations (e.g. Pigot et al., 2016; Remsen & Robinson, 1990).

For diet, we classified species in terms of whether they were (a) exclusively insectivorous ( $n = 500$ ) or whether the diet is supplemented by significant amounts (i.e. represents a substantial part of the food intake and is consumed at least seasonally) of (b) vertebrate prey ( $n = 42$ ), (c) fruit and/or other plant material ( $n = 119$ ) or if (d) species potentially consume all of these food types (omnivory;  $n = 121$ ). With respect to foraging mode, we considered whether species (a) obtain food by searching for hidden prey items (e.g. in decaying wood, under leaves, in bark or in crevices;  $n = 125$ ), (b) by gleaning from branches or foliage ( $n = 490$ ) or (c) by catching prey in flight ( $n = 167$ ). Classification of habitat follows Kennedy et al. (2016), who differentiated corvid species by the foliage density in which they are commonly found. We consider three categories: (a) dense foliage ( $n = 427$ ), (b) open habitats with limited foliage cover ( $n = 37$ ) or (c) habitats that represent an intermediate of (a) and (b;  $n = 318$ ). Finally, we determined the strata at which a species predominantly forages at, using the following categories (a) aerial ( $n = 13$ ), (b) canopy or subcanopy ( $n = 359$ ), (c) bush layer or understorey ( $n = 267$ ), (d) ground ( $n = 78$ ) or (e) a combination of two or more strata listed in (a–d;  $n = 65$ ). The complete species-level classifications are shown in Table S2. To investigate the interrelatedness between our ecological variables, we computed Goodman and Kruskal's tau statistic in the R package `GOODMANKRUSKAL` (Pearson, 2016). Tau represents an asymmetric measure of association between the categorical ecological variables. Values of tau range from 0 to 1 with higher values indicative of a better predictive ability. The resulting estimates suggest that our four ecological variables are relatively weak predictors of one another (Figure S1), justifying our approach to analyse their independent effects upon morphological variability.

Estimates of the phylogenetic relationships for the 782 corvid species were obtained from Kennedy et al. (2016). The original phylogeny generated by Jönsson et al. (2016) sampled ca. 85% of all corvid species using a combination of eight nuclear and four mitochondrial

loci. Bayesian methods were subsequently used to generate a time-calibrated tree. The phylogeny produced by Kennedy et al. (2016) built upon the initial analysis of Jönsson et al. (2016), adding the remaining unsampled species to the phylogeny as polytomies, with their placement based on taxonomic information. The branch lengths subtending these species were generated using the polytomy resolver method (Kuhn, Mooers, & Thomas, 2011). The maximum clade credibility tree generated from the pseudo-posterior distribution of phylogenies was used in the analyses described below and can be downloaded from Dryad (Kennedy, 2019). Because some species were placed in the phylogeny by taxonomic information alone irrespective of their ecological and morphological characters, this may result in a breakdown in the true patterns of phylogenetic trait structure, and consequently bias subsequent phylogenetic comparative analyses (Rabosky, 2015). We investigated this issue by performing the relevant comparative analysis described below both on the complete dataset of all 782 species, and following the removal of the 119 species placed in the phylogeny by taxonomy alone. In general, we recovered highly congruent results between these sets of analyses (Appendix S1B). We generally present results from the complete species-level dataset in the main text, highlighting any discrepancies with the analyses excluding the taxonomically placed species.

## 2.2 | Data transformation

Corvid passerines span a wide range of body sizes, with the smallest species weighing <10 g and the largest >1,000 g (Kennedy et al., 2012). The consequence of these size differences is that the original morphological measurements are strongly correlated with one another across species (mean  $r = .81 \pm .14$ ), with the distributions of each measurement being heavily right skewed (Figure S2). As commonly practiced in phylogenetic comparative studies that have data of this nature, we log-transformed the original morphological measurements (Figure S3) and performed a principal component analysis (PCA) on these values. The utility of PCA in this instance is to produce uncorrelated axes of morphological variation, from which PC axes corresponding to size and shape differences can be independently extracted from the data. The correlations of the original log-transformed morphological traits are shown in Table 1. PC1 (which explains 87% of the variance in the original data; Table 1) can be considered a strong proxy of overall body size while PC2–10 (which together explain the remaining 13% of the variation; Table 1) reflect different aspects of shape that are predominantly independent of size. Previous studies of passerines have suggested that axes explaining small amounts of variation in the original morphological data retain important biological information (Pigot et al., 2016; Ricklefs, 2005), and we further assessed this hypothesis here. Unless otherwise stated, all statistical analyses were performed both on the log-transformed measurements, and for the species scores of each of the 10 PC axes. Following criticisms about the use of PC scores that fail to correct for the non-independence of species-level data in phylogenetic comparative analyses (Uyeda, Caetano, & Pennell, 2015), we also confirmed the consistency of our main results

**TABLE 1** Loadings of the 10 log-transformed morphological measurements on the individual principal component axes

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10
Tarsus	0.27	0.04	-0.58	0.02	-0.38	-0.35	0.47	-0.22	-0.12	-0.20
Hallux	0.29	0.19	-0.33	0.05	0.16	0.32	-0.55	-0.22	-0.02	-0.54
Hallux + claw	0.30	0.13	-0.36	0.02	0.05	0.07	-0.26	-0.09	-0.16	0.81
Bill length	0.32	0.20	0.01	-0.06	0.18	0.63	0.54	0.34	-0.11	-0.02
Bill depth	0.39	0.28	0.28	-0.32	-0.58	-0.13	-0.26	0.41	0.07	-0.03
Bill width	0.30	0.20	0.50	-0.25	0.10	-0.03	0.16	-0.72	-0.05	0.04
Outer rectrix	0.29	-0.25	0.28	0.80	-0.32	0.15	-0.02	-0.09	-0.05	0.02
Longest rectrix	0.33	-0.85	-0.02	-0.39	0.02	0.09	-0.05	0.01	-0.05	-0.03
Longest primary feather	0.34	0.04	0.14	0.17	0.53	-0.54	-0.02	0.30	-0.39	-0.11
First secondary feather	0.31	<0.01	-0.07	0.11	0.26	-0.16	0.09	0.05	0.88	0.06
Variance explained	0.87	0.05	0.03	0.02	0.01	<0.01	<0.01	<0.01	<0.01	<0.01

using phylogenetically corrected principal component scores (Revell, 2009; see Appendix S1B).

