RESEARCH PAPER

Effects of phylogeny and geography on ecomorphological traits in passerine bird clades

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Abstract

Aim: To compare phylogenetic effects with geographic effects across multiple clades of passerine birds to understand the roles of evolutionary history and geographic patterns on the ecomorphological characteristics of species.

Location: Global.

Methods: We combine phylogenetic and geographic approaches to investigate and compare their effects on patterns of ecomorphological distinctness, i.e. the relative position of species in multidimensional ecomorphological trait space. The trait space was based on measurements from preserved specimens, representing ecologically relevant morphological adaptations across almost 500 species in eight clades of the order Passeriformes.

Results: Ecomorphological distinctness increased with phylogenetic distance across species in all clades, whereas there was no significant relationship between geographic and ecomorphological distinctness in any clade. However, we observed a significant interaction between phylogenetic and geographic effects on ecomorphological distinctness. Closely related species were ecomorphologically indistinct if in geographic proximity, while at large geographic distances, there was no relationship between phylogenetic and ecomorphological distinctness.

Main conclusions: We conclude that phylogenetic relationships are influential in shaping ecomorphological traits in passerine bird clades, but that this effect depends on the geographic distributions of species. Closely related species were only ecomorphologically similar when geographically close, suggesting a signal of allopatric speciation. Our results imply that studies identifying phylogenetic effects in species' traits should not focus exclusively on these but instead evaluate the interaction of phylogenetic effects with geographic effects.

KEYWORDS
ecomorphological divergence, geographic distribution, morphological adaptations, Passeriformes, phylogenetic signal, trait evolution

1 | INTRODUCTION

It is well known that both phylogenetic history and geography shape the evolution and maintenance of morphological diversity in clades.

Recent studies have focused on the evolution of morphological diversity in relation to colonization of new habitats (Jønsson, Lessard, & Ricklefs, 2015; Ricklefs, 2012), as well as on morphological and phylogenetic diversity of species assemblages along

environmental gradients (Dehling et al., 2014; Graham & Fine, 2008). However, there is still a limited understanding of the strength of the effects of phylogenetic relationships and geographic distributions of species on the patterns of morphological diversity of species within a clade (Simões et al., 2016). The combination of phylogenetic and geographic effects on morphological diversity within a clade has rarely been explicitly tested, and never consistently across multiple taxonomic clades (e.g. Harmon, Schulte, Larson, & Losos, 2003; Ricklefs, 2004; Miller, Zanne, & Ricklefs, 2013; but see Lovette, Bermingham, & Ricklefs, 2002).

We address phylogenetic and geographic effects on the morphological diversity of clades by studying the ecomorphological distinctness of 491 species in eight avian clades. Ecomorphological approaches are valuable in describing the ecological niche of species as morphology often reflects species' ecology in terms of morphological adaptations to the environment (Karr & James, 1975; Ricklefs & Miles, 1994; Williams, 1995; Woodward, Winn, & Fish, 2006). We define ecomorphologically distinct species as those that have unusual or extreme trait combinations in comparison to other species within their clade (e.g. Maglianesi, Blüthgen, Böhning-Gaese, & Schleuning, 2014).

The distribution of ecomorphological traits within a clade is affected by the shared ancestry of closely related species that are often more morphologically similar than distantly related species (Losos, 2008). Hence, some phylogenetic effects on ecomorphological distinctness would be expected, signified by an increase in ecomorphological distinctness with greater phylogenetic distances between species, i.e. greater phylogenetic distinctness. As a consequence, a particularly steep increase in ecomorphological distinctness with phylogenetic distinctness is expected under phylogenetic niche conservatism with particularly high morphological similarity in closely related species (e.g. Ackerly, 2009). By contrast, small increases in ecomorphological distinctness with phylogenetic distinctness or no relationship between the two would be expected under a process, among others, of convergent evolution (e.g. Harmon, Kolbe, Cheverud, & Losos, 2005). In any case, the presence of some phylogenetic effect is expected even under simple evolutionary models such as Brownian motion, i.e. trait evolution resembling a random walk through time (Losos, 2008).

The geographic distribution of species within a clade may also influence ecomorphologial distinctness due to processes such as interspecific competition or allopatric speciation. If geographically overlapping species compete with each other, and if the degree of competition is correlated with similarity in ecomorphological traits, co-occurring (sympatric) species would be expected to be ecomorphologically more distant than geographically nonoverlapping (allopatric) species, to avoid interspecific competition (e.g. Davies, Meiri, Barraclough, & Gittleman, 2007; Rodríguez-Gironés & Santamaría, 2007). Alternatively, if allopatric speciation leaves a geographic signal on the ecomorphological diversity of species, species that are close in geographic space (allopatric or in secondary sympatry) would be expected to be ecomorphologically similar and phylogenetically close. Thereby one would expect phylogenetic and geographic effects to interact, as there should be a positive relationship among ecomorphological and phylogenetic distinctness for geographically close but not for geographically widely separated species (e.g. Cardillo & Warren, 2016).

It is still not clear how ecomorphological divergence (i.e. the evolution of ecomorphological distinctness) is connected to both the phylogenetic history and geographic distribution of species within clades (Simões et al., 2016), and whether one of these effects plays a more prominent role in shaping ecomorphological diversity than the other. Previous studies suggest that phylogenetic effects rarely influence the distribution of ecomorphological traits (Freckleton, Harvey, & Pagel, 2002; Harmon et al., 2010; Nyári & Reddy, 2013), yet some cases have been observed in which signatures of both evolutionary and geographic effects can be detected (e.g. *Anolis* lizards; Thorpe, Surget-Groba, & Johansson, 2008; Mahler, Revell, Glor, & Losos, 2010). Previous attempts to understand morphological diversity have not compared this combination of phylogenetic and geographic effects on ecomorphological traits consistently across different taxonomic clades (e.g. Harmon et al., 2003; Ricklefs, 2004; but see Lovette et al., 2002). Although inferring evolutionary processes from the ecomorphological diversity that they generate has proven difficult (Warren, Cardillo, Rosauer, & Bolnick, 2014), a comparative approach across multiple clades could test the consistency of these patterns.

We combine ecological and evolutionary approaches by testing how ecomorphological diversity of species within eight different avian clades is related to both the phylogenetic history and the geographic distributions of the species. If phylogenetic history leaves a signal on ecomorphological diversity, we expect that phylogenetically distinct species, i.e. more distantly related species are also ecomorphologically distinct. If competition leaves a signal on ecomorphological patterns, we expect that geographic distinctness (i.e. greater geographic distances between species distributions) is negatively related to ecomorphological distinctness (i.e. that more closely located species are more distant in ecomorphological space). Alternatively, if allopatric speciation leaves a signal on ecomorphological distinctness, we expect an interaction effect of geographic with phylogenetic distinctness. We address this question across eight avian clades that differ in phylogenetic age and geographic distribution, to assess whether patterns are general among different taxonomic groups. We compare radiations of similar species richness within one order, facilitating the comparison of patterns across the selected clades.

