ORIGINAL ARTICLE

Range size patterns of New World oscine passerines (Aves): insights from differences among migratory and sedentary clades

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ABSTRACT

Aim To quantify the contributions of environment, phylogeny and geography to variation in the breeding and non-breeding geographical range sizes of oscine passerines.

Location Western Hemisphere.

Methods Breeding range sizes were estimated for 420 species, and non-breeding ranges were estimated for 122 migratory species. Phylogenetic, environmental and geographical (spatial) eigenvectors were used to partition cross-species variation in range size. The strengths of environmental and phylogenetic signals were quantified and compared among all species, and between migratory and sedentary oscines.

Results Phylogenetic, environmental and geographical structure explained most of the variation in range size, accounting for 95% of the variation in breeding range sizes of migratory birds. The three components overlapped extensively, with most variation explained by differences in environmental niches. Models for breeding ranges of migratory species contained the strongest phylogenetic, environmental and geographical signals at the species level. In contrast, models for non-breeding ranges of migratory species contained the weakest phylogenetic and environmental signals (5.7% and 65.2% of variance explained, respectively). The phylogenetic signal was consistently stronger for migratory breeding ranges than for the other groups.

Main conclusions Oscine range sizes contain a low to moderate phylogenetic signal that overlaps with environmental and geographical associations. The significance of phylogenetic signal suggests that the evolution of range size is not entirely labile, which is probably a result of the non-labile evolution of associated traits. Environmental, geographical and phylogenetic variables can account for most of the variance in species-level range size, with qualitatively similar patterns for migratory and sedentary species. Nonetheless, the stronger environmental and phylogenetic signals in the breeding ranges of migratory species may reflect both that migration is a phylogenetically conserved trait and that the subset of species able to breed in 'recently' deglaciated regions is more severely constrained by macroclimatic filtering.

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INTRODUCTION

Geographical range size represents one of the major features of species on which macroecologists have focused, and there is abundant literature on Rapoport's rule (Rapoport, 1982), which states that range sizes are larger in cold, extra-tropical climates than in tropical climates. The conditions under which Rapoport's rule applies have been the subject of much debate (e.g. Kolasa *et al.*, 1998; Gaston & Chown, 1999; Hernández-Fernández & Vrba, 2005). In particular, the distribution of bird range sizes has received attention at both regional (Hawkins & Diniz-Filho, 2006) and global (Orme *et al.*, 2006) scales. For instance, Rapoport's rule is found only in certain areas (e.g. the Holarctic), where the seasonal variability hypothesis (Stevens, 1989) or the hypothesized effect of glaciations extirpating small-ranged species (Rohde, 1996) could explain the larger ranges at higher latitudes. Conversely, bird geographical ranges are smaller in montane areas, suggesting limits due to habitat availability (Hawkins & Diniz-Filho, 2006; Orme *et al.*, 2006). Despite efforts to find a 'one size fits all' explanation, no single ecological hypothesis seems sufficient to explain range size patterns.

Aside from ecological constraints, geographical range sizes are likely to be influenced by evolutionary dynamics. Whereas a macroevolutionary perspective focuses on the extent to which geographical ranges could be inherited from ancestors (e.g. owing to the inheritance of specific traits determining the size of the range each species could attain; see below), a microevolutionary view centres on how phenotypic plasticity in the environmental tolerances of populations would define the species' range boundaries (Stevens, 1989). The extent to which these mechanisms apply is not well resolved. Following a report of substantial species-level heritability of range size in extinct marine molluscs (Jablonski, 1987), attempts were made to measure the phylogenetic signal in range sizes among extant terrestrial species: it was found to be weak or non-existent (Gaston, 1998; Webb & Gaston, 2003, 2005; and references therein). Range size is a dynamic feature, often showing a process of growth and contraction over the evolutionary lifetime of a species (Gaston, 1998; Jones *et al.*, 2005; Pigot *et al.*, 2012) that may confound phylogenetic signal in range size. On the other hand, range sizes undoubtedly reflect species traits to some extent (e.g. body size, dispersal ability, tolerance to environmental stresses, and/or degree of generalism in terms of habitat use or diet), many of which appear to be strongly conserved during cladogenesis (Freckleton *et al.*, 2002), so it would be surprising if there were no phylogenetic signal in range size at all (see e.g. Pocock *et al.*, 2006; Bocxlaer *et al.*, 2010; Buckley, 2010). A summary of 16 data sets by Waldron (2007) reported statistically significant phylogenetic structure in range sizes in 11 of them. Of five analyses of various bird clades, three found heritability at some level. More recently, Borregaard *et al.* (2012) showed that current range size patterns could have been shaped by inheritance from ancestors, reinforcing the idea that evolutionary dynamics have left an imprint in geographical ranges.

Measuring the extent to which range size variation is related to evolutionary dynamics is complicated because the evolutionary signal might overlap with that derived from effects of current environmental constraints, or from spatially structured biotic factors (e.g. geographical cohesiveness in the dispersal of individuals). Freckleton & Jetz (2009) recently addressed this by proposing a method for cross-species analysis (*sensu* Gaston *et al.*, 2008) that uses generalized least squares (GLS) regression to simultaneously measure contributions of space and phylogeny to range size (or any other trait). A drawback of this technique is that the environmental and geographical ranges of each species were characterized by midpoints, with a serious loss of information (Ruggiero & Hawkins, 2006). For example, this technique would consider the geographical distance between a species with a Pan-American distribution and one occurring only in Panama to be minimal. Machac *et al.* (2011) used a similar approach but complemented it with calculations of additional geographical distances between ranges. They found that range size relationships with phylogeny and geography differed depending on what spatial measurements were employed. These inconsistencies highlight the need for alternative methods to quantify influences of environment and/or geographical location in cross-species analyses of range size.

