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The evolution of morphological diversity in continental assemblages of passerine birds

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Understanding geographic variation in the species richness and lineage composition of regional biotas is a long-standing goal in ecology. Why do some evolutionary lineages proliferate while others do not, and how do new colonists fit into an established fauna? Here, we analyze the morphological structure of assemblages of passerine birds in four biogeographic regions to examine the relative influence of colonization history and niche-based processes on continental communities of passerine birds. Using morphological traits related to habitat choice, foraging technique, and movement, we quantify the morphological spaces occupied by different groups of passerine birds. We further quantify morphological overlap between groups by multivariate discriminant analysis and null model analyses of trait dispersion. Finally, we use subclade disparity through time to assess the temporal component of morphological evolution. We find mixed support for the prediction, based on priority, that first colonizers constrain subsequent colonizers. Indeed, our results show that the assembly of continental communities is idiosyncratic with regards to the diversification of new clades and the filling of morphospace.

KEY WORDS: Coexistence, macroecology, macroevolution Passeriformes, priority effect.

A central goal in ecology is to understand the processes driving geographic patterns of species richness (Darwin 1859; Wallace 1876; Hillebrand 2004; Mittelbach et al. 2007). Colonization history and historical contingency, in general, might exert a strong influence on the contemporary composition of regional assemblages of species (Ricklefs and Schluter 1993; Chase 2003; Fukami et al. 2007; Fukami and Nakajima 2011). Accordingly, the representation of clades in regional communities could be strongly affected by the order in which clades have colonized a given region, such that initial colonization is associated with an advantage—a phenomenon known as a priority effect (Sutherland 1974; Cole 1983; Drake 1991; Chase 2003). However, new colonists to a region also might possess advantages that allow them to diversify at the expense of previously established groups (Simpson 1953; Givnish 1997; Schluter 2000; Lovette et al. 2002). Finally,

regional patterns of species richness might be determined solely by local conditions, such that the structure of species assemblages arises from niche-based processes (e.g., niche differentiation and environmental filtering, MacArthur and Levins 1967; Dayan and Simberloff 2005; Chase and Myers 2011; HilleRisLambers et al. 2012). Here, we investigate how spatio-temporal patterns of morphological diversity in continental passerine birds (Aves: Passeriformes) reflect the potential impacts of colonization history and niche-based processes in the assembly of continental avifaunas.

The geographic location and history of a region undoubtedly influences its occupation by major clades of organisms. Some clades have ancient roots within a region, whereas others appear as colonists after diversifying elsewhere (Moen et al. 2009). Whether a clade diversifies following colonization of a new geographic area is poorly understood. Although ecologists often

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assume that "niche saturation" constrains diversification ("ecological limit hypothesis"; Schluter and Grant 1984; Cornell and Lawton 1992; Ricklefs 2006; Phillimore and Price 2008; Rabosky and Lovette 2008; Rabosky 2009), direct evidence supporting this hypothesis is scarce (Ricklefs 2010, 2012; Wiens 2011). Moreover, few studies have investigated morphological diversification in a biogeographically explicit context (but see Mahler et al. 2010; Schenk et al. 2013).

The timing of colonization might determine the rate and direction of morphological evolution (Schenk et al. 2013). For example, the first clade to colonize a continent might fill much of the available niche space through adaptive radiation (Osborn 1902; Simpson 1953), constraining diversification of subsequent colonizers to ecological space left open by established clades, constituting "priority" or "pre-emptive" effects (Vanette and Fukami 2014). Accordingly, we would expect diversification of late-arriving clades to be slower and to minimize ecological overlap with resident species. Although ecological space is often difficult to quantify, the positions of passerine bird species in morphological space, based on measurements of the wings, legs, and bill, are directly related to diet, foraging substrate, and foraging movements (Ricklefs and Travis 1980; Miles and Ricklefs 1984; Grant 1986; Carrascal et al. 1990).

In this comparative biogeographic study, we quantify the degree of morphological differentiation among the four major passerine groups (basal oscines, suboscines, core Corvoidea, and Passerida; Barker et al. 2002, Ericson et al. 2002, Jønsson et al. 2011, Aggerbeck et al. 2014) in relation to the time of appearance of each group on several continents. To quantify morphological differentiation, we take three approaches. First, we examine the morphological space occupied, which we estimate by the standard deviations of species scores on each of seven principal components axes. Second, we use the reassignments of species into groups in a series of discriminant analyses to estimate the degree to which different groups overlap in morphological space. The greater the proportion of incorrectly reassigned species, the more a particular group overlaps others. Third, we combine multivariate statistics and null model analyses and ask whether morphological differentiation is greater than expected under a random draw from the global species pool, and a more geographically restricted regional species pool, for each passerine clade.

To quantify historical patterns of morphological disparity, we use a time-calibrated phylogeny for passerine birds and calculate morphological subclade disparity through time (DTT). Combining these analytical approaches, we ask: (1) to what degree has the morphological diversification of one passerine group influenced that of the others within a particular region? and (2) how might the early arrival and establishment of one group within a particular region have impacted the taxonomic and morphological diversification of subsequent arrivals?