2 | MATERIALS AND METHODS

2.1 | Data preparation

We selected eight monophyletic clades across the order of passerine birds (Aves: Passeriformes) to test the influence of phylogenetic and geographic effects on the ecomorphological distinctness across species among and within the clades. Passerines have a relatively uniform morphology, which enables a better comparison of similar

structures across multiple families. Clades of different ages (between approximately nine and 24 million years) have been selected from different parts of the passerine tree, and constitute families or monophyletic subclades of families (Cardinalidae, Parulidae: *Setophaga-Myiothlypis* clade, Muscicapidae: *Oenanthe-Monticola* clade, Turdidae: genus *Turdus*, Hirundinidae, Vireonidae, Corvidae: genus *Corvus*, and Tyrannidae: Xolmiini clade; see Appendix S1 in Supporting Information for species lists and Appendix S2 for genera). These were chosen based on the following criteria: they must (a) have approximately the same number of species (see Appendix S1), (b) have high phylogenetic resolution, (c) represent a variety of feeding strategies and dietary guilds, and (d) show a considerable degree of morphological trait diversity within the clade. The clades have varying geographic distributions (Xolmiini, Vireonidae, *Setophaga-Myiothlypis*, and Cardinalidae: Americas; *Oenanthe-Monticola*: Asia, Africa, and Europe; Hirundinidae: Worldwide; *Corvus*: Worldwide except South America; *Turdus*: Worldwide except Australia). Species names follow IOC taxonomy v. 5.01 (Gill & Donsker, 2015; see Table S1.1 in Appendix S1 and supplementary methods in Appendix S2).

We quantified the ecomorphological traits of 491 species in these clades using nine morphological trait measurements (of the beak, wings, tail, and tarsi) of preserved specimens. The selected measurements are closely related to specific ecological niche dimensions such as diet and foraging behaviour (e.g. Grant & Grant, 2006; Jønsson et al., 2012), aerial movement and dispersal distance (e.g. Calmaestra & Moreno, 2000; Dawideit, Phillimore, Laube, Leisler, & Böhning-Gaese, 2009), as well as bipedal locomotion (e.g. Fitzpatrick, 1985), and can thus be used to reflect ecomorphological relationships (e.g. Ricklefs, 2012; Winkler & Leisler, 1992). We measured morphological traits of 2,465 preserved specimens belonging to 491 species of the total 526 species described in the eight clades from four museum collections (Table S1.1 in Appendix S1). We only took trait data from adult individuals and aimed to measure two females and two males of each species. The methodology largely followed Eck et al. (2011) except for bill dimensions (see supplementary methods in Appendix S2 for full description). We additionally measured any available morphologically distinct subspecies to account for intraspecific variation. In many cases, we therefore obtained data from more than four individuals per species (average number of individuals per species = 5.03, min = 1, max = 29). To account for variation in body sizes across all clades, the body mass of each species was included as the tenth variable in analyses, obtained from a public database (Wilman et al., 2014).

Prior to analysis, measured values for each trait were averaged across all specimens in each species irrespective of sex. We checked that within-species trait variation was lower than the variation between species (data not shown). Where available, trait data for morphologically distinct subspecies were included unweighted in the overall species average. Species averages were log-transformed, then standardised to a mean of 0 and a standard deviation of 1. To reduce dimensionality, species ecomorphological trait averages and body mass were subjected to a combined principal components analysis (PCA). Ecomorphological trait space was characterised using PC1 and PC2 as these axes represented 94.2% of the explained variance in our data (Table S2.2 in Appendix S2). The trait space included all eight clades to ensure comparability, but analyses of distinctness were conducted within each clade separately. To directly determine the effect of phylogenetic distinctness of a species on its position in ecomorphological trait space, we obtained dated phylogenies from birdtree.org (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) and created consensus trees for each clade (1,000 trees per clade, 25% burn-in removed, 95% maximum clade credibility) using TreeAnnotator, enabled in BEAST 1.8 (Drummond, Suchard, Xie, & Rambaut, 2012). Geographic data of breeding ranges were obtained for all species of all clades (Holt et al., 2013) to determine the effect of geographic distances and overlap among species.

2.2 | Distinctness quantification

To determine the phylogenetic and geographic effects on ecomorphological distinctness, we calculated average distinctness values for each species across all species pairs within the clade in ecomorphological trait space (mean ecomorphological distinctness, MED), on the phylogeny (mean phylogenetic distinctness, MPD), and in geographic space (mean geographic distinctness, MGD). We also calculated the distances between nearest neighbour pairs in ecomorphological trait space (nearest neighbour ecomorphological distance, NNED) and the phylogenetic and geographic distances between these pairs (nearest neighbour phylogenetic distance, NNPD, and nearest neighbour geographic distance, NNGD).

Ecomorphological distinctness for each species was measured as the mean pairwise ecomorphological distance (MED) to all other species within the clade in trait space, where a greater value indicates greater distinctness (Laliberté & Legendre, 2010). This measure was chosen over morphological "originality" of each species (distance to the centroid) as we wanted to determine the ecomorphological position of each species relative to all other species of the clade rather than to a mean clade value. Ecomorphological distances between nearest neighbours in trait space (NNED) were calculated by extracting the shortest distance to a neighbouring species within the same clade from the pairwise ecomorphological distance matrix for each species (see Dehling et al., 2014).

Pairwise phylogenetic distances were calculated between all possible species pairs for each clade. Using these distances, we calculated the mean phylogenetic distance (MPD) between species pairs, where a greater mean distance indicates greater distinctness (Webb, Ackerly, McPeek, & Donoghue, 2002). We also calculated the phylogenetic distance between each nearest ecomorphological neighbour pair (NNPD). We consider these methods more relevant to our objective than the phylomorphospace approach (Revell, 2012; Sidlauskas, 2008), as we wanted to quantify phylogenetic signal rather than control for it.

The geographic range data were used to address the degree of range overlap between species within a clade (Cardillo & Warren, 2016). Across all species pairs, the mean of pairwise geographic distances between each of the grid cells of one species' breeding range

to all grid cells of another species' breeding range was calculated to obtain a value of mean geographic distinctness (MGD) for each species, where a greater mean distance indicates greater distinctness. MGD values were log-transformed, as we observed a large variation in the scale of MGD within and between the clades. Using the pairwise distance matrices, we additionally extracted the geographic distance between nearest ecomorphological neighbour pairs (NNGD), which were also log-transformed.