### 2.3 | Comparing models of morphological evolution

To assess whether the generation of morphological differences among corvid species is consistent with ecological selection pressures through time, we compared the fit of models of trait evolution that approximated this and alternative evolutionary processes. To reconstruct the evolutionary history of our ecological variables, we used likelihood-ratio tests to compare the relative fit of continuous time reversible Markov models in which all transition rates were constrained to be equal (ER), or allowed to vary independently (ARD), between the character states of our four ecological variables. As these tests consistently showed that the ARD model provided a significantly better fit across all ecological variables ( $p < .05$ ), we estimated the ancestral states of their respective characters using this model. We estimated character history by implementing stochastic character mapping in the R package *PHYTOOLS* (Revell, 2012), producing 100 maps for each ecological variable (Figures S4–S7). Subsequently, we fit four different univariate models of continuous trait evolution (single optima Brownian motion [BM1], multirate Brownian motion [BMS], single optima Ornstein–Uhlenbeck (OU) [OU1] and multimodal OU [OUM]), using the R package *OUwie* (Beaulieu & O'Meara, 2016).

The four evolutionary models that were compared can be briefly summarized as follows. Brownian motion (BM) models the scenario in which continuous traits can evolve through time in any direction, with the expected differences accrued among taxa being solely proportional to the time since divergence from a common ancestor. Variance in trait values under BM is determined by the evolutionary rate (the  $\sigma^2$  parameter), which we estimated either as a single rate for all species across the phylogeny (BM1), or with several discrete rate classes (BMS). The Ornstein–Uhlenbeck (OU) model extends the BM framework to capture the potential constraints of evolution in terms of how continuous traits evolve towards one (OU1) or several (OUM) optima (Butler & King, 2004; Hansen, 1997). We performed

these model comparisons to test whether the trends of morphological evolution were consistent with processes that are independent of ecological influences, or that varied in terms of evolutionary rates (BMS model), or selective optima (OUM model) between ecological character states. We assessed the fit of the BMS and OUM models utilizing the internal node states recorded from the stochastic character maps of each ecological variable to define selective regimes. Models were subsequently fit across 100 stochastic character maps per variable. The measurements of all individuals (Kennedy, 2019) were used to estimate measurement error for each species, which we incorporated into these analyses to improve the accuracy of the parameter estimates across all models. Model fit was evaluated by calculating Akaike Information Criteria (AIC) values for all models, with average AIC values estimated for the 100 evaluations of the BMS and OUM models, respectively.

### 2.4 | Morphological variation across ecological character states

To further quantify the extent to which morphology varies within and between ecological characters, we used phylogenetic ANOVA in the R package *PHYTOOLS* (Revell, 2012). This approach implements the methods of Garland, Dickerman, Janis, and Jones (1993), who proposed that to account for the non-independence of species-level data in these analyses, continuous trait evolution should first be modelled along the phylogeny in accordance with BM. We repeated the simulations of trait evolution under BM 1,000 times for each measurement/PC axis to estimate a distribution of  $F$ -statistics that provide the critical values from which we can reject the null hypothesis that there are no differences in morphology between the ecological character states. We also used the empirical  $F$ -statistics to assess which measurements or PC axes are most strongly differentiated by the character states of the four ecological variables. To estimate the variance in morphology that can be explained by the ecological variables, we computed  $R^2_{lr}$  values using the R package *RR2* (Ives & Li, 2018). Following Ives (2018),  $R^2_{lr}$  values represent a partial  $R^2$  that is



estimated to reflect the likelihood of observing the data in a phylogenetic least squares regression using a set of predictors, compared to models in which the intercept is the only predictor.  $R^2_{lr}$  values were estimated for the four ecological variables modelled individually, and also as combined predictors.

Using the R package *GEIGER* (Harmon, Weir, Brock, Glor, & Challenger, 2008), we also investigated morphological differences in multivariate trait space among ecological character states, using phylogenetic MANOVA (Garland et al., 1993). One of our main aims in these analyses was to determine how the morphological differences in ecological character states become more or less diagnosable depending on the number of PC axes analysed in combination, and whether these differences reflect the variance each axis explains in the original morphological data. We therefore repeated these analyses by incrementally removing the PC axes that explained the least variance in the data, until we were left only with PC1 (e.g. all PC axes, PC9-1, PC8-1, etc.). As above, *F*-statistics were compared to assess the relative degree to which the morphological trait values are divergent among the ecological character states.

## 2.5 | Predicting membership of ecological character states by species morphology

We performed linear discriminant analyses (LDA) to determine how well species-level membership of the ecological character states could be predicted from morphology. LDA assesses linear combinations of continuous characters that best separate two or more discrete classes. In our case, this reflects whether combinations of the morphological measurements can associate species to their correct ecological character state or not. In addition to performing the LDA analyses upon the full complement of log-transformed measurements, as above, we incrementally removed PC axes from PC10-1, to eventually only consider PC1, assessing the classification accuracy for each combination of axes. *K*-fold cross-validation was used to determine classification accuracy, with our dataset divided into 10 equal sized samples ( $K = 10$ ). Nine subsamples were used to train the model, with a single subsample retained to test the model. The cross-validation method was repeated *K* times, such that all subsamples were used in both the training and test datasets. Classification accuracy reflected the percentage of species accurately associated with the correct ecological character state. We repeated the LDA analysis upon PC scores simulated under a BM model 1,000 times, to assess classification accuracy as a consequence of morphological similarity due to the influence of shared ancestry alone.