Here, we explore the extent to which phylogeny, environment and the geographical distribution of species relate to the cross-species variation in range size of New World oscine passerines. We also introduce a novel eigenvector-based methodology which circumvents the loss of information generated by reducing environmental and geographical variation for species to midpoints. We focus on birds, which may represent an unusual group for studying geographical range dynamics because many migrate seasonally, and for many of these only their breeding distributions are known (see Orme *et al.*, 2006; Pigot *et al.*, 2010). At the same time, however, oscines embody interesting biological features. First, they constitute a relatively uniform group in terms of general ecology and body size (Chesser & Levey, 1998). Second, their evolutionary origins are known, with most lower-rank clades having radiated within the New World, especially in the Neotropics (Levey & Stiles, 1992; Rappole, 1995; Chesser & Levey, 1998; Ericson *et al.*, 2003; Weir *et al.*, 2009) subsequent to their arrival through the Bering Strait within the last 15 million years (Jahn *et al.*, 2004). Third, many oscines are migratory and have distinct breeding and non-breeding ranges (well documented in the New World), often thousands of kilometres apart, which allowed us to compare migratory and sedentary (non-migratory) groups and breeding and non-breeding ranges of migratory species. Fourth, this migratory behaviour has been proposed to have appeared recently (throughout the Pleistocene; see Milá *et al.*, 2006), and could be a phylogenetically structured characteristic associated with specific physiological, behavioural and/or dietary adaptations (see Levey & Stiles, 1992), which in turn could determine responses to macroclimatic gradients.

We had three expectations regarding range size patterns. First, because biological traits influence range size (e.g. Böhning-Gaese *et al.*, 2006), and because some of these traits are evolutionarily conserved (Freckleton *et al.*, 2002), we expected a non-random phylogenetic signal for range size. However, as expansions and contractions of species ranges are also associated with variation in environmental conditions over time, including those derived from human activities (e.g. climate change or anthropogenic alteration of habitats), we did not expect this phylogenetic signal to be strong (Jones *et al.*, 2005; Böhning-Gaese *et al.*, 2006). Second, migratory birds often form subsets of phylogenetically closely related species sharing physiological, behavioural and/or dietary traits (Levey & Stiles, 1992; Chesser & Levey, 1998; Boyle & Conway, 2007), and have larger ranges than sedentary species (Salewski & Bruderer, 2007), leading us to expect a stronger phylogenetic signal among migratory species. Finally, migration has been proposed to originate within species inhabiting southern, tropical areas that began flying north to breed (the 'southern-home theory'; see Levey & Stiles, 1992) taking advantage of the resource peak of the northern spring–summer (Croat, 1975; Levey, 1988; Blake & Loiselle, 1991; Boyle & Conway, 2007; but see Salewski & Bruderer, 2007). In order to breed in the north, migratory species would require broader environmental tolerances (i.e. even in summer, species breeding in the Nearctic may encounter colder temperatures than tropical breeders; e.g. see Rodríguez *et al.*, 2008), and thus their breeding ranges are likely to encompass broader environmental variation. For all of the above reasons, we predicted a stronger environmental signal in the breeding range sizes of migratory species than in those of sedentary species.

Bearing in mind these predictions, we addressed the following five questions. (1) What are the geographical patterns in species richness and range size of New World oscine groups defined by their sedentary/migratory behaviour? (2) Is this behaviour a phylogenetically conserved characteristic? (3) Is this also true for their geographical range sizes? (4) To what extent do the phylogeny, current environment and geographical distribution of oscines relate separately and in concert to range size variation? (5) Are there differences in these patterns between migratory and sedentary species, and between breeding and non-breeding ranges of migrants?

MATERIALS AND METHODS

Bird data

The breeding and non-breeding ranges of 420 species of native oscines included in the supertree of Jønsson & Fjeldså (2006) were extracted from the database available at http://www.natu-reserve.org/getData/birdMaps.jsp/ (accessed November 2011) (Ridgley *et al.*, 2003). Island endemics and species whose ranges extend beyond the Western Hemisphere were not considered for analysis (see Appendix S1 in Supporting Information for a list of species and their $\log_{10}$-range sizes). Four range sizes were quantified: breeding ranges of all species, year-round ranges of sedentary species, and breeding and non-breeding ranges of migratory species. Although island endemics were excluded, island distributions of species also occurring on the mainland were included in range size calculations, but passage ranges were not. The data were binned in a 9319-km^2 grid in a Behrmann projection, and mean $\log_{10}$-range sizes were calculated for each cell to explore and compare the geographical patterns in range size for all, migratory and sedentary species.

We also generated species richness maps based on the breeding and non-breeding ranges of all, sedentary and migratory species. Richness patterns for all New World bird species based on breeding ranges have been documented (e.g. Hawkins *et al.*, 2006), but as far as we know richness patterns for migratory species in their winter ranges have not been mapped. Local migration and other movements occur for some sedentary species, but we defined our migratory subset of species as long-distance migrants only, as identified in Ridgley *et al.* (2003). Although our data set included *c.* 30% of New World oscine species, their richness patterns should be representative (we found they were similar to those of all birds as reported in Hawkins *et al.*, 2006; see below) and were used to compare differences among the migratory and sedentary species and to facilitate interpretation of the range size patterns.

Geographical, environmental and phylogenetic filtering

To separate the independent and covarying influences of environmental factors, phylogenetic relationships and geographical structure on range size across species, we conducted a filtering procedure similar in logic to spatial (Borcard & Legendre, 2002) or phylogenetic (phylogenetic eigenvector regression, PVR; Diniz-Filho *et al.*, 1998) filters. Several methods have been proposed to address this issue by reducing all variability in environmental conditions within species ranges to midpoints (as in Freckleton & Jetz, 2009) or by translating phylogenetic relationships into an assemblage (grid-based) context, where modelling is performed (Terribile *et al.*, 2009; Safi & Pettorelli, 2010). A novel aspect of our approach is that analyses are conducted at the cross-species level and account for the environmental and geographical variation contained within the range sizes of species instead of averaging the values across geographical units (i.e. grid cells) to perform a regression based on those units (e.g. Ramirez *et al.*, 2008; Morales-Castilla *et al.*, 2012).