2.3 | Statistical analyses

We tested five different methods to determine the phylogenetic effect on the patterns of ecomorphological distinctness in trait space: (a) Mixed-effects models between ecomorphological and phylogenetic distinctness values across all species in all clades; (b) regressions of the same relationship within each clade; (c) mixed-effects models equivalent to (a) across all nearest neighbour distances in all clades, (d) regressions of the same relationship across nearest neighbour distances within clades; and (v) phylogenetic signal of MED within clades (λ; Pagel, 1999). These methods test for a phylogenetic effect against different null models: (a) and (c) no phylogenetic effect (slope estimate of zero) in the mixed-effects models (for MED and NNED); (b) and (d) a random-shuffle null model (i.e. random shuffling of species' identities across the tips of the phylogeny) to account for the topology of the phylogenetic tree in regression analyses within clades (for MED and NNED); (v) two null models, the random-shuffle model and a Brownian motion process of trait evolution (random walk of evolution), in phylogenetic signal analyses (for MED only).

Mixed-effects models were fitted across all species in all eight clades, where MED was the response variable and MPD the fixed variable. We allowed random slopes and intercepts for each clade, to model clade variation in relationships between ecomorphological and phylogenetic distinctness. We ran equivalent models between NNED and NNPD values to further determine the phylogenetic effect on ecomorphological distances between nearest neighbours. To assess whether clades significantly differed in their relationships of ecomorphological to phylogenetic distinctness, the mixed-effects models across all clades (for MED and NNED) were also fitted with clade as a fixed effect and the interaction of clade with the phylogenetic predictor variable. In addition, regression models within clades tested the phylogenetic effect on ecomorphological distinctness in each clade separately against the random-shuffle null model (for MED and NNED). As a more conventional measure of the phylogenetic pattern in trait values across species, the phylogenetic signal metric λ was calculated to distinguish the observed phylogenetic pattern from both a random phylogenetic distribution and from the distribution expected under a Brownian motion process of trait evolution.

To determine the effect of geographic distinctness on the patterns of ecomorphological distinctness, we used the equivalent methods (a)-(d) for geographic distributions of species with the same null models. We tested for significant differences between clades in these models as described above for the phylogenetic mixed-effects models.

Furthermore, we used two methods to test the relative strengths of phylogenetic and geographic effects on ecomorphological distinctness. Firstly, we constructed a mixed-effects model with both phylogenetic and geographic distinctness as fixed effects across all species in all clades. We constructed an equivalent model for nearest ecomorphological neighbour distances with both the phylogenetic and geographic distances of nearest ecomorphological neighbours as fixed effects across all clades. Both models additionally assessed whether the phylogenetic variable significantly differed in its relationship of the ecomorphological distinctness with the geographic variable by including an interaction of MPD with MGD, and NNPD with NNGD. Secondly, we inferred the relative contributions of phylogenetic and geographic distinctness to the ecomorphological distinctness of species within each clade using the method described by Freckleton and Jetz (2009). While our mixed-effects model simply looks for a relationship between observed ecomorphological and phylogenetic or geographic patterns, Freckleton and Jetz's method does not estimate interaction effects. Instead it uses an a Brownian motion model of trait evolution as the null model (λ-statistic; Pagel, 1999; Freckleton et al., 2002) to estimate the phylogenetic and geographic effects in each clade by directly incorporating a variance-covariance matrix for the phylogenetic relationships and a pairwise distance matrix for geographic ranges of species. The values of the geographic distance matrix were first log-transformed, and then standardised to range between 0 and 1. This method estimates three parameters, which represent the relative contributions of phylogenetic effects (λ'), geographic effects (φ) as well as unexplained effects (γ) that are independent of phylogenetic and geographic effects.

3 | RESULTS

The constructed ecomorphological trait space represents the position of each species relative to all others in the clade based on their ecomorphological traits, and the arrangement of all eight clades in this trait space relative to each other (Figure 1). Factor loadings indicated that all variables were approximately equally important for PC1; this axis therefore represented a proxy of overall body size (representing 82.6% of the variation, Table S2.2, S2.3 in Appendix S2). PC2 represented wing shape and tarsus length (explaining 11.6% of the variation, Figure 1, Table S2.3). The PC scores on these two axes were used to characterize the ecomorphological trait space of the species (see Methods; Figure 1).

3.1 | Phylogenetic and geographic effects on ecomorphological distinctness

The mixed-effects model across all species in all clades showed a significant positive relationship between ecomorphological and phylogenetic distinctness, meaning ecomorphological distinctness increased with phylogenetic distance between species (Table 1, Figure 2a). Clade never significantly affected the other fixed effects when tested as a fixed effect with interaction term (with MPD, MGD,
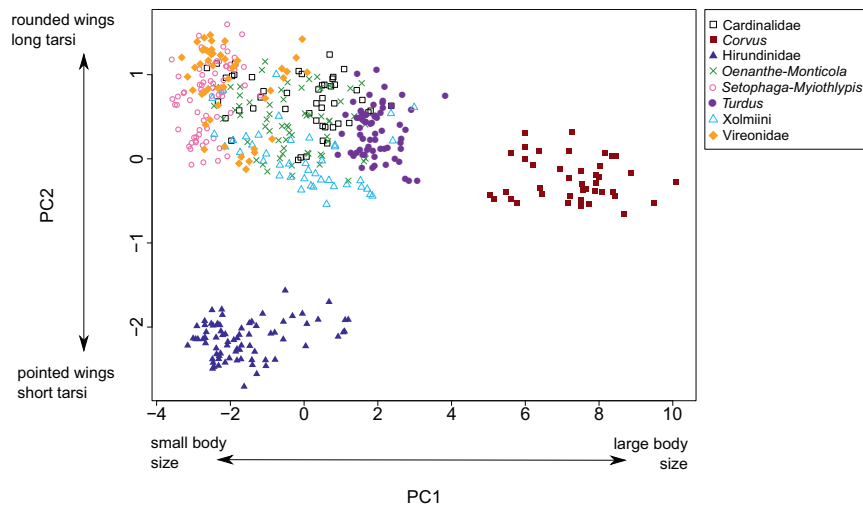
FIGURE 1 The ecomorphological distribution of 491 species in eight monophyletic clades (Cardinalidae, *Corvus*, Hirundinidae, *Oenanthe-Monticola* clade, *Setophaga-Myiothlypis* clade, *Turdus*, Xolmiini clade and Vireonidae), indicated by coloured symbols. The PCA was run across species averages of ten traits: nine ecomorphological measurements (wing length and pointedness (measured as Kipp's distance); bill length, width and height; tail length; tarsus length, as well as sagittal and distal tarsal diameters) and body mass. Higher scores for PC1 were associated with larger body size, while lower scores were associated with smaller body size. PC2 represented wing shape and tarsus length, where high scores for PC2 were associated with rounded wings (i.e. smaller Kipp's distance) and longer tarsi, while lower scores indicated pointed wings (i.e. higher Kipp's distance) and shorter tarsi

NNPD or NNGD; Table S2.4 in Appendix S2), therefore we controlled for clade as a random effect in the main models presented here (Table 1). Regressions within clades showed an overall positive trend between ecomorphological and phylogenetic distinctness, but significance compared to the random-shuffle null model varied across clades (Table 2, Figure 2a). Ecomorphologically distinct species were significantly distant on the phylogeny in *Oenanthe-Monticola* and allies (Muscicapidae), Xolmiini (Tyrannidae) and Vireonidae. The explanatory power in these models was weak, with most clades having $R^2 < 0.1$ values. We estimated Pagel's λ of ecomorphological distinctness as a direct measure for phylogenetic signal, and found some variation of phylogenetic signal among the clades. Pagel's λ was significantly higher than expected from the random-shuffle null model in all but two clades, but only significantly different from the Brownian motion null model in four clades (Table 2).