Methods

MORPHOLOGICAL AND PHYLOGENETIC DATA

Our study draws on morphological data for 1579 species of passerine birds (deposited in Dryad) of which 1329 species (84%) occur in the four tropical continental regions. This constitutes morphological data for 620 (out of 2184 species, 28%) species from the Neotropics (excluding the Caribbean), 271 (out of 1176 species, 23%) species from the Afrotropics (excluding Madagascar), 240 (out of 952 species, 25%) species from the Orient (including the Greater Sunda Islands and the Philippines), and 239 (out of 857 species, 28%) species from Australasia (excluding New Zealand). The species used for the morphological analyses represent a broad selection of taxa covering 96% of families and 60% genera (for details see Ricklefs 2012). The characters examined (lengths of the wing, tail, tarsus, and middle toe, and the length, width, and depth of the culmen measured at the base) represent various aspects of morphological adaptation to differences in habitat use and foraging strategies (Miles and Ricklefs 1984; Miles et al. 1987; Ricklefs 2012).

A time-calibrated phylogeny for the 1579 measured passerine species was accessed on www.birdtree.org (Jetz et al. 2012) and included 620 species from the Neotropics (335 suboscine species, 262 passerid species, 23 core corvoid species), 271 species from the Afrotropics (220 passerid species, 49 core corvoid species, two suboscine species), 240 species from the Orient (182 passerid species, 46 core corvoid species, 12 suboscine species), and 239 species from Australasia (87 basal oscines, 61 passerid species, 90 core corvoid species, one suboscine species). The dataset included 225 species of core corvoids, 903 species of passerids, 368 species of suboscines, and 88 species of basal oscines globally, including the Holarctic region of the northern hemisphere. The phylogenetic hypothesis used for the analyses in this article is a supertree with placement of 66% of the species based on molecular data and placement of the remaining 34% of species based on current taxonomy (see Jetz et al. 2012). Although we rely on a complete phylogeny for birds, it is important to be aware that the underlying phylogenetic data are not perfect (Ricklefs and Pagel 2012). Because of this uncertainty in both phylogenetic placement and clade age, morphological variance may be poorly estimated in the downstream analyses.

DISCRIMINANT ANALYSES OF CONTEMPORARY MORPHOLOGICAL OVERLAP

First we compared passerine morphological diversification between the four passerine groups (basal oscines, suboscines, core Corvoidea, and Passerida) globally, based on a principal components analysis (PCA) calculated from the covariance matrix of seven log-transformed variables measured on all 1579 passerine bird species. Using the same PCA, we compared the

morphological diversification of the four passerine clades present in each of the four tropical continental regions (Neotropics, Afrotropics, Orient, and Australasia). The first principal component represented a general size axis accounting for 69–83% of the total variance, followed by component 2 (broad and deep beaks relative to short tails: 6–14% of total variance; Tables S1 and S2).

We then conducted another principal components analysis based on the 1316 species that occur in the four focal regions. We excluded swallows (Hirundinidae), which exhibit outlier morphology adapted to aerial foraging. The first principal component represented a general size axis accounting for 77% of the total variance (standard deviation = 0.387), followed by component 2 (broad and deep beaks relative to short tails: 8.3%; 0.127) and component 3 (long tarsi and toes relative to thin beaks: 6.5%; 0.112). The remaining components, representing about 8% of the variation in total, are associated with various shape axes, but do not have clear interpretations. We calculated an index to the overall morphological space occupied, which was the square root of the sum of the eigenvalues of the principal components, essentially a diagonal through the multivariate space. A separate index for shape only was calculated as the square root of the sum of eigenvalues 2 through 7. The standard error of the size and shape space indices is the standard error of the standard deviation (s), which is approximately $s/\mathrm{sqrt}[2(n-1)]$. For $n = 25, 50, 100, 200$, and 500, $1/\mathrm{sqrt}[2(n-1)] = 0.14, 0.10, 0.07, 0.05$, and 0.03 (Tables S3 and S4).

We conducted discriminant analyses (SAS Procedure DISCRIM) based on the seven principal component scores. The program returns a matrix of generalized squared distances between the centroids of each group and a reclassification of each species into one of the groups based on the posterior probability of membership in that group. The generalized squared distance between two groups is the square of the ratio of the Euclidean distance to the within-group standard deviation of species scores on the discriminant axis (Table S5).

NULL MODEL ANALYSES OF CONTEMPORARY MORPHOLOGICAL OVERLAP

Contemporary patterns of passerine morphological overlap were compared between the first group to colonize a region and all subsequent groups to colonize that region. First, we created a pairwise matrix of morphological distances between species. To do so, we averaged morphological values across specimens for each species. Then, we calculated pairwise distances in multivariate morphological space among all possible species pairs using Mahalanobis's (1936) descriptive statistic. The Mahalanobis distance accounts for the variance of each variable and the covariance between variables and therefore does not require prior transformation of the data beyond the initial log transformation. From this matrix, the distance between each species of group A (first

colonizers) to all species of group B (subsequent colonizers) was calculated. Morphological overlap was estimated as the median of all these pairwise distance values.