## 3 | RESULTS

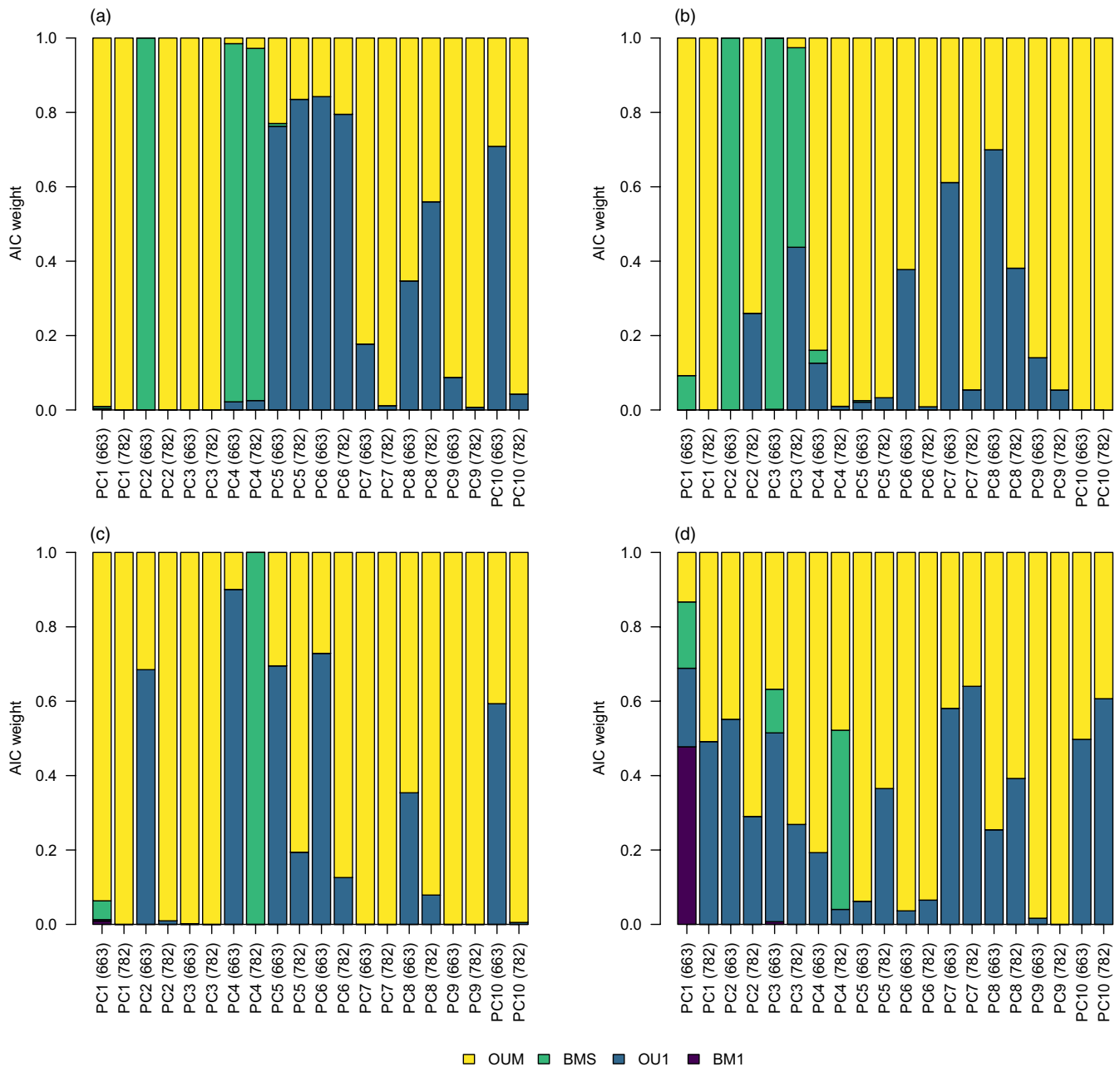
### 3.1 | Comparing models of morphological evolution

Comparisons of the fit of different models of continuous trait evolution are presented in Figure 2 and Tables S3–S10. For the log-transformed

measurements of the 782 species, for all but a single trait (longest rectrix) we generally recovered strong support for the OUM model across the four ecological variables (Tables S3–S6). For analyses of the 663 species for which DNA sequence data were available, we continued to recover strong support for models which support the influence of ecology upon patterns of morphological evolution, although with increased support for the BMS model at the expense of OUM (Appendix S1B). With respect to the PC axes, we similarly found strong support for the OUM model in the majority (26/40) of comparisons (foraging mode 6/10 axes, diet 8/10 axes, strata 9/10 axes and habitat 3/10 axes; Figure 2; Tables S7–S10), although this number was reduced when only analysing species sampled in the phylogeny by DNA sequence (foraging mode 4/10 axes, diet 5/10 axes, strata 4/10 axes and habitat 5/10 axes; Figure 2; Tables S11–S14). For both the log-transformed morphology and PC axes, the favoured evolutionary trends are in many instances consistent with selection towards different morphological optima, with those optima varying among the ecological character states. However, in the case of habitat, for all but two PC axes (PC4 and PC9) we cannot fully discount the possibility that the underlying processes generating morphological variation was ecologically neutral (Appendix S1B). BMS was the favoured model for PC2 and PC3 in the food and foraging classifications upon excluding the taxonomically placed species (Figure 2), and also for PC4 in the cases of food (all analyses), strata and habitat (only for the analyses excluding the taxonomically placed species; Figure 2). These results suggest heterogeneity in the rates of evolution for these PC axes (Figure 2; Tables S8–S10).