In contrast to ecomorphological distinctness, the ecomorphological distance between nearest ecomorphological neighbours was not explained by their phylogenetic distances across clades (mixed-effects model, Table 1), though we found a significant negative relationship of NNED and NNPD between species pairs in one of the within-clade models (Xolmiini, Table 2). This implies that nearest ecomorphological neighbours in Xolmiini, which are separated by small distances in trait space, are more distantly related on the phylogeny than expected under the random-shuffle null model.

We compared the ecomorphological distinctness of species across all clades with their geographic distinctness in a mixed-effects model to infer the geographic effects on species' distributions in ecomorphological space and found a negative, but nonsignificant relationship (Table 1, Figure 2b). Furthermore, we found no significant differences in the relationships among clades (Table S2.4,

Figure 2b). Clade-level regressions of ecomorphological and geographic distinctness showed an apparently greater variation in slopes among clades than we observed between ecomorphological and phylogenetic distinctness. None of these slopes significantly differed from expectations under the random-shuffle null model (Table 2, Figure 2b). The explanatory power in these models was weak, with most clades having $R^2 < 0.1$ values. Similarly, the distance between nearest ecomorphological neighbours could not be explained by geographic distances between these species pairs within or across clades, supporting our other findings (mixed-effects model across clades in Table 1, within-clade regressions in Table 2).

3.2 | Combined effects of phylogeny and geography

The mixed-effects model investigating the combined effects of phylogenetic and geographic distinctness on ecomorphological distinctness across clades showed positive phylogenetic and geographic effects on ecomorphological distinctness, and also a significant negative interaction effect between these fixed effects (Table 1). The geographic effect on ecomorphological distinctness was only significant in the interaction with phylogenetic distinctness, where the relationship between ecomorphological and phylogenetic distinctness was positive only at low values of geographic distinctness, but nonexistent at high values (Figure 3). In the combined mixed-effects model for NNED, neither phylogenetic nor geographic distances between nearest ecomorphological neighbour pairs significantly influenced their distance in ecomorphological trait space, nor did we observe a significant interaction effect between NNPD and NNGD (Table 1).

TABLE 1 Results of mixed-effects models across all species of all clades testing the relationships of mean ecomorphological distinctness (MED) against mean phylogenetic distinctness (MPD) and mean geographic distinctness (MGD) separately and in combination, and the same models for nearest neighbour ecomorphological distances (NNED) against their phylogenetic (NNPD) and geographic distances (NNGD). Combined models include a test for an interaction between the phylogenetic and geographic variables (indicated by *). Number of species analysed in each model are indicated by *n*. Mixed-effects models detail the overall slope estimate, its *t*-value, degrees of freedom (d.f.), and its significance (*p*); the estimated variation in slopes among clades (var, random effect); and goodness of fit of the model to the data (conditional R^2)

	n	Estimate	*t*	d.f.	*p*	var	R^2
MPD	456	0.045	4.006	5.899	0.007[a]	<0.001	0.676
MGD	453	−0.141	−0.640	9.299	0.537	0.003	0.476
NNPD	456	−0.001	−1.564	2.944	0.218	<0.001	0.115
NNGD	453	<−0.001	−0.192	302.100	0.848	<0.001	0.098
Combined effects of							
MPD	451	0.443	2.997	35.170	0.005[a]	<0.001	0.580
MGD		1.076	2.640	31.270	0.013[a]	0.076	
MPD*MGD		−0.047	−2.752	34.510	0.009[a]		
Combined effects of							
NNPD	451	−0.003	−1.479	6.860	0.144	<0.001	0.113
NNGD		−0.003	−0.725	32.630	0.469	<0.001	
NNPD*NNGD		<0.001	0.813	31.730	0.417		

[a]$p < 0.05$.

The results from partitioning the variance in ecomorphological distinctness across species into phylogenetic and geographic effects corroborated these results, but also showed a general pattern of decreasing phylogenetic effects with decreasing taxonomic level (i.e. from family to subclade to genus level; Figure 4). In most clades, ecomorphological distinctness seemed to be heavily influenced by phylogenetic effects (λ'), while there were substantial unknown effects (γ), which were independent of phylogenetic and geographic effects (Table S2.5 in Appendix S2). This relationship was not observed in *Turdus*, in which ecomorphological distinctness was explained completely by independent effects (γ). We observed no direct geographic effect in any of our clades (Figure 4).

4 | DISCUSSION

The objective of this study was to test the effects of phylogenetic and geographic distance on distances in ecomorphological trait space of species within and across eight clades of Passerines. Effects of phylogenetic and geographic distinctness were not independent of each other, and the significance of the geographic effect on ecomorphological diversity was influenced by the phylogenetic distinctness of species. When testing phylogenetic and geographic effects separately across species in the eight individual clades we observed consistent phylogenetic effects on ecomorphological distinctness, but no direct geographic effects. These patterns across clades were fairly homogeneous despite having selected clades of different phylogenetic ages and geographic distribution patterns, with no significant differences among clades. Significant effects were only observed for MED, not nearest neighbour ecomorphological distance, so the

described effects are not entirely consistent down to the level of species pairs that are closest in ecomorphological trait space.

While phylogenetic effects were more influential than geographic effects in shaping the traits of species across clades, these effects depended on the geographic distribution of species. In close geographic proximity, closely related species were also closer in ecomorphological trait space (i.e. there was a significant positive relationship between ecomorphological distinctness and phylogenetic distinctness). In contrast, when species were not in geographic proximity, this relationship was not observed. Close geographic proximity in our case does not distinguish whether species ranges are completely, partly or not overlapping, so geographically close species could be sympatric (i.e. coexisting in the same geographic area) or allopatric (i.e. occurring in separate, nonoverlapping geographic areas). If sympatric species compete, a negative relationship between geographic distance and ecomorphological distinctness is expected (Dayan & Simberloff, 2005). We found instead that geographic distance modified phylogenetic effects on ecomorphological distinctness, which could suggest that these patterns have been shaped by a process of allopatric speciation. Under such a scenario, comparatively recently split species would still be ecomorphologically relatively similar due to a lack of competitive effects on ecomorphological divergence (Pigot & Tobias, 2013; Price, 2008).