The method comprises three steps (Fig. 1). First, the relationships among species relative to each component (geographical, environmental and phylogenetic) are computed and expressed as pairwise distance matrices. Each matrix is computed independently and contains distances between species according to geography (i.e. reflecting overlap levels between presences/absences of species pairs as measured by the Hellinger distance; Legendre & Gallagher,
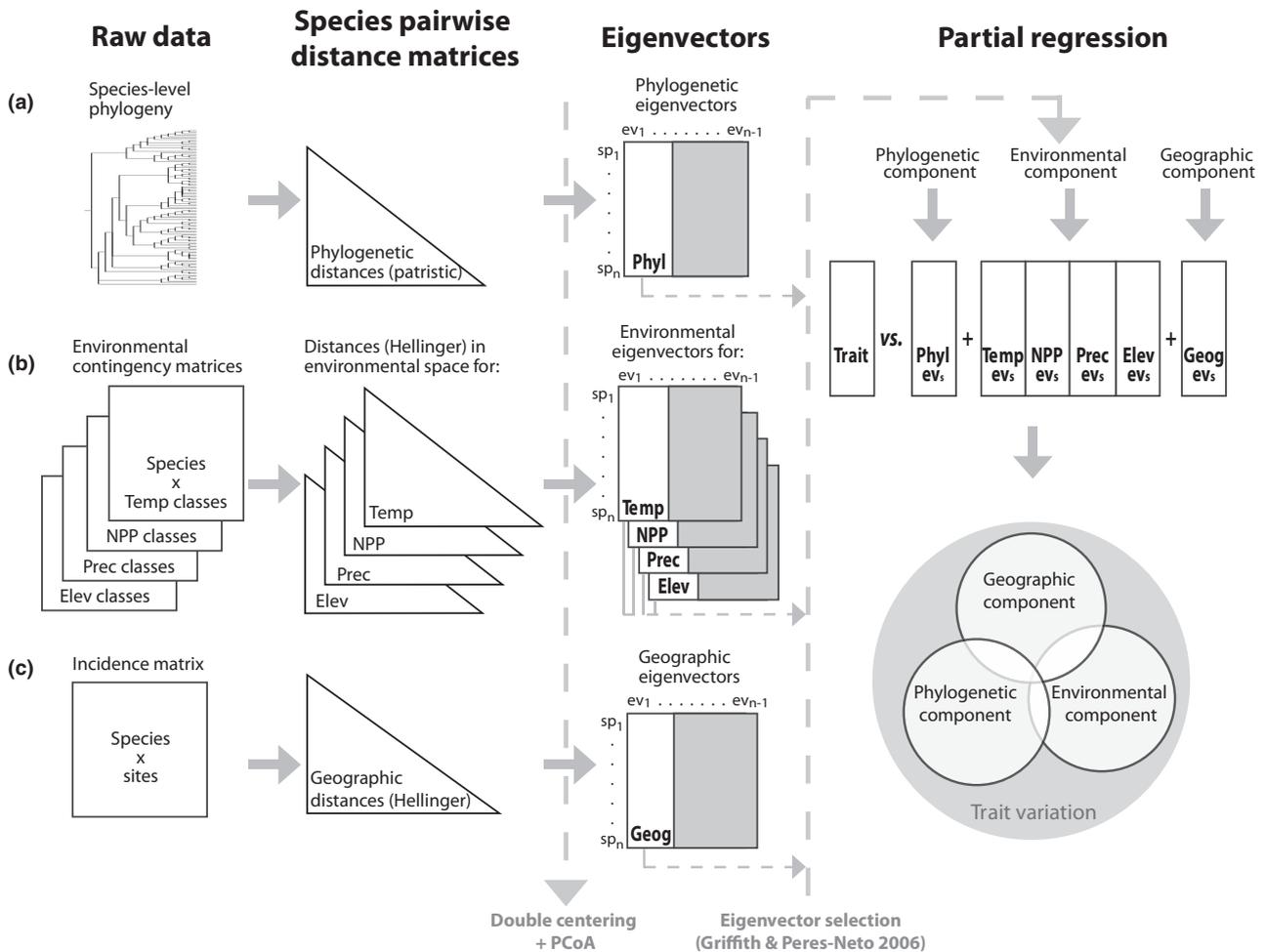
Figure 1 Summary of the eigenvector-based approach used to partition range size variation of New World oscines into its (a) phylogenetic, (b) environmental and (c) geographical components. The procedure is as follows. (1) Raw data for each of the components are transformed into a pairwise distance matrix. Hellinger distances are used for each environmental matrix and for the distributional matrix. (2) Distance matrices are decomposed into eigenvectors using principal components analysis. (3) A subset of eigenvectors is selected for each component using the algorithm of Griffith & Peres-Neto (2006) to minimize residual autocorrelation. (4) Selected eigenvectors are included as response variables in a partial regression. Note that the steps followed for the phylogenetic component are equivalent to performing phylogentic eigenvector regression (Diniz-Filho *et al.*, 1998). Abbreviations: Temp, temperature; NPP, net primary productivity; Prec, precipitation; Elev, range in elevation.

2001), environmental conditions or phylogeny. The phylogenetic pairwise distance matrices were generated by measuring patristic distances among species based on pruned phylogenies (see below), and the environmental and geographical distance matrices were built based on environmental contingency matrices or species presence–absence matrices, respectively. Environment was defined with respect to four variables (see 'Environmental correlates of range sizes' for details) binned in 45 equal-interval classes. For each variable, we counted the number of grid-cells that each class was represented within each species' geographical range. By doing so, we accounted for the frequency of each environmental equal-interval class in each species' range. This information was utilized to build environmental contingency matrices that were later transformed into pairwise distance matrices. To compute the environmental and geographical distance matrices, we used Hellinger distances in order to minimize

two problems common to highly dispersed (i.e. zero-inflated) matrices, namely the 'double-zero problem' and the 'species-abundance paradox' (Legendre & Legendre, 1998; Gagné & Proulx, 2009). Second, each matrix was double-centred and converted into a set of eigenvectors through a principal coordinates analysis, with a subset of eigenvectors representing each matrix to be used as predictors of range size. The selection of eigenvectors is a critical issue, because both the number of eigenvectors and the existence of autocorrelation in the residuals (of a regression of the response variable, range size in our case, on the eigenvectors) can affect the results, which has led to criticisms of eigenvector-based approaches (Rohlf, 2001; Freckleton *et al.*, 2011). However, these issues were recently addressed by Diniz-Filho *et al.* (2012), who evaluated multiple methods for eigenvector selection. Accordingly, the algorithm proposed by Griffith & Peres-Neto (2006) was used to select the smallest set of

eigenvectors needed, in order to reduce the autocorrelation in the residuals to non-significant levels ($P > 0.05$) (see Appendix S2). Third, OLS partial regressions were performed to partition the amounts of variation in range size associated with the three sets of eigenvectors representing each component (i.e. geographical, environmental and phylogenetic) across species. In our analysis the procedure was repeated for all oscine ranges, ranges of sedentary species, migratory non-breeding ranges and migratory breeding ranges. To evaluate the consistency between our method and that proposed by Freckleton & Jetz (2009) we repeated the variation partitioning analyses utilizing their method (see Appendix S3).