### 3.2 | Correlations between ecological and morphological traits

We tested whether the distribution of the morphological trait values varied between ecological character states using phylogenetic ANOVA. The results of these tests are presented in Table 2; Figures S8–S15. For the log-transformed traits, we consistently recovered highly significant differences among the character states of the four ecological variables, with the means and variation showing similar patterns among the individual character states irrespective of the specific morphological trait considered (Figures S8–S11). Because of the strong positive correlations between the original trait values, these results suggest that overall size differences are the primary determinant of these relationships. This interpretation is further corroborated by the results of the phylogenetic ANOVAs with respect to PC1, which was the only PC axis found to show significant variation among all four ecological variables (Table 2). Differences in the distribution of PC1 values were also consistent in trend to those of the log-transformed measurements (Figures S12–S15). Significant variation among the ecological character states for the species-level values of the shape PC axes (PC2-10) was also recovered (Table 2; Figures S12–S15). However, considering the individual shape PC axes, the prevalence of significant differences depended upon the ecological variable analysed (Table 2). Only two axes (PC4 and PC8) showed no significant differences between any of the ecological variables (Table 2). Together, these findings imply that once



**FIGURE 2** Bar plots showing the Akaike Information Criteria (AIC) model weights of four univariate evolutionary models (BM1, OU1, BMS and OUM) fit individually to PC1-10. Bars denoted (663) represent the results from models fit to the PC scores of the 663 species sampled in the phylogeny based on molecular sequence data, whereas those referred to as (782) also include those species added to the phylogeny using taxonomic information alone. The AIC values for the BMS and OUM models from which the AIC weights were derived represent the mean values from the model evaluations, using the internal node states of 100 individual stochastic character maps that approximated the evolutionary history of the ecological character states. Plots are shown for the following ecological variables (a) foraging mode, (b) diet, (c) strata and (d) habitat

size differences have been accounted for, distinct aspects of shape variation fluctuate in their importance when attempting to discriminate between the character states of different ecological variables. It is notable that significant differences among ecological character states were recovered among PC axes that explained minor amounts of variation in the original morphological measurements (Tables 1, 2). 95% confidence ellipses highlighting variation in the PC axes between ecological

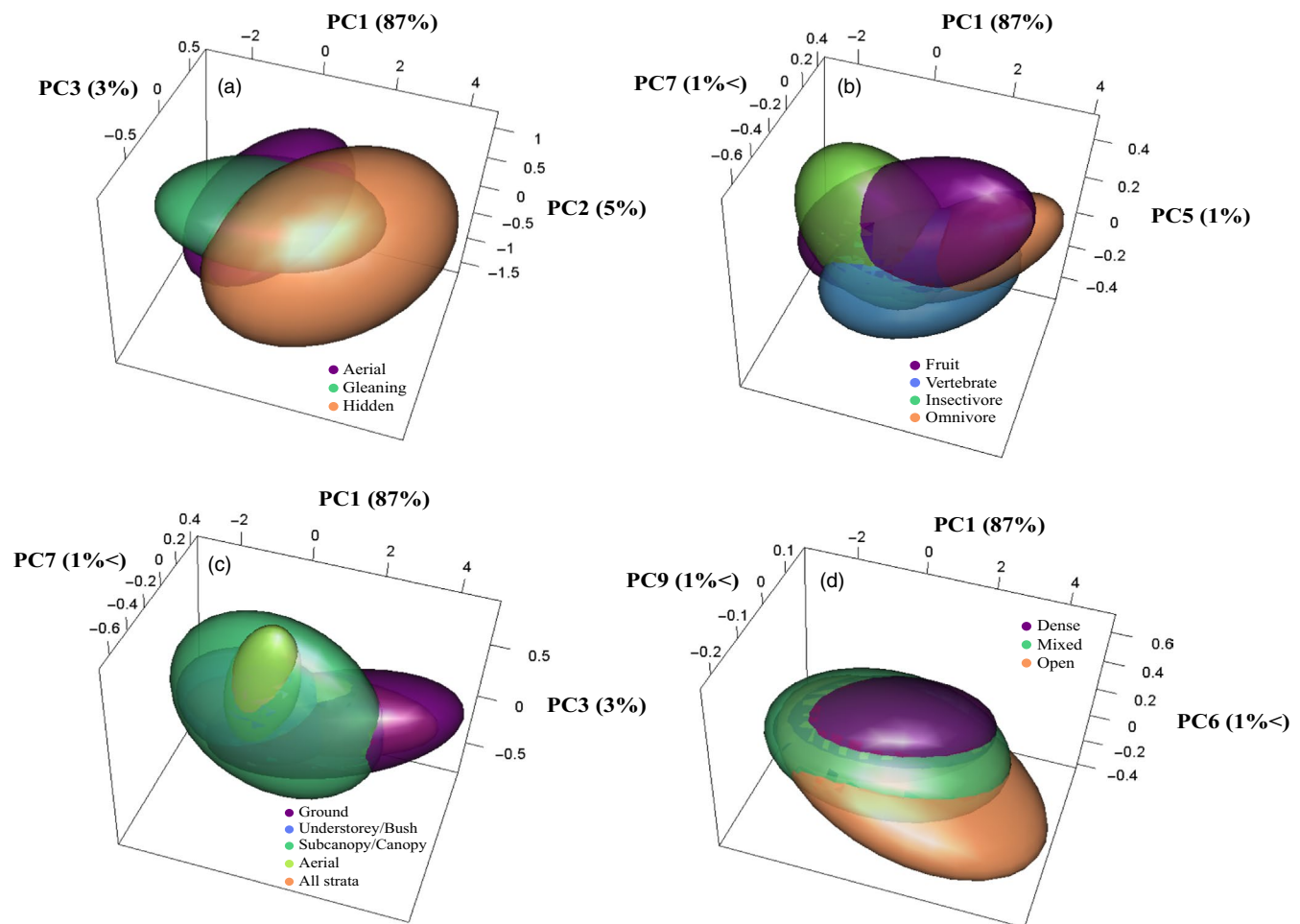
character states are shown in Figure 3. Despite clear differences in the distributions of the trait values,  $R^2$  values suggest that for both the log-transformed morphological measurements and the individual PC axes, ecological character states have limited ability to explain morphological variation among the Corvids (Tables 2; Table S15).