Similar to findings in another single clade of birds (Tobias et al., 2014), we found that when species were not in geographic proximity (i.e. had clearly separated ranges) both distant and close relatives could be ecomorphologically similar. This pattern could be driven by a mix of processes, including ecological and geographic opportunity. The geographic separation of species may allow these to diversify in traits after they enter a new habitat with no ecological limits to
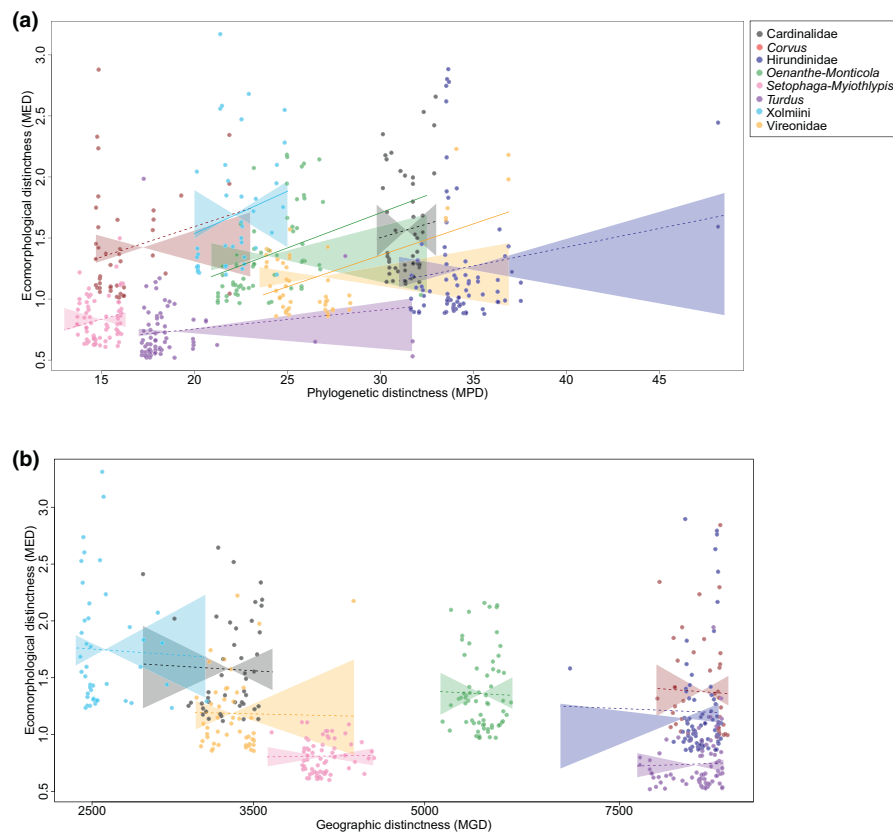
FIGURE 2 Mixed-effects models across all species with random slopes and intercepts for each clade, for ecomorphological distinctness (MED, the mean pairwise distance of a species to all other species in the same clade measured in the trait space shown in Figure 1) as response variable, and for the fixed effects (a) phylogenetic distinctness (MPD, the mean pairwise phylogenetic distance to species in the same clade measured in million years) and (b) geographic distinctness (MGD, the mean pairwise geographic distance to species in the same clade measured in km and log-transformed). Both models incorporated clade allocation as the random effect. Each clade is shown in a different colour, where each point represents one species. Observed slopes for each clade are from the model across clades; they are shown as solid if the correlations were significant in the linear regressions of the individual clade, and as dashed if not. Additionally we show 95% confidence intervals derived from a null model for each clade (shaded polygons; random shuffling of phylogenetic (a) and geographic (b) distinctness values across the entire clade)

diversity (ecological opportunity; Wiens, 2011), so that they may become dissimilar to their geographically remote relatives; or they may maintain their traits as they would be released from congeneric competition (geographic opportunity; Simões et al., 2016). These patterns have been observed in the Caribbean Anoles, where distantly related species living in allopatry have developed remarkably similar traits (Harmon et al., 2005; Mahler et al., 2010). These species show a decrease in adaptive differentiation among islands, following initial increases in disparity through the availability of ecological opportunities.

The nonindependence of phylogenetic and geographic effects affecting the distribution of species in trait space shows that the phylogenetic pattern in morphological diversity cannot be interpreted accurately without also considering the geographic proximity of species. The importance of jointly investigating phylogenetic and geographic influences on species' traits is also emphasized by Freckleton and Jetz (2009), who show that traits often exhibit both phylogenetic and spatial structures. While their combined influences on

speciation rates and diversification patterns have frequently been considered (Barrera-Guzmán, Milá, Sánchez-González, & Navarro-Sigüenza, 2012; Graham, Ron, Santos, Schneider, & Moritz, 2004; Mittelbach & Schemske, 2015; Near & Benard, 2004), few studies have synthesized these approaches in relation to morphological variation (Harmon, Melville, Larson, & Losos, 2008; Velasco et al., 2016). Of the studies that have considered the influence of both historical and spatial data, some also find an influence of geography on morphological evolution (e.g. Harmon et al., 2008). Therefore, especially when studying groups of species, their geographic distributions should be controlled for, particularly for sympatric species.

When testing the phylogenetic effects without consideration of the influence of geography on these patterns, we found consistent effects on ecomorphological distinctness across all species in all clades, but the strength of these effects within clades appeared to be quite variable. Due to the influence of geography on the phylogenetic effect on ecomorphological distinctness, it is difficult to interpret these results without also considering the contribution of geographic

TABLE 2 Results of separate linear regression models for each clade of mean pairwise ecomorphological distance (MED) against mean pairwise phylogenetic distance (MPD) and mean pairwise geographic distance (MGD), and the same models for nearest neighbour ecomorphological distances (NNED) against their phylogenetic (NNPD) and geographic distances (NNGD). This shows test results against the random-shuffle null model, and the phylogenetic signal in MED tested against the random-shuffle and the Brownian motion null model. Number of species analysed in each clade are indicated by n. The phylogenetic signal of each group (λ) is shown with significance of λ compared to two null models: no phylogenetic signal, i.e. random shuffling of species on tree p(λ = 0); and phylogenetic signal in accordance with Brownian motion process p(λ = 1). For regression models, each section details the estimated slope; significance of phylogenetic/geographic isolation compared to the random-shuffle null model (p.null); and goodness of fit of the regression model to the data (R^2)