Phylogenetic signal in range size

The phylogeny of Jønsson & Fjeldså (2006) was initially pruned to include only the 420 species included in the present analysis, and it was then pruned to build phylogenetic trees for the 298 sedentary species and for the 122 migratory species. All three phylogenies were used to compute phylogenetic signal metrics.

We tested for phylogenetic signal following Kozak & Wiens (2010). Log-likelihoods were calculated for three models of evolution to assess whether the best fit was provided by a Brownian motion model of gradual drift (Pagel's $\lambda = 1$), an Ornstein–Uhlenbeck model of constrained evolution (stabilizing selection; see Hansen et al., 2008), or a white noise model (Pagel's $\lambda = 0$). We also compared the strength of phylogenetic signal among the different bird groups using Blomberg's K (Blomberg et al., 2003), which varies from 0 to ∞, where $K = 1$ indicates Brownian motion. Finally, we checked for consistency of our phylogenetic component calculated through PVR (Diniz-Filho et al., 1998) with the other phylogenetic metrics. Although the R^2 from a PVR is not considered a conventional measure of phylogenetic signal (it is not a process-based metric), it quantifies the amount of variation in range size described by phylogenetic relationships among species. To test our first prediction (a stronger phylogenetic signal in breeding ranges of migratory species), we used the D metric of Fritz & Purvis (2010) to confirm that migratory behaviour is phylogenetically conserved. The D metric can be used to calculate the phylogenetic signal of binary traits (in our case, 0 = sedentary, 1 = migratory), and thus it identifies whether migratory species represent a phylogenetically non-random group of species. D is 1 for random distributions of the trait, > 1 for an overdispersed trait, 0 if the trait is distributed as expected under Brownian motion, and < 0 if the trait is more phylogenetically conserved than under a Brownian expectation.

To test the statistical significance of the phylogenetic metrics, likelihood ratios were used to infer the most likely model of evolution; a randomization of the data among species was used for Blomberg's K; and null models generated by taking 1000 random samples of the log-transformed range sizes without replacement and regressing them against the selected subset of vectors were used for the PVR. Polytomies

in the phylogeny were resolved randomly by zero-length branches.

Because the phylogeny of Jønsson & Fjeldså (2006) does not include branch lengths, we evaluated the robustness of our results by comparing them with those obtained using the phylogeny of Jetz et al. (2012). The results were virtually identical, because the latter supertree assumes the topology of Jønsson & Fjeldså, and so to reduce redundancy the latter results are not reported.

Environmental correlates of range sizes

Our goal was not to generate detailed predictive environmental models but to evaluate the extent to which each of four environmental predictors (below) contributed to the environmental component of range size for each group of birds. The environmental influences were calculated using the adjusted R^2 yielded by the eigenvectors representing each environmental variable. The focus was on variables expected to be associated with bird distributions and thus with the size of the geographical ranges. Mean temperature of the breeding season (months of northern summer, May–August) was extracted from the BIO1 database in WorldClim (http://www.worldclim.org/; accessed February 2013), and mean temperature of the non-breeding season (months of northern winter, November–February) was used for the non-breeding ranges of migratory birds. This variable is considered an important environmental driver of Rapoport's rule because it relates to extra-tropical species having broader thermal tolerances and hence showing larger geographical extents (Stevens, 1989). Average net primary productivity (NPP; data available at: http://sedac.ciesin.columbia.edu/es/hanpp.html/, accessed February 2013) was included because range size, particularly for the case of migratory birds, has been associated with resource availability (Shaffer et al., 2006). This variable was generated for both the breeding and the non-breeding season as for temperature. Average precipitation during the breeding and non-breeding seasons (extracted from the BIO12 database in WorldClim) was used as a secondary indicator of productivity (Stevens, 1989). Range in elevation within cells using all pixels (calculated from the 30-arcsecond digital elevation model gtopo30) was included because of the association between meso-scale temperature gradients and range sizes of New World birds (Hawkins & Diniz-Filho, 2006). Phylogenetic analyses and matrix computation were run in R, version 2.15.1 (R Development Core Team, 2011) and partial regressions were computed in sam, version 4.0 (Rangel et al., 2010).

RESULTS

Species richness gradients

The richness patterns for all species (Fig. 2a) and for non-migratory species (Fig. 2b) are almost identical in the Neotropics during the breeding season. Maximum richness
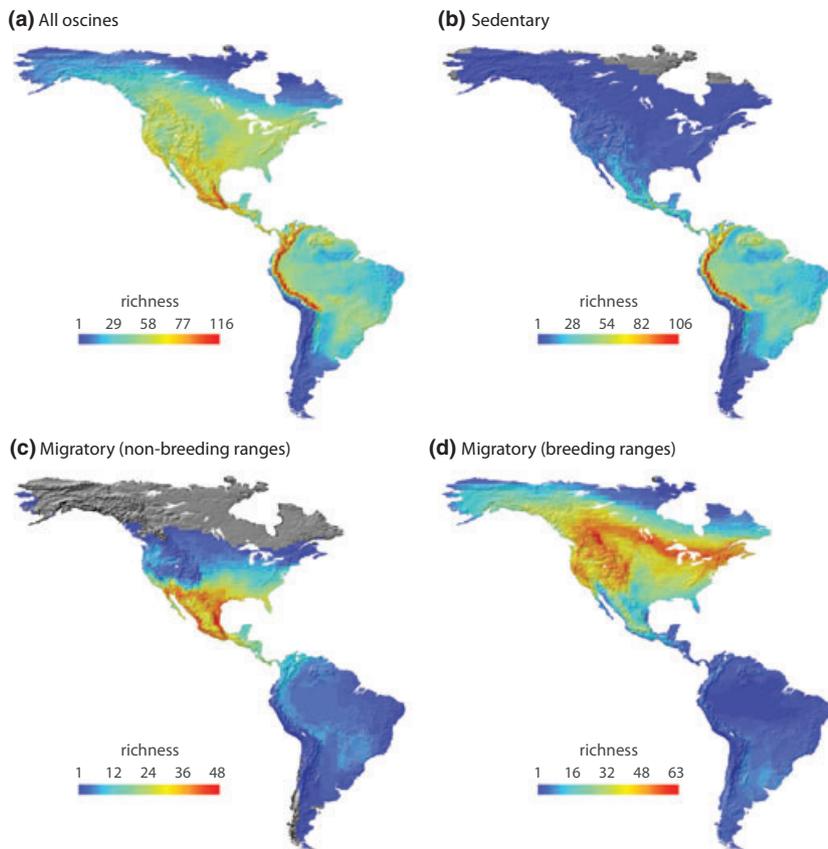
(a) All oscines