The relative extent to which the distribution of the log-transformed traits and PC axes differed among the four ecological variables was

**TABLE 2** *F*-statistics from phylogenetic ANOVAs that tested whether the distribution of the species scores on the individual PC axes were significantly different among the character states of each ecological variable.  $R^2_{lr}$  values are computed following Ives (2018), and represent a partial  $R^2$  value comparing the full model with the ecological variables as predictors, against a model that contains only the intercept. Combined variables reflect a model in which all four ecological variables were used as predictors simultaneously

	Foraging mode		Diet		Strata		Habitat		Combined variables
	<i>F</i> -statistic	$R^2_{lr}$	<i>F</i> -statistic	$R^2_{lr}$	<i>F</i> -statistic	$R^2_{lr}$	<i>F</i> -statistic	$R^2_{lr}$	$R^2_{lr}$
PC1	<b>191.29**</b>	.019	<b>294.77**</b>	.03	<b>70.26**</b>	.01	<b>17.7**</b>	.001	.055
PC2	<b>27.67*</b>	.034	4.1	.012	10.46	.028	1.44	.021	.073
PC3	<b>84.84**</b>	.038	11.96	.005	<b>19.43**</b>	.062	<b>8.11*</b>	.007	.091
PC4	10.75	.002	8.3	.003	2.08	.021	0.26	.03	.045
PC5	5.18	.002	<b>37.43**</b>	.009	<b>16.1*</b>	.023	3.5	.021	.05
PC6	5.72	.006	18.97	.004	<b>16.15*</b>	.022	<b>25.29**</b>	.027	.047
PC7	20.36	.007	<b>20.78*</b>	.01	<b>28.88**</b>	.017	3.13	.001	.033
PC8	13.73	.014	6.37	.002	6.59	.013	3.79	.01	.045
PC9	<b>26.53*</b>	.012	7.45	.013	<b>46.67**</b>	.057	<b>34.93**</b>	.021	.084
PC10	6.91	.006	<b>23.48*</b>	.002	3.77	.015	3.85	.018	.033

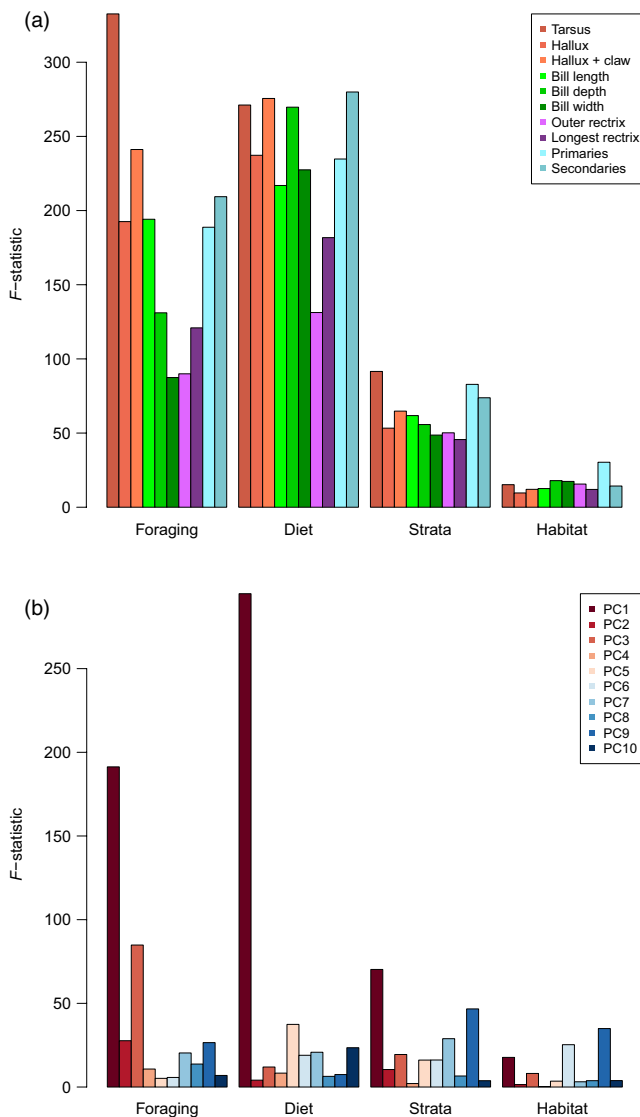
Note: Significant differences among the PC scores across the character states are highlighted in bold; <0.001\*\* and <0.01\*. Results denoted by \* become non-significant upon applying the Bonferroni correction.



**FIGURE 3** 95% confidence ellipses showing variation in the PC axes among the character states of four ecological variables: (a) foraging mode, (b) diet, (c) strata and (d) habitat. For each ecological variable, different combinations of PC axes are shown that emphasize the divergence between character states



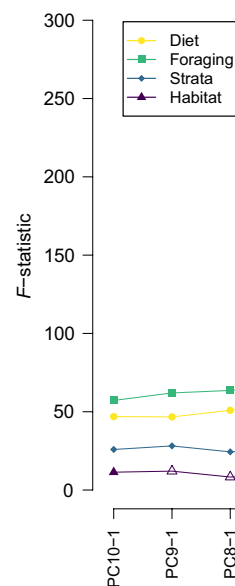
determined through comparison of the  $F$ -statistics derived from the ANOVAs and MANOVAs. For both the log-transformed morphology and PC axes, we consistently found that foraging and dietary variables had far larger  $F$ -statistics (implying greater differentiation in the distribution of trait values among the ecological character states) compared to either the strata or habitat classifications (Figure 4). With respect to univariate analyses of the PC axes, variation among the ecological character states is greatest for PC1 compared to any of the remaining PC axes, although the shape axes (PC2-10) also showed significant differences (Figures 4, 5; Figures S12–S15). In accordance with these findings, values of the  $F$ -statistics from the MANOVAs increase upon combining fewer PC axes from PC10-1 to PC1.