We quantified the deviation of the observed pattern of morphological overlap from a distribution of random values of morphological overlap created with a null model. The null model consisted of resampling morphological values only for the taxon of subsequent colonizers (B), while keeping the observed morphological values for the first colonizer taxon (A) constant among simulations. Such an approach was necessary to assess potential priority effects. That is, we were interested in testing whether the morphology of subsequent colonizers (taxon B) diverged significantly from first colonizers (taxon A) relative to a random draw of species (taxon B), *including those that do not occur* on the focal continent. Using this approach, one can determine whether morphological evolution in new colonizers (taxon B) resulted in divergence or convergence with respect to previous colonizers (taxon A). We used the New World as the regional species pool for the Neotropics and the Old World and Australasia as the regional species pool for the Afrotropics, the Orient, and Australasia. Observed values of morphological overlap (overlap$_{obs}$) between taxon pairs A and B were compared to 10,000 simulated values of morphological overlap (overlap$_{null}$) to assess statistical significance.

To enable comparisons among taxonomic groups and continents, the magnitude of the morphological deviation was quantified by calculating a standardized effect size (SES) of morphological overlap between each of the group comparisons. The SES of morphological overlap was obtained by subtracting the mean of null overlap values (overlap$_{null}$) from the observed value (overlap$_{obs}$) and dividing the difference by the standardized deviation of null overlap values (overlap$_{null}$). A similar approach has been employed in studies that quantify phylogenetic spacing (Webb et al. 2002), except that we replaced the phylogenetic distance matrix with a morphological distance matrix. SESs of morphological distances indicate significant divergence of morphologies when SES > 1.96 and significant convergence when SES < −1.96. We initially quantified SES of morphological distances using two different species pool definitions: all species in the world (global pool) and all species in either the New World or Old World (regional pools), depending on the location of the focal continent. Refining our definition of the species pool to include only species from regions adjacent to that of the focal region serves several purposes. First, a smaller species pool size often decreases the chance of committing a type I error in null model analyses (i.e., incorrect rejection of a true null hypothesis). Second, because of our focus on morphological evolution following colonization, the pool should include those species that most likely represent the sister lineages to those new colonizers. It is difficult to know exactly which lineages are sisters and we

assumed that they were best represented by the contemporary species in the taxon of interest from nearby continents. Both results are reported in Table S6 but we only discuss the results of the regional pools in the discussion. All null model analyses were conducted in R (R Development CoreTeam. 2013).

ANALYSES OF HISTORICAL MORPHOLOGICAL OVERLAP

Following Harmon et al. (2003), we calculated mean subclade DTT for principal component 1 (size) as well as for two shape metrics: (1) beak length/height ratio, which to some extent reflects foraging adaptation; and (2) wing length/tarsus length ratio, which to some extent reflects habitat and substrate adaptation. Disparity represents the proportion of the variance in a morphological variable that occurs among species within subclades. Thus, at the stem of a clade, where only a single lineage exists, all the variance is represented in the present-day descendants of that lineage and disparity is 1; at the present time, when each lineage is a single species, the disparity is 0.

We then generated DTT plots using the average squared Euclidean distances, which partition the contemporary morphological diversity among lineages existing at each time point during the history of the clade following Harmon et al. (2003). Observed morphological disparity among lineages was compared with expected disparity based on simulating (10,000 simulations) morphological characters evolving under a random walk on the phylogenetic tree (Harmon et al. 2003). The higher the value of this *relative* disparity, the greater the average morphological space occupied by subclades relative to the morphological disparity of the taxon as a whole, and the greater the morphological overlap between subclades. We also calculated the morphological disparity index (MDI), which quantifies the overall difference in relative disparity of a clade compared to the expectation under the Brownian motion null model, and the corresponding significance level following Harmon et al. (2003) and Slater et al. (2010). Negative MDI values indicate lower subclade disparity than expected under Brownian motion. All analyses were conducted in R using the packages APE (Paradis et al. 2004) and GEIGER (Harmon et al. 2008).

Results and Discussion
MORPHOLOGICAL SPACE AND SUBCLADE DTT

Upon entering a new region free of competitors, predators, and pathogens, a lineage might undergo rapid diversification with respect to number of species as well as to form and function (Simpson 1944; Nee et al. 1992; Foote 1994; Schluter 2000; Jønsson et al. 2012; Rabosky et al. 2014), although a recent meta-analysis across vertebrates and invertebrates found little evidence for relatively rapid morphological differentiation early

in the evolutionary histories of most clades (Harmon et al. 2010). Eventually, however, under the ecological limit and niche saturation hypotheses, one presumes that ecological space is filled and species diversification slows (Phillimore and Price 2008; Rabosky and Lovette 2008; Rabosky 2009).