(b) Sedentary

(c) Migratory (non-breeding ranges)

(d) Migratory (breeding ranges)

Figure 2 Species richness gradients for the species of New World oscine passerines in the data set based on four range size metrics. (a) Richness of all species considering their breeding ranges ($n = 420$); (b) richness of sedentary species only ($n = 298$); (c) richness of migratory species while in their non-breeding ranges ($n = 122$); and (d) richness of migratory species while in their breeding ranges ($n = 122$).

occurs in the tropical Andes and mountain ranges of tropical Mexico. In contrast, both all oscines and sedentary oscines are not particularly rich in the lowland tropics, which is reflected by the species richness of all oscines being higher in parts of temperate North America than in the Amazon Basin (Fig. 2a). This latter pattern is not found for sedentary species (Fig. 2b), reflecting the fact that most extratropical North American species are migratory (Fig. 2c,d). Most of our migratory oscines are distributed in Mexico and the southern USA during northern winter, with no migratory species overwintering in northern Canada (Fig. 2c). During the northern summer, returning migrants generate a band of high richness near the USA–Canadian border and southwards in the Rocky Mountains and Pacific slopes (Fig. 2d).

Range size gradients

Rapoport's rule is found in North America for all groups (Fig. 3), with broad ranges on average across most of Canada (except in north-eastern Nunavut), moderate ranges in the eastern USA, and narrow ranges in the south-western USA southwards. However, this gradient is more abrupt for sedentary species (Fig. 3b) and is shifted southwards for the non-breeding ranges of migrating oscines (Fig. 3c). Range size patterns of all and sedentary species in South America differ substantially from those in North America (Fig. 3a,b),

with broad average ranges in north-eastern Brazil and the narrowest ranges in the Andes. Patterns for migratory species are qualitatively similar (Fig. 3c,d), in that the largest ranges are found in the Amazonian Basin, although non-breeding ranges are not small in the Andes (Fig. 3c). Overall, all combinations of ranges have a similar pattern: Rapoport's rule in North America and its converse in South America.

Relative contribution of each environmental variable

The explanatory power of saturated multiple regression models for range size including the vectors representing the variation of each environmental variable was strong, ranging from 63% for non-breeding ranges of migratory species to 88% for breeding ranges of migrants (Table 1). Although the overlap among the proportions of range size explained by each environmental variable was large, their relative explanatory power differed among groups (Table 1). Eigenvectors representing productivity and temperature were most strongly associated with both breeding and non-breeding ranges of migratory oscines. Vectors selected for productivity and precipitation explained most of the variation in range size for all species, and the variation in range sizes of non-migratory species was equally explained by the eigenvectors of temperature, productivity and precipitation (Table 1). Range in elevation had low to moderate explanatory power for all groups.
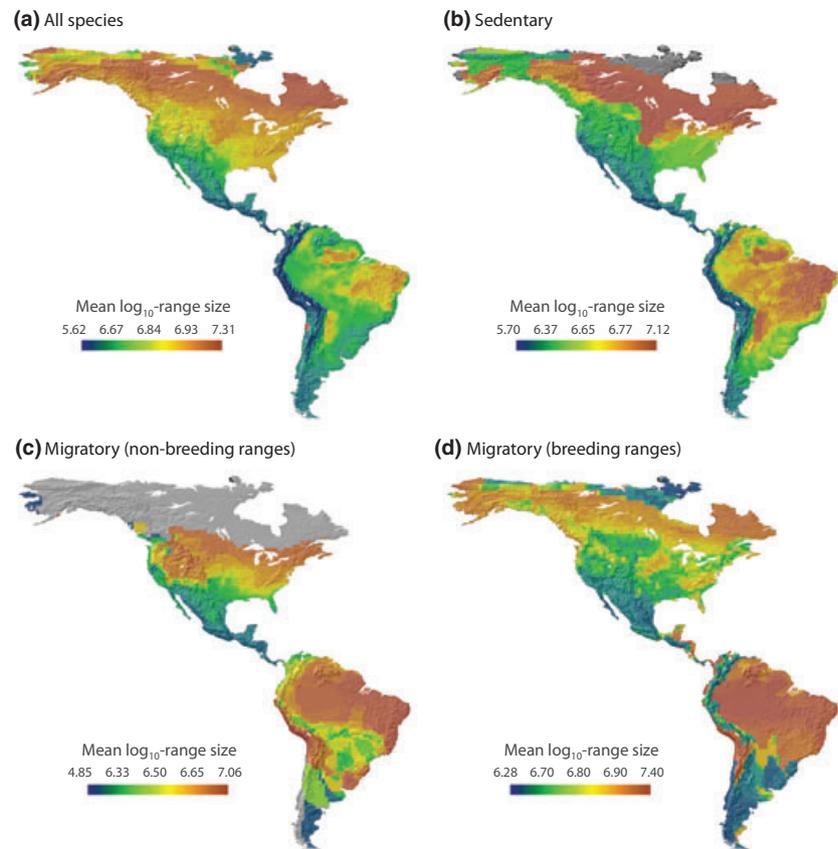
(a) All species

(b) Sedentary

Mean log$_{10}$-range size

5.62 6.67 6.84 6.93 7.31

Mean log$_{10}$-range size

5.70 6.37 6.65 6.77 7.12

(c) Migratory (non-breeding ranges)

(d) Migratory (breeding ranges)

Mean log$_{10}$-range size

4.85 6.33 6.50 6.65 7.06

Mean log$_{10}$-range size

6.28 6.70 6.80 6.90 7.40

Figure 3 Mean range sizes (log$_{10}$-transformed km²) for the species of New World oscine passerines in the data set for (a) all species considering their breeding ranges ($n = 420$), (b) sedentary species only ($n = 298$), (c) non-breeding ranges of migratory species ($n = 122$), and (d) breeding ranges of migratory species only ($n = 122$).