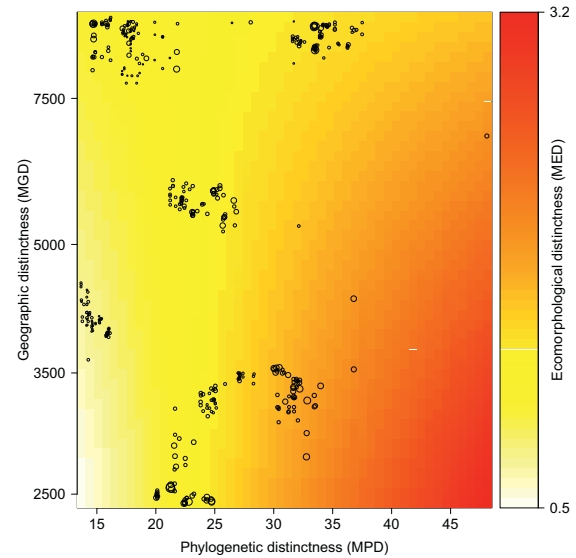| | Phylogenetic effects | | | | | | | | | | Geographic effects | | | | | | |
| | Phylogenetic signal | | | | MPD | | | NNPD | | | MGD | | | | NNGD | | |
	n	λ	p(λ = 0)	p(λ = 1)	Slope	p.null	R^2	Slope	p.null	R^2	n	Slope	p.null	R^2	Slope	p.null	R^2
Cardinalidae	48	0.906	<0.001*	0.549	0.076	0.180	0.019	0.001	0.170	0.018	45	0.517	0.347	0.004	−0.008	0.154	0.027
Corvus	41	0.375	0.359	0.069	0.037	0.106	0.039	−0.006	0.083	0.057	42	−1.578	0.150	0.026	−0.001	0.427	0.001
Hirundinidae	78	0.938	<0.001*	0.247	0.034	0.077	0.033	−0.001	0.220	0.008	79	0.441	0.395	0.001	0.001	0.332	0.002
Oenanthe	62	0.781	<0.001*	<0.001*	0.075	<0.001*	0.185	−0.001	0.260	0.007	65	−0.196	0.420	0.004	0.005	0.228	0.010
Setophaga	69	0.618	0.015*	0.011*	0.033	0.125	0.012	0.001	0.361	0.003	64	0.166	0.344	0.002	0.001	0.378	0.001
Turdus	67	0.000	>0.999	<0.001*	0.003	0.339	0.001	−0.003	0.149	0.015	68	0.812	0.074	0.033	−0.006	0.156	0.017
Xolmiini	42	0.840	0.005*	0.002*	0.101	0.032*	0.087	−0.004	0.036*	0.082	43	−1.345	0.148	0.025	0.003	0.427	0.002
Vireonidae	49	0.916	<0.001*	0.078	0.067	<0.001*	0.435	0.000	0.347	0.002	47	1.743	0.059	0.073	0.007	0.127	0.026

*$p < 0.05$.

FIGURE 3 Trend surface plot showing the interacting effects of phylogenetic and geographic distinctness on ecomorphological distinctness as estimated in the combined model across all species in the eight clades. Circles depict the position of the observed species data, and circle size corresponds to the level of observed ecomorphological distinctness. The colour surface shows the fitted relationship of ecomorphological distinctness (MED) with both phylogenetic (MPD) and geographic distinctness (MGD) across 451 species
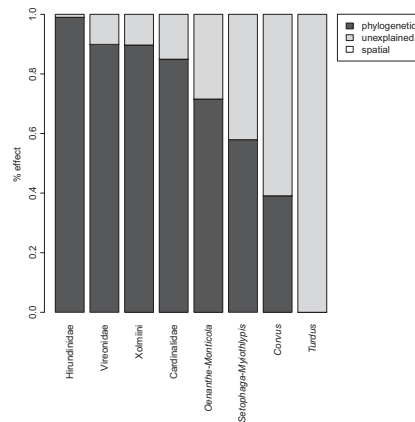

FIGURE 4 Partitioned contributions of phylogenetic, spatial and unexplained independent effects on the variance in ecomorphological distinctness of species within each clade. Variance was partitioned into phylogenetic (λ', dark grey), spatial (φ) and unexplained independent (γ, light grey) components. The results were ordered by the strength of the phylogenetic effect, and showed no spatial effect on ecomorphological distinctness in any of our clades

distribution. Although we observed consistently positive phylogenetic effects across clades overall, this variation in strength within clades could suggest that different processes influence patterns of ecomorphological distinctness to different degrees in each clade. Previous studies have distinguished between different phylogenetic patterns in morphological diversity, for example citing processes

such as phylogenetic niche conservatism or weaker evolutionary effects as having driven these patterns (Bravo, Remsen, & Brumfield, 2014; Hawkins, Diniz-Filho, Jaramillo, & Soeller, 2007; Miller et al., 2013). Other studies investigating species' occupation of niche space have come to similar conclusions, observing strong phylogenetic signal but no independent influential geographic signal (e.g. Miller et al., 2013; Verbruggen et al., 2009). Our finding of a significant interaction with geographic effects leads us to conclude that such results need to be evaluated with the geographic influences on phylogenetic patterns in morphological diversity taken into account (Pigot & Tobias, 2013). Due to lower statistical power we could not test the interaction between phylogenetic and geographic effects in the individual clades. Instead we tested individual null models within all clades. Mixed-effects models, regressions, phylogenetic signal, and variance partitioning each used different approaches to calculate the phylogenetic effect on ecomorphological distinctness. However, the different approaches across clades agree on strong phylogenetic and weak or no geographic effects, supporting our interpretations above despite observed variation in within-clade results, which may also be caused simply by the lower sample size within clades.

Geographic distinctness of species within clades had no direct effect on patterns of ecomorphological distinctness alone, but influenced the relationship between phylogenetic and ecomorphological distinctness. Our results suggest that the geographic signal on its own is either completely absent or has not been preserved within these clades. No geographic signal of competition would be preserved if allopatric speciation with later sympatry is observed for ecomorphologically similar species (Cardillo & Warren, 2016; but see Pigot & Tobias, 2013). We therefore also lack evidence for direct competition effects in these clades, though competition might have played a role in secondary contact among closely related species. The lack of geographic signal may also be due to our measure of geographic distinctness, which is measured only at a broad geographic scale (i.e. the degree to which extent-of-occurrence range maps in general overlap). Variations in geographic scale have previously been suggested to influence patterns of species distributions and diversity, and may therefore also influence patterns of morphological diversity within clades (Cardillo & Warren, 2016; Graham & Fine, 2008). We observed no geographic signal at the relatively rough spatial grain (100 × 100 km grid cells) of the geographic ranges of our species, though some signal may be observed at smaller scales of habitat partitioning, which is beyond the spatial scale captured in our geographic distinctness measure. It is well known that phylogenetically close, ecomorphologically similar and competing bird species separate themselves across space much more finely, for example across different habitat types in the same region (e.g. *Sylvia* warblers in Mediterranean regions; Laube, Graham, & Böhning-Gaese, 2013 and references within), or across different canopy layers in the same forest (e.g. *Setophaga* warblers; MacArthur, 1958). Across clades, however, the interaction between geographic and phylogenetic effects implies that geographic effects are not independent from phylogenetic effects.