**FIGURE 4** Bar plots showing  $F$ -statistic values computed from ANOVAs comparing the distributions of (a) the log-transformed morphological traits and (b) the species scores on the 10 PC axes, as a factor of the character states of foraging mode, diet, strata and habitat. Higher  $F$ -statistic values reflect greater divergence in the morphological trait distributions between character states

### 3.3 | Predicting membership of ecological character states from morphology

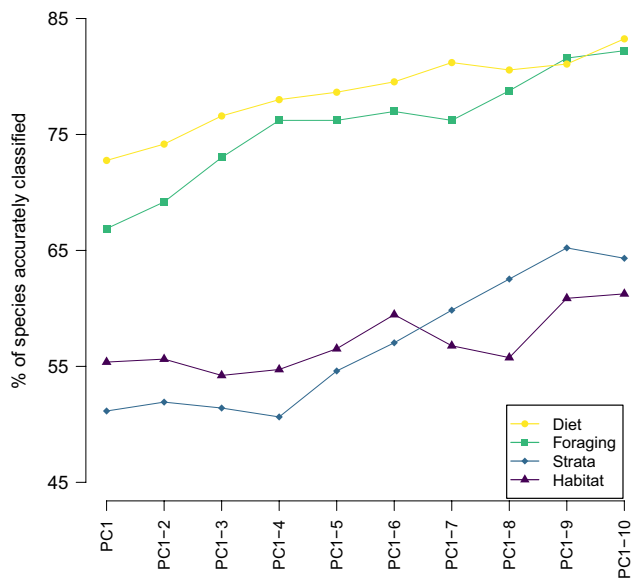
The results from our LDAs show that species-level membership of ecological character states can be well predicted from our morphological measurements (Figure 6) with an accuracy that is substantially higher than when randomly assigning species to different states, or analysing trait data simulated under BM, except in the case of habitat (Figure S16). In line with our previously discussed results, foraging and dietary characters are predicted with the greatest accuracy, such that 82% or 83% of species are assigned to the correct character state, respectively, when analysing the full morphological dataset (Figure 6). Upon combining the food and foraging categories into a single variable, the percentage of correctly assigned species decreases to 69% (Figure S17). However, despite the finer division of the ecological character states as a consequence of combining these variables, classification accuracy remains comparatively higher than for either the strata (66%) or habitat (61%) classes (Figure 6; Figure S17). Across all ecological categories, combining additional PC axes before performing the LDA tended to increase the classification accuracy of species (Figure 6). However, plateaus in classification accuracy for habitat and strata occur when considering the lower PC axes (PC2-4), while this also occurs among the intermediate axes for foraging mode (PC4-7; Figure 4; Figure S16). As such, the additional classification accuracy gained from adding individual PC axes does not linearly reflect the amount of variation they explain in the original morphological data (Table 1), meaning that minor



**FIGURE 5**  $F$ -statistics computed from MANOVAs comparing multivariate combinations of the PC axes among the character states of the foraging mode, diet, strata and habitat variables. Higher  $F$ -statistic values reflect greater divergence in the morphological trait distributions between the ecological character states. Filled symbols indicate that the combinations of PC scores were significantly different ( $p = .05<$ ) between character states

axes of morphological variation are disproportionately important in discriminating between ecological character states (Tables S3, S4, S16 and Figures S16–S22).

The coefficients of linear discriminants determined from analysing the log-transformed morphology (Table 3) show the relative



**FIGURE 6** Percentage of species accurately classified to the correct ecological character state from linear discriminant analyses of the 10 principal component axes, performed separately for each ecological variable. Each point represents a separate analysis in which the scores from the single PC axes were progressively removed, beginning with a combination of all axes (PC10-1) until only the axis that explained the most variation in the original morphological data (PC1) was considered

importance of the original measurements in accurately classifying species into their respective ecological character states. For the food and foraging categories (both individually and when combined into a single variable), tarsus, hallux and hind claw measurements had the greatest influence differentiating the character states, with the wing and bill measurements of secondary importance (Table 3; Table S13). Upon combining the food and foraging categories into a single variable, the comparative importance of bill width and depth influencing classification accuracy became slightly more apparent (Table S17). In contrast, wing morphology was most important for differentiating habitat classes, while tarsus and hallux also made substantial, but lesser contributions (Table 3). Considering strata, tarsus, hallux, hind claw and wing morphology had similar importance in differentiating the character states (Table 3). Tail measurements made limited contributions to the linear discriminants of all four ecological variables (Table 3).

## 4 | DISCUSSION

For a globally distributed and speciose radiation of passerine birds, our analysis demonstrates that morphological divergence is generally consistent with the prevalence of ecological selection pressures through time (Figure 2; Figures S8–S15). Consequently, membership of ecological character states can be predicted with relatively high accuracy from morphology (Figure 6). In contrast, ecological variables are extremely weak predictors of morphological variability (Table 2; Table S15). Therefore, although broad ecological strategies can be predicted by morphological differences among species (Figure 6), extensive morphological variation within individual ecological character states is

**TABLE 3** Coefficients of linear discriminants from the LDA analyses performed upon the 10 log-transformed morphological traits that attempted to classify species among the character states of four discrete ecological variables

	Foraging		Food			Strata				Habitat	
	LD1	LD2	LD1	LD2	LD3	LD1	LD2	LD3	LD4	LD1	LD2
Tarsus	4.02	-1.81	-1.63	-0.26	-0.92	6.06	2.83	-2.69	4.72	4.47	1.22
Hallux	-2.43	-5.61	6.44	15.15	-5.59	-6.49	-2.80	2.83	11.89	1.57	1.17
Hallux + claw	0.30	10.40	-6.65	-13.12	5.67	3.64	0.54	-5.64	-13.96	-5.98	-1.26
Bill length	2.24	0.13	1.94	1.02	-1.90	0.02	-0.93	0.58	2.98	-0.22	-1.59
Bill depth	0.05	-3.38	-0.62	-0.45	-5.13	-1.04	-1.23	0.48	-2.29	0.88	-1.74
Bill width	-2.80	2.17	-2.49	-2.69	3.24	0.54	1.62	-1.74	-1.37	-0.37	-0.10
Outer rectrix	-2.79	2.74	1.03	-1.42	-1.64	0.36	0.55	-0.83	0.62	0.09	-3.20
Longest rectrix	-0.28	1.34	-0.58	0.15	-0.92	-0.09	0.63	-0.12	-1.05	0.43	-1.13
Primaries	2.25	3.95	0.80	0.81	-0.46	3.73	-8.12	-4.53	2.15	9.60	1.21
Secondaries	2.19	-8.39	-2.23	1.77	8.70	-3.93	7.38	13.05	-2.77	-9.93	6.68
Proportion of trace	0.84	0.16	0.76	0.16	0.09	0.53	0.28	0.17	0.02	0.9	0.1