Table 1 Contributions of the eigenvectors selected for each environmental variable (TEMP, temperature; NPP, net primary productivity; PREC, precipitation; ELEV, range in elevation – see text for details) to the environmental component of range size for each New World oscine group. The coefficients of determination for multiple regressions including all environmental factors are shown (R^2_{ENV}) as the adjusted R^2. Note that there is overlap between the associations of the eigenvectors selected for each variable and range size.

Oscine group	r^2_{TEMP}	r^2_{NPP}	r^2_{PREC}	r^2_{ELEV}	R^2_{ENV}
All oscines ($n = 420$)	0.194	0.728	0.648	0.410	0.769
Sedentary ($n = 298$)	0.747	0.746	0.755	0.586	0.758
Migratory non-breeding ($n = 122$)	0.625	0.591	0.128	0.281	0.633
Migratory breeding ($n = 122$)	0.819	0.878	0.064	0.495	0.884

Phylogenetic signal in range size

As expected, phylogenetic signal in range size was generally weak, although differences were found among groups. Range size fitted significantly better to the Ornstein–Uhlenbeck model of evolution than to the Brownian motion model for all groups, and than to white noise for all groups except for the non-breeding ranges of migratory oscines (Table 2). Non-breeding ranges of migratory species consistently had no detectable phylogenetic signal (not significantly different

from random based on Blomberg's K, Table 2). In contrast, the signal in breeding ranges of migrants was the strongest of all groups, with the phylogenetic vectors explaining as much as 24% of the variation in range size. The phylogenetic signal of all species and non-migratory species was similarly weak, although significantly different from the random expectation according to Blomberg's K, and PVR R^2 for these groups ranged from 12% to 16% (Table 2). In addition, the phylogenetic signal for migratory behaviour indicated that this trait was highly phylogenetically conserved ($D = -0.505$, $P < 0.001$).

Partitioning geographical, environmental and phylogenetic components of range size

Partial regressions including geographical, environmental and phylogenetic components accounted for most of the species-level variation in range size of every group of birds (coefficients of determination ranged from 0.828 to 0.949) (Fig. 4a–d, see also Appendix S3). In general, the overlapping influences of both the geographical and environmental components explained more variation in range size for all groups (Fig. 4). The association of the environmental component with range size independent of the other components was the secondary predictor explaining more variation in range size of all groups, with the exception of the non-breeding ranges of migratory species for which the geographical component alone was the second most important predictor

Table 2 Metrics of phylogenetic signal in range size of four groups of New World oscine birds. Log-likelihoods for the fit of Ornstein–Uhlenbeck [Ln*L*(OU)], Brownian motion [Ln*L*($\lambda = 1$)], and absence of phylogenetic signal [Ln*L*($\lambda = 0$)] are shown with probability values resulting from comparing the OU fit against the other two models. Blomberg's *K* is also shown, with the probability of its value being equal to the random expectation. The R^2 from the phylogenetic eigenvector regressions (PVRs) considered as our phylogenetic component are reported to evaluate consistency with the other metrics.

Oscine group	Ln*L*(OU)	Ln*L*($\lambda = 0$)	Ln*L*($\lambda = 1$)	$P < [\lambda = 0]$	$P < [\lambda = 1]$	*K*	$P < [K = 0]$	PVR R^2	PVR R^2_{null}	R^2_{null} SE
All oscines	−500.8	−519.8	−513.1	< 0.001	< 0.001	0.011	0.005	0.157	0.007	0.005
Sedentary	−365.2	−371.5	−377.6	< 0.001	< 0.001	0.014	0.030	0.118	0.011	0.008
Migratory non-breeding	−87.7	−87.7	−95.8	0.802	< 0.001	0.030	0.350	0.057	0.014	0.014
Migratory breeding	−73.9	−77.6	−82.1	0.006	< 0.001	0.040	0.010	0.241	0.009	0.013

(a) All species

geography 61.4%

phylogeny 15.7%

environment 76.9%

(b) Sedentary

geography 52.3%

phylogeny 11.8%

environment 76.0%

(c) Migratory (non-breeding ranges)

geography 73.6%

environment 65.2%

phylogeny 5.7%

(d) Migratory (breeding ranges)