Among the regional clades considered in this analysis, the logarithm of the number of species was positively correlated with age of arrival (Spearman rank $r_S = 0.81$, $P = 0.001$, $n = 12$) and negatively correlated with order of arrival within a region ($r_S = -0.80$, $P = 0.002$). However, because age and order also were correlated ($r_S = -0.87$, $P = 0.0003$), we cannot separate the effects of age and order on species richness.

With respect to morphological diversity, we assessed the importance of priority effects in shaping passerine bird assemblages by explicitly comparing coexisting clades of passerine birds while taking into account their differing evolutionary histories. Although phylogenies provide insights into temporal diversification patterns of lineages, a high level of uncertainty remains about the diversification process owing to potentially unknown variable rates of extinction across the tree (Rabosky 2010). Consequently, determining the sequential arrival of particular clades in particular regions depends to some degree on the assumption that extinction has been on average the same in all clades. Analyses of the morphological space occupied by each of the major passerine clades show that the Passerida appears to have produced nearly the variance in size (PC1) and shape (PC2) exhibited by passerine birds as a whole (Fig. 1). In contrast, core corvoid and suboscine passerine birds have filled only parts of the morphological space occupied by passerines. Basal oscines, which occur only in Australo-Papua, show the same size variance as all passerine birds but are more restricted on the shape axis (PC2).

The similarity of the passerine morphological spaces in the four regions is further indicated by the proportion of misclassified species in a discriminant analysis of the regional passerine avifaunas. The percentage of wrongly placed species varied from 72% (Neotropics) to 66% (Afrotropics), 61% (Orient), and 46% (Australasia). Not surprisingly, owing to its isolation, and to it being the likely region of origin of oscine passerines—Passeriformes to the exclusion of suboscines (Barker et al. 2002; Ericson et al. 2002), Australasia has the most distinctive passerine fauna, and the fewest misclassified species. Overall, however, 64% of passerines were misclassified to the wrong continental region. The generalized squared distances between regions, which are scaled by the within-region variances on the discriminant axis, averaged only 0.48 (range: 0.23 [Neotropics-Afrotropics] to 0.91 [Neotropics-Australasia]), again showing the considerable overlap among the morphological spaces on each continent (Table S5). These results are in line with the analysis of Ricklefs (2012) in showing that globally the four passerine groups greatly overlap in morphological space with a strong central tendency,
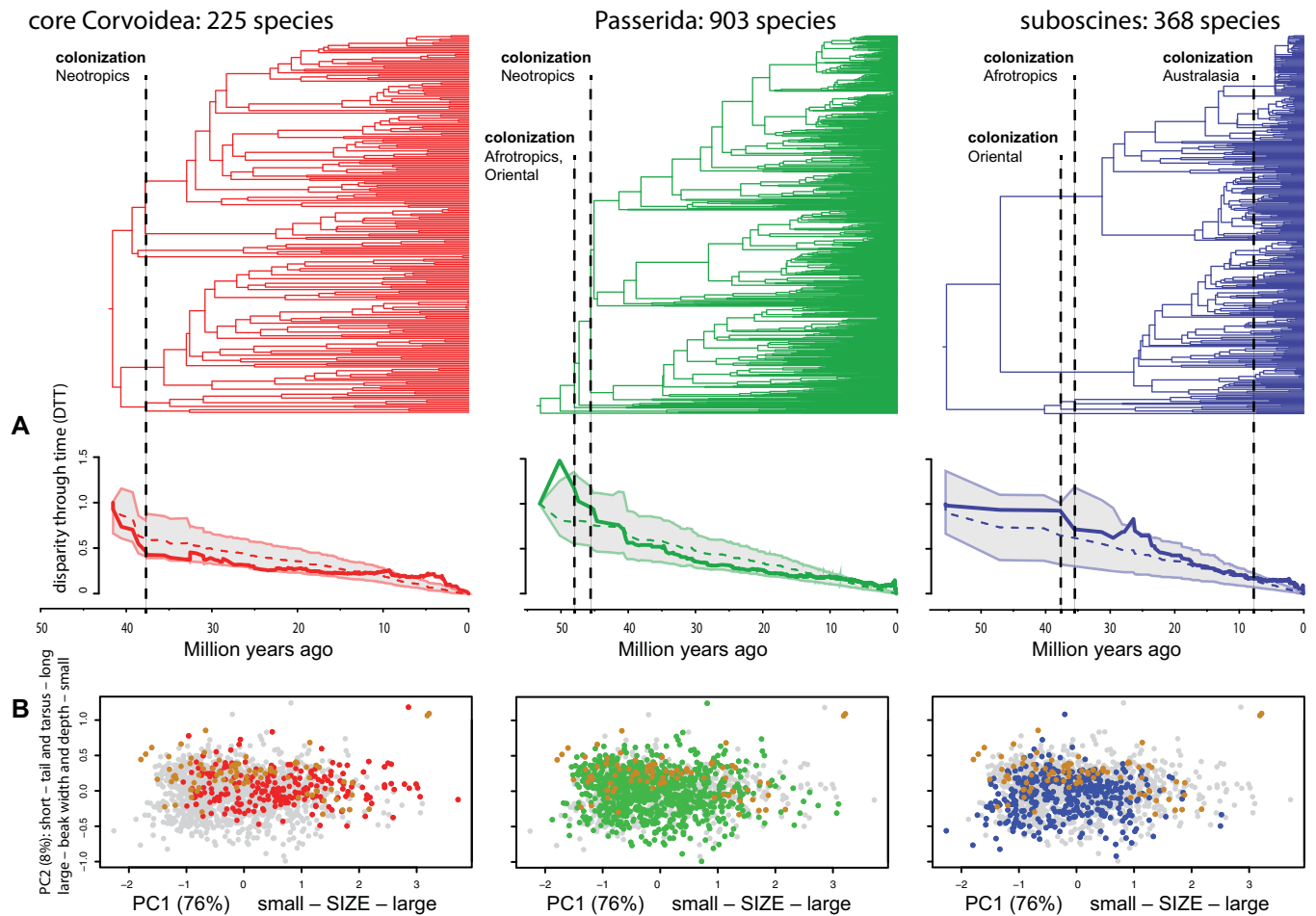
Figure 1. Phylogenies of the core Corvoidea (red), the Passerida (green), and suboscines (blue) including all taxa for which we have morphological measurements. (A) Disparity through time (DTT) plots of all seven PC axes combined. Average extant disparity at a given point in time is the average disparity of subclades whose ancestral lineages were present at that time relative to the disparity of the entire taxon. The dashed line indicates the median subclade DTT based on 10,000 simulations of character evolution on the phylogeny under Brownian motion. The shaded areas indicate the 95% DTT range for the simulated data. Vertical dashed lines indicate colonization of new regions. An early burst of morphological diversification would appear as a significantly low disparity value. (B) The morphological distribution on one size and one shape principal component axis against a background (light gray dots) of global passerine morphospace (*N* = 1579). Basal oscine passerines are indicated by brown dots on each of the panels.