**Note:** Proportion of the trace represents the between class variance among the ecological characters states that is explained by the successive linear discriminant functions (LD1, LD2, LD3 or LD4). Positive or negative values reflect the direction of the correlation between the log-transformed traits and the individual linear discriminant functions. The comparable importance of each morphological trait for the individual linear discriminants is reflected by the relative deviance of the respective values from 0.

apparent (Figures S8–S15). We reconcile these findings by concluding that different aspects of morphology can evolve in response to broadly similar selection pressures, and that divergent morphological forms can be adaptive in similar ecological contexts (Alfaro et al., 2005; Bock, 1959; Bock & van Wahlert, 1965; Wainwright et al., 2005).

The OUM model proposes the evolution of different morphological optima among each ecological character state, and commonly reflects the best fitting model of morphological evolution for all ecological variables except habitat (Figure 3; Tables S7–S14). OUM was commonly favoured over alternative models that approximate the processes of random walk (BM1), evolutionary constraints around a single selective optima (OU1) or variation in rates of morphological evolution (BMS; Figure 2). Trait measurements and PC axes whose trends of morphological evolution are best approximated by OUM are consistent with the influence of ecological selection pressures through time (Figure 2; Butler & King, 2004). The main message from these results is that models which account for ecological differences among species when assessing trends of morphological evolution, generally provide a better explanation of our data than those that do not. Considering the near global distribution of the Corvids (Jönsson, Fabre, Ricklefs, & Fjeldså, 2011; Kennedy et al., 2016), the implication of these findings is that unrelated and geographically separated species, which share ecological attributes, are evolving towards similar morphological optima as a consequence of these ecological selection pressures (Frédérich, Sorenson, Santini, Slater, & Alfaro, 2012; Gillespie, 2004; Hansen, 1997; Muschick, Indermaur, & Salzburger, 2012). However, as evidenced by the extensive morphological variation within character states (Figures S8–S15), and the limited explanatory power ecological variables have in accounting for morphological differences among species (Tables 2; Table S15), selection towards morphological optima are likely to be weak and potentially influenced by multiple other factors.

Foraging mode and diet more strongly differentiate corvid morphology in comparison to either habitat or strata (Table 2; Figures 4, 5). Although all four ecological variables have previously been shown to be correlated with passerine morphology (Benkman, 1993; Felice et al., 2019; Kennedy et al., 2016; Miles & Ricklefs, 1984; Navalón et al., 2019; Pigot et al., 2016; Richman & Price, 1992; Ricklefs & Travis, 1980; Robinson & Holmes, 1982; Schluter & Grant, 1984a; White, 2016), to our knowledge, the relative extent to which morphological divergence is driven by these different aspects of ecology has remained largely unexplored. Our main explanation for the different results among the variables is that foraging mode and diet are primarily associated with direct resource acquisition and use (Pigot et al., 2016; Ricklefs, 2005; Winkler & Leisler, 1985). Comparatively, habitat and strata are equally important in leading to the spatial differentiation of taxa, thus enabling congeners or taxa with otherwise similar ecologies to avoid direct competition with one another (MacArthur, 1958; Pigot & Tobias, 2013). Segregation of ecologically and morphologically similar congeners into different habitats is common in many corvid groups (e.g. *Dicrurus*, *Lanius*, and *Malaconotidae*) and thus

provides an important explanation for the generally weaker morphological differentiation between species that are members of the different habitat character states (Figures 2, 4–6). In addition, although habitat and strata are correlated with different morphological adaptations (Table 3; Figures S8–S15), these associations are also likely to be mediated by behavioural differences (Lapiedra et al., 2013; Robinson & Holmes, 1982), which we were unable to directly account for in this analysis.

Considering the analyses of the PC scores, by far the most variable axis, and the only one to differentiate all four ecological variables was PC1 (Table 2; Figure S12–S15). Given the strong positive correlation with the original morphological measurements (Table 1), we consider PC1 to be a good proxy for overall body size. In birds and throughout the animal kingdom more generally, body size is a core axis of niche differentiation, due to its robust association with prey size, the size of other consumed resources and/or resource monopolization (Lack, 1947; Hutchinson, 1959; Marki et al., 2019; Richman & Price, 1992; Wilson, 1975). Size (PC1) alone is a relatively weak predictor of the membership of the ecological character states (Figure 6), with the incorporation of shape dimensions necessary to improve classification accuracy when attempting to predict ecological differences among species (Figures 5, 6). In combination, PC2–10 only explain 13% of the overall variation in corvid morphology (individual axes explain between 5% [PC2] and <0.01% [PC10] of the overall variation; Table 1), yet the majority of these axes show significant variation between at least one set of ecological character states (Table 3; Figures S12–S15). Improved classification accuracy upon incorporating PC2–10 into the LDA analyses (Figure 6) supports the assertion that minor axes of morphological shape variation retain important information about species ecology (Pigot et al., 2016; Ricklefs, 2005; Ricklefs & Travis, 1980).