geography 76.7%

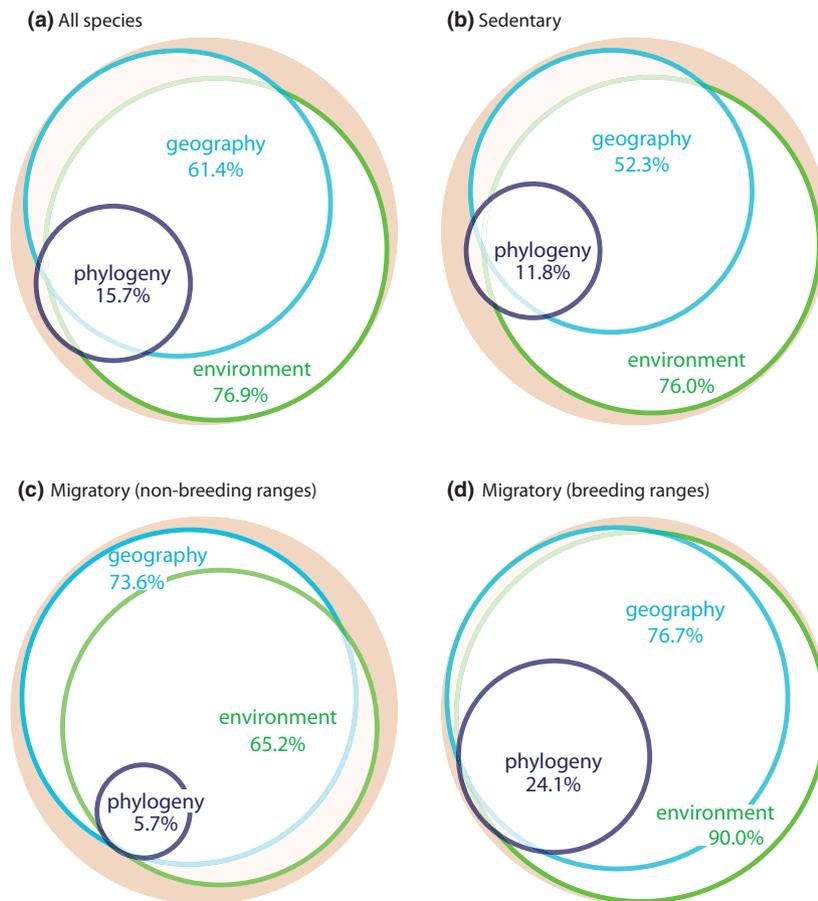phylogeny 24.1%

environment 90.0%

Figure 4 Partial regressions illustrating shared and independent relationships of the geographical (blue), environmental (green) and phylogenetic (purple) components as proportions of explained variation in range size of New World oscines in the data set for (a) all species (*n* = 420), (b) sedentary species (*n* = 298), (c) non-breeding ranges of migratory species (*n* = 122), and (d) breeding ranges of migratory species (*n* = 122). Circle size is proportional to the amount of variation in range size explained by each component, and the shaded circle in the background represents the total variation in range size.

(Fig. 4c). The association of the phylogenetic component with range size mostly overlapped with both geographical and environmental structure (Fig. 4), being greatest for the breeding ranges of migratory species ($R^2 = 0.238$). This suggests that the associations of breeding ranges of migratory species with environmental gradients (Fig. 4d) are more strongly phylogenetically conserved than those of other oscine ranges. It is noteworthy that whereas the overlap among the geographical and environmental components is due to environmental variables being spatially structured, the independent associations of the geographical component with range sizes correspond to other spatially structured processes not accounted for by our environmental variables

(including environmental variation occurring at other scales, biotic interactions, or range size dynamics in time).

DISCUSSION

Range size patterns of oscine passerines are very similar to patterns documented for all New World birds (Hawkins & Diniz-Filho, 2006; Orme *et al.*, 2006). Range size distributions of most migratory and sedentary species broadly follow Rapoport's rule in North America, but not across the entire continent (Fig. 3). Geographical patterns of ranges are similar for migratory and sedentary species, which is reflected in qualitatively similar partitions of geographical, phylogenetic

and environmental components (Fig. 4). Nonetheless, the breeding ranges of migratory species contain quantitatively stronger phylogenetic and environmental signals that are likely to be associated with the origination of migration in this highly mobile group of organisms.

In the Northern Hemisphere, broad ranges at high latitudes are believed to reflect species responses to highly variable winter temperatures. As noted by Stevens (1989), migratory birds are not exposed to severe winter conditions and so are not expected to follow Rapoport's rule. Nonetheless, Rapoport's rule holds in North America for both breeding and non-breeding ranges of migratory oscines (Fig. 3c,d), with a latitudinal shift in the maximum range sizes of each group. Migratory breeding ranges are associated primarily with productivity (Table 1), consistent with the hypothesis that summer ranges are configured to maximize primary productivity in order to permit the resource-demanding reproduction of these birds (see also Boyle & Conway, 2007). Non-breeding ranges are associated primarily with temperature (Table 1), specifically with winter temperatures that drive migratory species from Canada and Alaska, leaving behind a few widely distributed species that generate the largest average ranges in the north (Fig. 3c). Ranges of sedentary species have a stronger association with elevation, probably reflecting constraints on distributions in tropical mountains owing to short-distance turnover in local climates and vegetation coupled with a complex topography that limits dispersal (Ruggiero & Hawkins, 2008; Graham et al., 2010). Given that oscine richness is very high in mountainous areas (Fig. 2), the finding that half of the variation in sedentary and breeding migratory ranges can be explained by habitat availability (Hawkins & Diniz-Filho, 2006) (see Table 1) makes sense. As indicated for birds in general and in other parts of the world (Orme et al., 2006; Pigot et al., 2010), multiple processes influence range size patterns of oscines in North and South America.

Apart from differences in their distributions, an additional source of disparity among range sizes stems from the influence of evolutionary history. Although some previous analyses have found little or no phylogenetic signal in bird range sizes (Price et al., 1997; Waldron, 2007), we find evidence of phylogenetic conservatism in breeding ranges of New World oscines at low to moderate levels, with Ornstein–Uhlenbeck as the most likely model describing the evolution of range sizes of the groups showing phylogenetic signal (Table 2). This indicates retention of the 'trait' consistent with phylogenetic niche conservatism (Kozak & Wiens, 2010). Because the breeding ranges of migratory species experience geographical expansion as the birds migrate, and the species that are migratory are a non-random sample of the oscine phylogeny (see Results), the tendency towards larger breeding ranges shared by migratory species (see Fig. 5 and Fig. S1 in Appendix S3) is probably the reason for the stronger phylogenetic signal for this group.

Previous midpoint-based methods attempting to incorporate phylogenetic and spatial contributions to range sizes
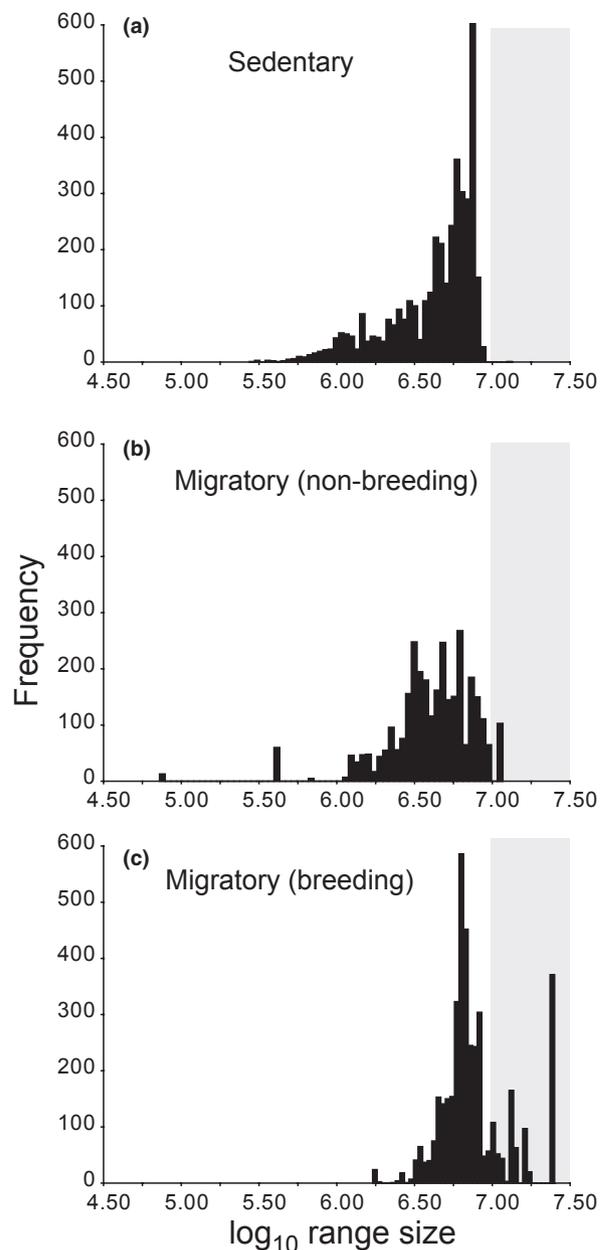