but at the same time showing that each of the four passerine subgroups has only filled parts of the morphological space on a global level.

The principal components analysis further revealed that the morphological space occupied by passerine birds in each region is similar (Fig. 2, Tables S3, S4), although size variation in the Afrotropics (0.326) and the Neotropics (0.373) is reduced compared to the Orient (0.407) and, especially, Australasia (0.465). Shape variation is more similar across the regions (0.192–0.231). For all passerines, regardless of region, size variation (0.387) and shape variation (0.211) are no greater, on average, than within the individual regions, indicating that the passerine faunas of the regions overlap substantially in morphological space. Moreover, the major passerine clades occupy partially overlapping

morphological spaces. On a global scale, the misclassification rates average 0.54, ranging between 0.42 (core corvoids) and 0.66 (passerids). Within continents, the misclassification rates are lower, averaging 0.14 (Afrotropics and Orient) to 0.39 (Australasia) and 0.44 (Neotropics), suggesting that the different clades occupy divergent parts of the morphological space within each continent, and within clades between continents.

These results indicate that passerine birds have evolved in a similar fashion within each of the regions, allowing them to fill largely the same morphological space in different regions irrespective of timing, source of origin, and evolutionary history. In addition, the different passerine clades have maintained minimal overlap in morphological space. One possible explanation for this morphological conservatism is that because species and
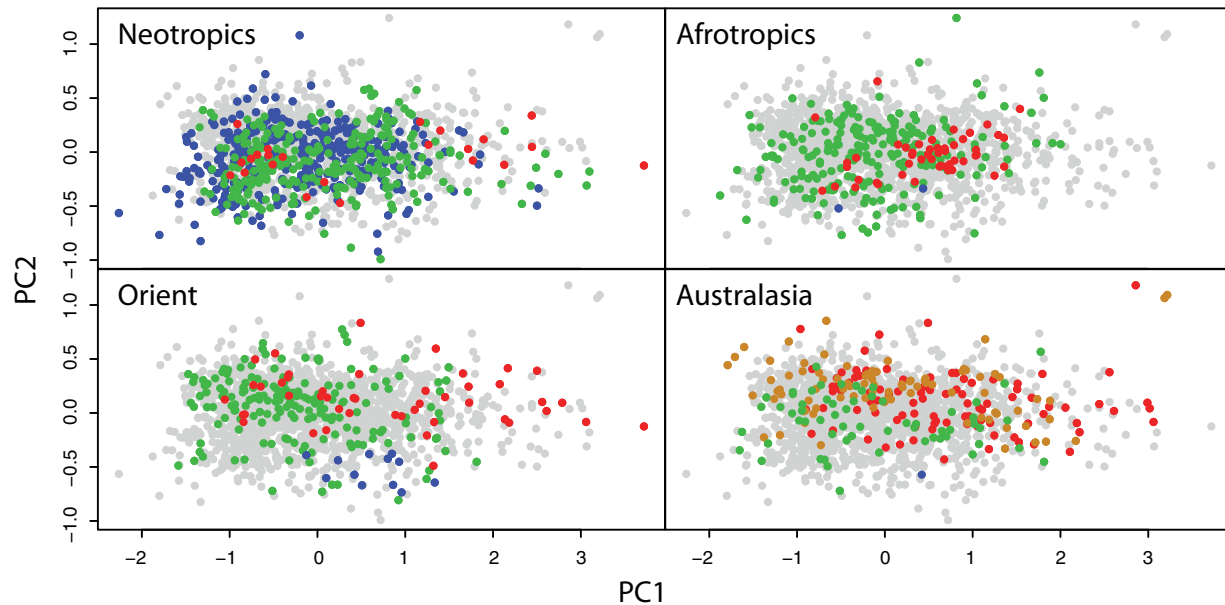
Figure 2. The morphological distribution on one size and one shape principal component axis against a background of the global passerine morphospace (*N* = 1579) for the four regions. Each colored (core Corvoidea = red, Passerida = green, suboscine = blue, basal oscine = brown) dot represents one species.