Our measure of ecomorphological divergence in trait space was based on ten traits, and was further reduced to the two main axes of the PCA. This may mask divergence in other traits, which may

have influenced the ecomorphological divergence of species (Maire, Grenouillet, Brosse, & Villéger, 2015), e.g. selective pressures associated with their habitat or climatic niche, competition with sympatric species of other clades, or other behavioural and morphological aspects (cf. Nyári & Reddy, 2013; Velasco et al., 2016). These were beyond the scope of this study but would be important to investigate in future analyses. As phylogenetic signal is known to be weaker in ecological traits than in morphological traits (Blomberg, Garland, & Ives, 2003; Böhning-Gaese & Oberrath, 1999; Freckleton et al., 2002), choosing ecomorphological traits in our comparative study across clades retained this phylogenetic signal of morphological traits, while still accounting for temporal or geographic variation of the ecological niche position of species.

Our study adds to scarce literature comparing patterns of trait distribution within and across clades (e.g. Harmon et al., 2010; Lovette et al., 2002), but contrasts to previous findings in that it suggests a homogeneous ecomorphological trait distribution pattern across clades despite different ages and geographic distributions of the eight clades. The ability of the models to detect a great amount of between-clade variation is reduced due to our limited number of clades. Nevertheless, as previous studies have often used studied a single clade, our analysis of eight independent clades therefore provides a broader inspection of the patterns of ecomorphological divergence. In previous studies, the rates of morphological evolution and speciation have both been shown to depend on clade age, where younger clades often show higher rates of morphological evolution than older clades (Harmon et al., 2010; Ricklefs, 2004). Thus, we expected to see variable ecomorphological distinctness patterns across clades with differing phylogenetic and geographic scales. This variation was not observed, despite selecting clades of similar species richness. Instead, clades in which relationships between ecomorphological and phylogenetic distinctness were statistically significant span different phylogenetic and geographic scales.

5 | CONCLUSIONS

In combining the patterns of morphological adaptations, phylogenetic relationships and geographic distributions of species, we were able to compare the roles of evolutionary history and geographic distribution of species in shaping trait diversity in clades. When comparing phylogenetic with geographic effects, the former appeared more important in determining distances between species in ecomorphological trait space. Our measure of geographic proximity did not appear to directly influence the ecomorphological distinctness of species in our clades. However, the geographic distance among species modified the relationship between ecomorphological and phylogenetic distinctness, which we interpret as a potential signal of allopatric speciation across clades; therefore, taking geography into account should become standard in future studies of trait divergence. We conclude that applying ecological community methods to monophyletic clades does not sufficiently capture the effects of some processes on trait divergence within clades, such as

interspecific competition. However, these methods can provide interesting insights into the interactions of trait evolution and geographic distributions of species and phylogenetic lineages.

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REFERENCES

Ackerly, D. D. (2009). Conservatism and diversification of plant functional traits: Evolutionary rates versus phylgoenetic signal. *Proceedings of the National Academy of Sciences USA*, *106*(Suppl), 19699–19706.

Barrera-Guzmán, A. O., Milá, B., Sánchez-González, L. A., & Navarro-Sigüenza, A. G. (2012). Speciation in an avian complex endemic to the mountains of Middle America (*Ergaticus*, Aves: Parulidae). *Molecular Phylogenetics and Evolution*, *62*, 907–920.

Blomberg, S. P., Garland, T. Jr, & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioural traits are more labile. *Evolution*, *57*, 717–745.

Böhning-Gaese, K., & Oberrath, R. (1999). Phylogenetic effects on morphological, life-history, behavioural and ecological traits of birds. *Evolutionary Ecology Research*, *1*, 347–364.

Bravo, G. A., Remsen, J. V., & Brumfield, R. T. (2014). Adaptive processes drive ecomorphological convergent evolution in antwrens (Thamnophilidae). *Evolution*, *68*, 2757–2774.

Calmaestra, R. G., & Moreno, E. (2000). Ecomorphological patterns related to migration: A comparative osteological study with passerines. *Journal of Zoology*, *252*, 495–501.

Cardillo, M., & Warren, D. L. (2016). Analysing patterns of spatial and niche overlap among species at multiple resolutions. *Global Ecology and Biogeography*, *25*, 951–963.

Davies, T. J., Meiri, S., Barraclough, T. G., & Gittleman, J. L. (2007). Species co-existence and character divergence across carnivores. *Ecology Lettres*, *10*, 146–152.

Dawideit, B. A., Phillimore, A. B., Laube, I., Leisler, B., & Böhning-Gaese, K. (2009). Ecomorphological predictors of natal dispersal distances in birds. *Journal of Animal Ecology*, *78*, 388–395.

Dayan, T., & Simberloff, D. (2005). Ecological and community-wide character displacement: The next generation. *Ecology Letters*, *8*, 875–894.

Dehling, D. M., Fritz, S. A., Töpfer, T., Päckert, M., Estler, P., Böhning-Gaese, K., & Schleuning, M. (2014). Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. *Ecography*, *37*, 1047–1055.

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973.

Eck, S., Fiebig, J., Fiedler, W., Heynen, I., Nicolai, B., Töpfer, T., ... Woog, F. (2011). *Measuring birds. Vögel vermessen*. Deutsche Ornithologen-Gesellschaft.

Fitzpatrick, J. W. (1985). Form, foraging behavior, and adaptive radiation in the Tyrannidae. *Ornithological Monographs*, *36*, 447–470.

Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: A test and review of evidence. *The American Naturalist*, *160*, 712–726.

Freckleton, R. P., & Jetz, W. (2009). Space versus phylogeny: Disentangling phylogenetic and spatial signals in comparative data. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 21–30.

Gill, F., & Donsker, D. (2015). IOC World Bird List (v 5.1). Retrieved from www.worldbirdnames.org/DOI-5/master_ioc_list_v5.1.xls

Graham, C. H., & Fine, P. V. A. (2008). Phylogenetic beta diversity: Linking ecological and evolutionary processes across space in time. *Ecology Letters*, *11*, 1265–1277.

Graham, C. H., Ron, S. R., Santos, J. C., Schneider, C. J., & Moritz, C. (2004). Integrating phylogenetics and environmental niche models to explore speciation mechanisms in Dendrobatid frogs. *Evolution*, *58*, 1781–1793.

Grant, P. R., & Grant, B. R. (2006). Evolution of character displacement in Darwin's finches. *Science*, *313*, 224–226.

Harmon, L. J., Kolbe, J. J., Cheverud, J. M., & Losos, J. B. (2005). Convergence and the multidimensional niche. *Evolution*, *59*, 409–421.

Harmon, L. J., Losos, J. B., Davies, T. J., Gillespie, R. G., Gittleman, J. L., Jennings, W. B., ... Mooers, A. O. (2010). Early bursts of body size and shape evolution are rare in comparative data. *Evolution*, *64*, 2385–2396.

Harmon, L. J., Melville, J., Larson, A., & Losos, J. B. (2008). The role of geography and ecological opportunity in the diversification of gay geckos (*Phelsuma*). *Systematic Biology*, *57*, 562–573.