Figure 5 Frequency distributions of New World oscines in the data set: (a) mean $\log_{10}$-range size (km²) for sedentary species ($n = 298$), (b) non-breeding ranges of migratory species ($n = 122$), and (c) breeding ranges of migratory species ($n = 122$). The background for mean $\log_{10}$-range size (km²) values above 7 are coloured in grey to facilitate comparison of maximum range sizes across groups.

reported that the net relative associations of phylogeny and space were nil for carnivores, and thus all cross-species variation in range size should be independent of both components (see Freckleton & Jetz, 2009). However, carnivore range size was later shown to be both spatially and phylogenetically constrained (Machac et al., 2011). This suggests that interpretations based on this method need to be cautious. Here, we show that for oscines the phylogenetic component

extensively overlaps with the environmental component in all range size groups (Fig. 4), suggesting environmental niche conservatism (*sensu* Desdevises *et al.*, 2003). Clearly, geographical ranges are shaped partly by biology, and hence species traits must influence range sizes, as shown by Böhning-Gaese *et al.* (2006), who linked dispersal ability to breeding, non-breeding and total range sizes among warblers. Many of these traits may be conserved during cladogenesis (which forms the basis for studies of phylogenetic conservatism of range size) while at the same time responding to environmental conditions. With respect to whether current environment is more important than historical evolutionary constraints in shaping oscine range sizes, our results through both the eigenvector method (Fig. 4) and the GLS approach (see Appendix S3) are consistent with those for mammals (Cooper *et al.*, 2011) in that niche variables (range size in our case) are more strongly affected by spatially structured environmental factors than by phylogenetic inertia, indicating that recent evolution influences the extent of geographical niches more than ancestral evolutionary events.

Consistent with expectation, we found quantitative differences in environmental and phylogenetic signals among sedentary and migratory ranges. In addition, differences were found among breeding and non-breeding ranges of migrants. These differences raise the question of why environmental and phylogenetic signals are not only stronger for breeding ranges of migratory species than for sedentary ranges, but also than for non-breeding ranges of migratory species. A plausible explanation lies in the 'southern home theory' of migration (Gauthreaux, 1982; Levey & Stiles, 1992). This proposes that migratory behaviour evolved in tropical species that were able to breed at higher latitudes, perhaps in connection with climate change; that is, species able to utilize the space opened by the retreat of the ice sheets at the end of each glacial cycle would have competitive advantages during reproduction (Lincoln *et al.*, 1998). An example of how post-glacial recolonization of niches could explain avian migration was provided by Milá *et al.* (2006), and the fact that a large number of migratory oscine clades originated within the Neotropics is consistent with this explanation (Levey & Stiles, 1992; Rappole, 1995; Chesser & Levey, 1998; Ericson *et al.*, 2003). This would also explain why non-breeding ranges are distributed mostly across Central America (Fig. 2c) and resemble sedentary ranges more than breeding ranges of migratories in their size distribution (Fig. 5). Furthermore, non-breeding ranges are more strongly correlated with sedentary ranges than with breeding ranges when the frequency distributions of the ranges within the environmental space are considered ($r_{\text{non-breeding vs. sedentary}} = 0.817$, $r_{\text{non-breeding vs. breeding}} = 0.584$). The 'southern home theory' can also explain differences between sedentary and breeding ranges of migratories in that sedentary species will have experienced less variable climates through time. Accordingly, sedentary oscines are preferentially distributed in tropical mountains or lowlands where climate has remained relatively stable, at

least during the last 21,000 years (Sandel *et al.*, 2011), and species have had more opportunities to diversify. In summary, we suspect that the stronger phylogenetic conservatism and greater influence of the environment on migratory breeding range sizes arises from the ability of migratory oscines to breed in areas where macroclimatic filtering is stronger owing to steeper environmental gradients at higher latitudes both seasonally and across eras (since the Last Glacia Maximum and perhaps during previous Pleistocene interglacial periods).

Finally, it is likely that factors not included in our analysis (e.g. interspecific competition) influence range sizes in different parts of the Western Hemisphere. Also, understanding what drives the spatial structure in range variation that appear to be independent of the abiotic environment (e.g. the amount of range size variation associated with the geographical component independently of the environmental and phylogenetic components, see Fig. 4) will probably require knowledge of specific biological traits that influence range size. Dispersal ability is a key trait (Böhning-Gaese *et al.*, 2006), but we lack these data across the species in our data set. We also acknowledge that, for the few migratory species breeding in areas that were never glaciated, explanations other than post-glacial colonization might be needed. For the moment it is clear that range sizes are evolutionarily constrained and that niche conservatism has a measurable influence on range size patterns, particularly for breeding ranges of migratory species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Species list with $\log_{10}$-transformed range sizes.

Appendix S2 Summary of the number of eigenvectors (k) selected for each of the components (phylogenetic, environmental and geographical), with Moran's I of residuals and associated P-values.

Appendix S3 Details on the range size variation partitioning analyses.

BIOSKETCH

Ignacio Morales-Castilla is interested in macroecology and biogeography with a focus on terrestrial vertebrates and the evolutionary determinants of their diversity gradients.

Author contributions: I.M-C., M.Á.R. and B.A.H. conceived the ideas; I.M-C. and R.K. collected the data; I.M-C. analysed the data; and I.M-C., M.Á.R. and B.A.H. led the writing.

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