entire clades continuously replace each other through time (Foote et al. 2007; Quental and Marshall 2014) such regional replacements may lead to a similar replacement of species and clades in morphological space without leaving a signature of an early burst in morphological diversity, which would otherwise be expected for colonizers entering "empty" areas, such as newly emerged oceanic islands (Osborn 1902; Simpson 1953; Schluter 2000).

Subclade DTT using PC1 (size) for the three passerine bird groups globally does not deviate significantly from the median subclade DTT based on 10,000 simulations of character evolution on the phylogeny under Brownian motion (core Corvoidea: *P* = 0.14, Passerida: *P* = 0.4, suboscines: *P* = 0.2; Fig. 1). A similar general pattern is apparent within regions (Fig. 3). Thus, our data do not support an early burst of morphological evolution, which accords with a meta-analysis of 49 animal clades (size and shape), of which only two datasets (body size in *Varanus* lizards and body shape in pygopodid lizards) produced weak support for an early burst model (Harmon et al. 2010). Interestingly, when Harmon et al. (2010) analyzed body size evolution in combined trees, the data for birds as a whole supported the early burst model. Within regions, we find no consistent pattern related to a particular trait or to the order of colonization. In most cases, disparity does not deviate significantly from the simulated median subclade DTT. The few significant deviations are either concentrated toward the present, which may be caused by within-species variation and the magnification of minor measuring uncertainties on recent time scales, or are associated with an abrupt increase or decrease in disparity with the first split in the phylogeny, which depends

on whether this produced two clades with similar or different morphology. Consequently, principal components, discriminant function, and DTT analyses indicate that passerine birds have evolved to fill largely the same morphological space globally and regionally. At regional scales, the four taxonomic groups exhibit significant partitioning of morphological space, but the differences between taxa cannot be assigned to an advantage of first colonizers (priority effect: Sutherland 1974; Cole 1983; Drake 1991; Chase 2003), nor do they indicate that later colonizers have an advantage over established groups (Simpson 1953; Givnish 1997; Schluter 2000).