Unlike our findings for PC1, PC2–10 show differences in terms of the individual ecological variables for which their distributions vary significantly (Figures S12–S15). Different aspects of shape likely vary in terms of their importance with respect to alternate ecological functions. It should be noted that two PC axes (PC4 and PC8) do not significantly vary among any of the ecological variables analysed (Table 2). The lack of significant variation in these instances may plausibly reflect the coarse resolution of our ecological categories. Variation in these morphological axes could also have been generated by selective processes related to ecology, but not captured by our variables (e.g. predator evasion, substrate type), or those unrelated to ecology, such as genetic drift (Lande, 1976) or sexual selection (Andersson, 1982). With regards non-ecological processes, sexual selection is likely to explain why analyses of the longest rectrix (for which PC4 is a strong correlate; Table 1) do not support evolutionary models consistent with selective optima, but rather variation in evolutionary rates (Figure 2; Figures S8–S11). Lineages which have experienced strong sexual selection have as a consequence had high rates of tail evolution, with some birds-of-paradise (e.g. *Astrapia*) and *Terpsiphone* flycatchers providing plausible examples of this influence among the Corvids. In the absence of a priori testing for a relationship with specific sets of ecological variables,

we suggest that the inclusion of a wide range of morphological traits (e.g. tarsus, hallux, claws, bills and wings) and associated PC axes are justified when attempting to study major ecological differences among species (Pigot et al., 2016; Ricklefs, 2005).

Assignment of species into the correct ecological character states can be achieved with a relatively high accuracy using the morphological measurements studied here (Figure 6; Figures S16–S22). Classification accuracy is substantially higher than expected given a random assignment of species into the character states, or when data simulated under BM are analysed, except in the case of the habitat categories (Figure S16). These results support previous findings about the ability of morphology to predict ecological strategies reported at the community scale (Miles et al., 1987; Pigot et al., 2016; Ricklefs & Travis, 1980). Different morphological traits vary in their importance for accurately classifying species among ecological categories, and some ecological categories can be predicted with a higher accuracy than others (Tables 2; Tables S16–S17 and Figures S18–S22). Key axes of differentiation likely reflect the progressively smaller legs/feet, relatively more projected wings and wider/shallower bills of aerial insect foragers in comparison to taxa that exploit larger prey towards the ground. The relative lengths of the primary and secondary flight feathers become comparatively more important discriminants of the habitat classes (Table 3) because the relative degree to which the wings are either projected or rounded (reflected by the ratio between the primary and secondary feathers) determines the capacity for manoeuvrability in dense vegetation, and propulsion during aerial flight (Claramunt et al., 2012; Kennedy et al., 2016; White, 2016). The importance of manoeuvrability upon both foraging mode and habitat preferences may also account for the similar linear discriminants of tarsus, hallux, hind claw and wing traits when classifying species by strata (Table 3). As previously suggested, the evolution of long tail feathers may be driven primarily by factors other than ecology, and correspondingly these measurements were consistently of minor importance in classifying species into ecological character states (Tables 3; Tables S16 and S17). In contrast, bill characters have long been considered to show a strong association with feeding ecology (Gill, 1995), with examples of bill divergence in a number of adaptive radiations used to illustrate this point (Jönsson et al., 2012; Schluter, 2000; Schluter & Grant, 1984a). When combining the dietary and foraging classifications into a single variable, we find that the influence of bill width and depth became more apparent in the discrimination of different ecological classes (Table S17). These differences make biological sense, considering the repeated evolution of wide flat bills among flycatchers that perform sallying manoeuvres (e.g. *Machaerirhynchidae*, *Monarchidae* and *Rhipiduridae*), and the deeper narrower bills among those that glean fruit (e.g. *Oriolidae* and *Paradisaeidae*).

A key message from the results of this analysis is that whereas morphology is generally a good predictor of broad ecological differences among species (Figure 6), ecological variables have limited ability to predict morphological variation (Table 2; Table S15; see also Felice et al., 2019; Miles & Ricklefs, 1984; Navalón et al., 2019).

These patterns are seemingly in contrast to the tight and reciprocal associations between ecology and morphology that have been shown among adaptive radiations, such as Darwin's finches and Hawaiian honeycreepers (Tokita, Yano, James, & Abzhanov, 2017). The coarse nature of the ecological character states may provide significant explanation for the lower explanatory power of the models using these variables to predict morphological variation (Felice et al., 2019). More refined ecological and morphological data that better reflect resource and substrate use are needed to further address this question. Although many morphological axes differ in their mean values between ecological character states, extensive morphological variation remains apparent within the individual character states (Figures S8–S15). As such, a range of different morphologies have evolved in response to the broad ecological strategies considered here. These findings are consistent with the concept of many-to-one mapping, in which a wide range of morphologies produce similar ecological functions (Bock, 1959; Bock & von Wahlert, 1965; Ricklefs & Miles, 1994; Wainwright et al., 2005). These trends have previously been noted in a number of different taxa, including the jaw morphology of labrid fish (Alfaro et al., 2005; Wainwright et al., 2005), and in the muscle size/hindlimb dimensions of *Anolis* lizards (Toro, Herrell & Irschick, 2004). Extensive variation of morphology among sets of taxa with similar ecologies may well represent a general feature among vertebrate groups.

Here we present evidence to support the interrelationship between ecological and morphological traits among a species-rich radiation of passerine birds, extending support for these correlations from the community to global scale. In many instances, morphological variability among corvid species is consistent with the presence of different selective optima between ecological strategies. Variation in body size broadly differentiates a number of ecologies; however, axes of shape variation are equally important in refining our capacity to accurately associate species to specific ecological character states. Despite statistical differences in the morphological values among ecological character states, these same character states are themselves weak predictors of morphological variation reflecting the diversity of morphological forms than can evolve in response to similar selection pressures. These results support the hypothesis that many-to-one mapping may represent a general feature of the relationship between ecology and morphology across the tree of life. Directly considering the functional role of morphological traits, and establishing their relationships with ecological characters should represent a primary aim of future eco-morphological analyses. In the absence of such assessment, we propose that the inclusion of multiple morphological traits and their associated axes of variation are warranted in analyses that aim to understand the accumulation of ecological diversity through time and space.

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## 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., P.Z.M., J.F. and C.R. interpreted the analyses and wrote the manuscript.

## DATA AVAILABILITY STATEMENT

The mean morphological measurements and ecological character states are provided in Table S2. The morphological measurements of individual specimens can be downloaded from the Dryad Digital Repository: <https://datadryad.org/stash/dataset/doi:10.5061/dryad.fbg79cncr6> (Kennedy, 2019).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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