Harmon, L. J., Schulte, J. A., Larson, A., & Losos, J. B. (2003). Tempo and mode of evolutionary radiation in iguanian lizards. *Science*, *301*, 961–964.

Hawkins, B. A., Diniz-Filho, J. A. F., Jaramillo, C. A., & Soeller, S. A. (2007). Climate, niche conservatism, and the global bird diversity gradient. *The American Naturalist*, *170*(Suppl), S16–S27.

Holt, B. G., Lessard, J.-P., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitrov, D., ... Rahbek, C. (2013). An update of Wallace's zoogeographic regions of the world. *Science*, *339*, 74–79.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*, 444–448.

Jønsson, K. A., Fabre, P.-H., Fritz, S. A., Etienne, R. S., Ricklefs, R. E., Jørgensen, T. B., & Irestedt, M. (2012). Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proceedings of the National Academy of Sciences USA*, *109*, 6620–6625.

Jønsson, K. A., Lessard, J.-P., & Ricklefs, R. E. (2015). The evolution of morphological diversity in continental assemblages of passerine birds. *Evolution*, *69*, 879–889.

Karr, J. R., & James, F. C. (1975). Eco-morphological configurations and convergent evolution in species and communities. In M. Cody & J. Diamond (Eds.), *Ecology and evolution of communities* (pp. 258–291). Cambridge, MA: Harvard University Press.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits: A distance-based framework for measuring from multiple traits functional diversity. *Ecology*, *91*, 299–305.

Laube, I., Graham, C., & Böhning-Gaese, K. (2013). Intra-generic species richness and dispersal ability interact to determine geographic ranges of birds. *Global Ecology and Biogeography*, *22*, 223–232.

Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, *11*, 995–1003.

Lovette, I. J., Bermingham, E., & Ricklefs, R. E. (2002). Clade-specific morphological diversification and adaptive radiation in Hawaiian

songbirds. *Proceedings of the Royal Society B: Biological Sciences*, *269*, 37–42.

MacArthur, R. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology*, *39*, 599–619.

Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant − Hummingbird networks in the neotropics. *Ecology*, *95*, 3325–3334.

Mahler, D. L., Revell, L. J., Glor, R. E., & Losos, J. B. (2010). Ecological opportunity and the rate of morphological evolution in the diversification of greater Antillean anoles. *Evolution*, *64*, 2731–2745.

Maire, E., Grenouillet, G., Brosse, S., & Villéger, S. (2015). How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Global Ecology and Biogeography*, *24*, 728–740.

Miller, E. T., Zanne, A. E., & Ricklefs, R. E. (2013). Niche conservatism constrains Australian honeyeater assemblages in stressful environments. *Ecology Letters*, *16*, 1186–1194.

Mittelbach, G. G., & Schemske, D. W. (2015). Ecological and evolutionary perspectives on community assembly. *Trends in Ecology & Evolution*, *30*, 241–247.

Near, T. J., & Benard, M. F. (2004). Rapid allopatric speciation in logperch darters (Percidae: *Percina*). *Evolution*, *58*, 2798–2808.

Nyári, Á. S., & Reddy, S. (2013). Comparative phyloclimatic analysis and evolution of ecological niches in the scimitar babblers (Aves: Timaliidae: *Pomatorhinus*). *PLoS ONE*, *8*, e55629.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*, 877–884.

Pigot, A. L., & Tobias, J. A. (2013). Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters*, *16*, 330–338.

Price, T. (2008). *Speciation in birds*. Greenwood Village: Roberts and Company.

Revell, L. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223.

Ricklefs, R. E. (2004). Cladogenesis and morphological diversification in passerine birds. *Nature*, *430*, 338–341.

Ricklefs, R. E. (2012). Species richness and morphological diversity of passerine birds. *Proceedings of the National Academy of Sciences USA*, *109*, 14482–14487.

Ricklefs, R. E., & Miles, D. B. (1994). Ecological and evolutionary inferences from morphology: An ecological perspective. In P. C. Wainwright, & S. M. Reilly (Eds.), *Ecological morphology* (pp. 13–41). Chicago, IL: The University of Chicago Press.

Rodríguez-Gironés, M. A., & Santamaría, L. (2007). Resource competition, character displacement, and the evolution of deep corolla tubes. *The American Naturalist*, *170*, 455–464.

Sidlauskas, B. (2008). Continuous and arrested morphological diversification in sister clades of characiform fishes: A phylomorphospace approach. *Evolution*, *62*, 3135–3156.

Simões, M., Breitkreuz, L., Alvarado, M., Baca, S., Cooper, J. C., Heins, L., . . . Lieberman, B. S. (2016). The evolving theory of evolutionary radiations. *Trends in Ecology & Evolution*, *31*, 27–34.

Thorpe, R. S., Surget-Groba, Y., & Johansson, H. (2008). The relative importance of ecology and geographic isolation for speciation in anoles. *Philosophical Transactions of the Royal Society B*, *363*, 3071–3081.

Tobias, J. A., Cornwallis, C. K., Derryberry, E. P., Claramunt, S., Brumfield, R. T., & Seddon, N. (2014). Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature*, *506*, 359–363.

Velasco, J. A., Martinez-Meyer, E., Flores-Villela, O., García, A., Algar, A. C., Köhler, G., & Daza, J. M. (2016). Climatic niche attributes and diversification in *Anolis* lizards. *Journal of Biogeography*, *43*, 134–144.

Verbruggen, H., Tyberghein, L., Pauly, K., Vlaeminck, C., Van Nieuwenhuyze, K., Kooistra, W. H. C. F., . . . de Clerck, O. (2009). Macroecology meets macroevolution: Evolutionary niche dynamics in the seaweed Halimeda. *Global Ecology and Biogeography*, *18*, 393–405.

Warren, D. L., Cardillo, M., Rosauer, D. F., & Bolnick, D. I. (2014). Mistaking geography for biology: Inferring processes from species distributions. *Trends in Ecology & Evolution*, *29*, 572–580.

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, *33*, 475–505.

Wiens, J. J. (2011). The causes of species richness patterns across space, time, and clades and the role of "ecological limits". *The Quarterly Review of Biology*, *86*, 75–96.

Williams, E. E. (1995). The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. In T. Dobzhansky, M. K. Hecht, & W. C. Steere (Eds.), *Evolutionary biology* (pp. 47–89). New York, NY: Springer US.

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Evolution*, *95*, 2027.

Winkler, H., & Leisler, B. (1992). On the ecomorphology of migrants. *Ibis*, *134*, 21–28.

Woodward, B. L., Winn, J. P., & Fish, F. E. (2006). Morphological specializations of baleen whales associated with hydrodynamic performance and ecological niche. *Journal of Morphology*, *267*, 1284–1294.

BIOSKETCH

Anna Phillips is a PhD student interested in vertebrate phylogeography and macroevolution. Her current work focuses on inferring ecological and evolutionary patterns and processes from trait distributions of avian species.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.