CONTEMPORARY MORPHOLOGICAL OVERLAP AND PRIORITY EFFECT

We find evidence of morphological differentiation between first and second colonizers in the Australasian and Oriental regions, but not in the Afrotropical or Neotropical regions (Table 1). In the Oriental region, where the Passerida were the initial colonists, the next colonizing clade (core Corvoidea, SES = 16.01) differs significantly morphologically from the initially established group. The same is true in the Australasian region, where the basal oscines were the initial colonists, followed by the Passerida (SES = 1.90) and the core Corvoidea (SES = 2.97). In the Afrotropical region, the two large passerine groups (the Passerida and the core Corvoidea) are morphologically more convergent than expected by chance (SES = −2.21), and in the Neotropics we find neither unexpected divergence nor convergence of morphological occupancy.
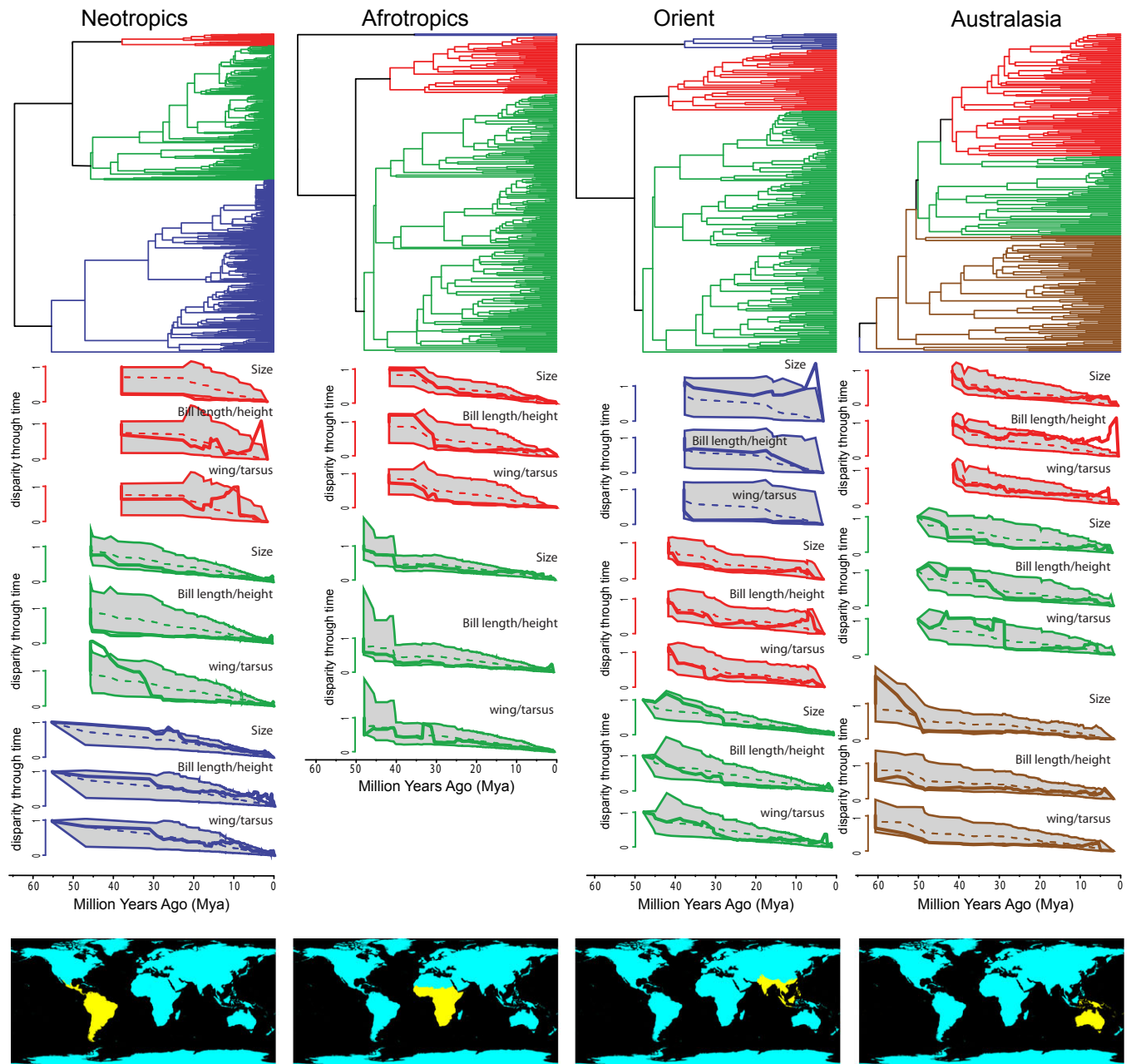
Figure 3. Phylogenies for all passerine species for which we had morphological measurements for the Neotropics (*N* = 620), Afrotropics (*N* = 271), Orient (*N* = 240), and Australasia (*N* = 242). Major passerine groups are basal oscines = brown, suboscines = blue, Passerida = green, core Corvoidea = red. The phylogenies are rotated such that clades that have persisted for the longest time are at the bottom. Below the phylogenies are the mean subclade disparity through time (DTT) plots for size, bill shape, and wing/tarsus ratio for each major passerine group. The dashed line indicates the median subclade DTT based on 10,000 simulations of character evolution on the passerine phylogeny under Brownian motion. The shaded areas indicate the 95% DTT range for the simulated data. High values indicate high within clade disparity, whereas low values indicate high among clade disparity (early burst). Two characteristics of the lineage through time (LTT) plots should be interpreted cautiously: (1) spikes toward the present, which may be caused by within-species variation and the magnification of minor measuring uncertainties on recent time scales and (2) the abrupt increase or decrease with the first split in the phylogeny, which depend on whether the first split in a phylogeny produces two clades with similar or different morphology.

Table 1. Morphological overlap among co-occurring groups of passerine birds (suboscines, basal oscines, Passerida, core Corvoidea) in the Australasian, Oriental, Afrotropical, and Neotropical regions.

	First colonizer	Second colonizer	Third colonizer	SES value for first versus second colonizer	SES value for first/ second versus third colonizer
Neotropics	Suboscines	Passerida	Core Corvoidea	−0.16	−0.11
Afrotropics	Passerida	Core Corvoidea	–	**−2.21**	–
Oriental	Passerida	Core Corvoidea	Suboscines	**16.01**	1.50
Australasia	Basal oscines	Passerida	Core Corvoidea	1.90	**2.97**

Contemporary patterns of overlap are quantified with standardized effect size (SES) of morphological distances. SES values > 1.96 indicate significant (in bold) divergence of morphologies and SES values < −1.96 indicate significant (in bold) convergence. We quantified SES of morphological distances using two different species pool definitions: all species in the world (global pool) and all species in either the New World or Old World (regional pools) depending on the location of the focal continent. The results presented here are for the regional species pools, which are overall similar to the global species pools (see Table S6).

Although no general pattern of morphological evolution emerges for first, second, or third colonizers in a region, "priority effects" might push late colonizers into open ecological or morphological space. Using null model analyses of the contemporary morphological distribution, we find that subsequent colonizers diverge morphologically from established clades in two of the four regions (Table 1). Thus, it appears that morphological diversification early in the evolutionary history of a group may, in some cases, lead the second group to diversify in a different morphological space. To our knowledge, such historical priority effects on the morphological diversification of entire bird clades have not been reported before, although historical priority effects are known from the fossil record (e.g., Wesley-Hunt 2005; Tyler and Leighton 2011; Wilson 2013). Moreover, Schenk et al. (2013) documented historical priority effects in continental assemblages of muroid rodents, whereby first colonizers appeared to inhibit the diversification of second colonizers, consistent with their constraining ecological opportunity.

Priority effects are difficult to determine, as the colonization of a continental region by a major clade might involve numerous dispersing lineages over long periods. The phylogenetic relationships among the contemporary species within each region do indicate an order of diversification in many cases. For example, in Australasia the clade with the deepest history of diversification in the contemporary avifauna comprises the basal oscines, followed by the passerids and core corvoids. The passerids precede the core corvoids in the other continents, as well, and the suboscines precede both in the Neotropics. The morphological spaces occupied by passerids are rather similar in size on the major continents, varying in the size dimension between 0.32 and 0.38, and shape between 0.19 and 0.21 (Table S4), regardless of whether passerids were the first major passerine clade (Afrotropics and Orient) or second (Neotropics and Australia). The core corvoids occupy spaces having very different dimensions in the different continents, ranging on the size axis between

0.24 (Afrotropics) and 0.61 (Neotropics) and on the shape axes between 0.13 (Neotropics) and 0.22 (Australia).

Whether a major passerine clade diversifies early or late within a continental region appears to have little effect on the morphological space occupied by the clade. For example, the continent of Australia supported the diversification first of the basal passerines (size = 0.48, shape = 0.20), followed by the passerids (0.38, 0.19) and the core corvoids (0.43, 0.22); in the Neotropics, the suboscines (0.36, 0.22) were followed by the passerids (0.37, 0.19) and the core corvoids (0.61, 0.13). Thus, although each of the major clades of passerine birds occupies somewhat nonoverlapping portions of the morphological space, the order of appearance of a clade within a region appears not to influence its morphological diversity at the present time.

Conclusions

This analysis addresses the build-up and coexistence of passerine bird assemblages in explicit spatial and temporal contexts. Using morphology as a proxy for niche space, our analyses do not support early bursts of morphological evolution for either the first or for subsequent colonizers of a particular region. We find mixed support for priority effects, as null models support morphological differentiation between first and second colonizers in only two out of four regions. Finally, our analyses show that passerine birds largely occupy the same morphological space globally and regionally, but that the four passerine groups individually are fairly well separated in morphological space within the four regions. Our results indicate that the relative timing of colonization does not predict the extent of diversification within a region for a given group. Instead, it is likely that species within passerine clades are continuously replacing each other, which may lead to a more gradual filling of niche space over time, as opposed to rapid filling during an initial burst. In the long run, each clade occupies a characteristic part of the morphological space within a region,

indicative of evolutionary conservatism in filling ecological niche space within continental avifaunas.

Of course, external morphology is not a completely adequate proxy for a species' ecology; species clearly diversify along trait axes that are not perceived in external morphology (e.g., Ricklefs 1996). In addition, morphological diversification within a region might depend on the morphology of the initial colonist(s), which, without a fossil record, is unknowable. Alternatively, birds might be sufficiently generalized that small differences in morphology/ecology are sufficient to allow them to persist without diverging dramatically from other species. We also acknowledge that random extinctions of individuals and/or entire clades (Ricklefs and Jønsson 2014) could bias results and interpretations by obliterating the full history of diversification within a region.

DATA ARCHIVING
The doi for our data is 10.5061/dryad.qk461.

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

Table S1. Distribution statistics for the ln-transformed original variables based on average values for 1579 passerine bird species.

Table S2. A principal components analysis was performed on the covariance matrix of the log-transformed original seven trait measurements across all passerine birds, and PC axis scores were calculated for each species.

Table S3. Standard deviations of principal component scores for all passerine species in the four regions and within each of the regions (excluding Hirundinidae, which exhibit outlier morphology).

Table S4. The principal component scores for each of the major passerine clades (excluding Hirundinidae, which exhibit outlier morphology), and for the core corvoids and passerids in each of the continental regions.

Table S5. Generalized square morphological distances between the passerine avifaunas (excluding Hirundinidae, which exhibit outlier morphology) and between the major clades of passerines in each continental region.

Table S6. Seven morphological traits were used to calculate Euclidean distances in trait space between all species of group A and all species of group B, for each region.