

LATITUDINAL VARIATION IN SUBSPECIFIC DIVERSIFICATION OF BIRDS

Paul R. Martin^{1,2,3,4} and Joshua J. Tewksbury^{1,5}

¹*Department of Biology, University of Washington, Box 351800, 24 Kincaid Hall, Seattle, Washington 98195*

²*Yanayacu Biological Station, Cosanga, Napo, Ecuador*

³*Department of Biology, Queen's University, Kingston, Ontario K7L 3N6 Canada*

⁴*E-mail: pm45@queensu.ca*

⁵*E-mail: tewksjj@u.washington.edu*

Received February 19, 2008

Accepted July 15, 2008

Patterns of evolution are believed to vary latitudinally, but our understanding of this variation remains limited. Here we examine how patterns of subspecific diversification vary within species of birds, specifically addressing three questions: (1) Are subspecies more numerous at lower latitudes within species, consistent with greater phenotypic differentiation at lower latitudes? (2) If there are more subspecies at lower latitudes within species, can area of breeding range explain this relationship? and (3) how do latitudinal differences in subspecies within species vary geographically across the globe? Using all species with five or more subspecies from 12 of the most diverse families of birds in the world, we found consistently more subspecies at lower latitudes across all families, both hemispheres, and all continents examined. Despite the positive influence of area on the number of subspecies within species, area did not explain the greater number of subspecies at lower latitudes within species. Global patterns of subspecies support the idea that phenotypic differentiation of populations is greater at lower latitudes within species. If subspecies density provides an index of rates of incipient speciation, then our results support evolutionary hypotheses for the latitudinal diversity gradient that invoke higher tropical speciation rates.

KEY WORDS: Biodiversity, latitude, latitudinal gradients, population differentiation, speciation, subspecies.

Evolutionary processes such as selection, drift, and gene flow vary in their strength and importance over latitude (Darwin 1859; Wallace 1878; Dobzhansky 1950; Fischer 1960; Schemske 2002; Mittelbach et al. 2007), but the texture and the consequences of this variation are poorly understood. One of the potential consequences of latitudinal variation in evolutionary processes is variation in population differentiation. Population differentiation is of biological importance because of its central relationship to adaptive differentiation and allopatric speciation (Mayr 1942, 1963; Coyne and Orr 2004).

How does population differentiation vary latitudinally and across the globe? This question has been difficult to address because there are few broad global datasets that contain information on population differentiation across many species. Arguably the largest and most complete set of data on this subject comes from

subspecific differentiation in birds, and a number of previous studies have used patterns of avian subspecific diversity to examine correlates of differentiation (Rensch 1933; Møller and Cuervo 1998; Belliure et al. 2000; Mayr and Diamond 2001; Newton 2003; Sol et al. 2005). Most recently, Phillimore et al. (2007) examined global patterns of subspecies richness across all species of birds in the world, and found several correlates of high subspecific differentiation, including breeding range area, occurrence on islands and in montane regions, habitat heterogeneity, and latitude in the southern, but not in the northern, hemisphere (Phillimore et al. 2007).

Previous studies of subspecies richness have focused on comparisons across species, in part because across-species comparisons do not require details of the distributions of subspecies that are cumbersome to generate. Comparing the number of subspecies

across species, however, can lead to results that are difficult to interpret. Where speciation involves the “budding” off of peripheral, isolate populations, sister species could often display opposite patterns—the more ancestral species retaining a large number of subspecies, the derived member having no subspecies at all. In these cases, the mean number of subspecies per species may not positively covary with rates of diversification. To avoid this potentially confounding issue, here we focus on patterns of subspecific distribution within species, and specifically within species that have many (five or more) subspecies. We then use the distribution of subspecies within these species to test hypotheses regarding subspecific diversification relative to latitude, and the influence of area on subspecific diversification.

EVOLUTIONARY HYPOTHESES FOR THE LATITUDINAL DIVERSITY GRADIENT

Examining patterns of population differentiation can provide insight into evolutionary hypotheses for the present-day latitudinal diversity gradient if population differentiation provides an index of incipient diversification and speciation (Mittelbach et al. 2007; see Supporting Appendix S1 for support). In a recent review, Mittelbach et al. (2007) classified evolutionary hypotheses for the latitudinal gradient into two broad categories: in the first, diversification rates are similar between temperate and tropical regions, but time for diversification has been greater in the tropics, and in the second diversification rates are higher in the tropics, resulting from either higher speciation rates or lower extinction rates at lower latitudes. A higher density of subspecies at lower latitudes within species would support the second group of hypotheses that invoke higher tropical diversification rates through speciation.

Here we use subspecies distributions within focal species to address three questions: (1) Are subspecies more numerous at lower latitudes within species, consistent with greater phenotypic differentiation at lower latitudes?, (2) If there are more subspecies at lower latitudes within species, can area of breeding range explain this relationship?, and (3) how do latitudinal differences in subspecies within species vary geographically across the globe? We further gathered available molecular phylogenetic data on focal groups to provide a historical, evolutionary context to variation in subspecies density over latitude.

Materials and Methods

We followed familial taxonomy of Monroe and Sibley (1993) and specific and subspecific taxonomy of Dickinson (2003). We mapped breeding distributions of focal taxa using a diverse array of literature (Supporting Appendix S2). Maps were created using ArcGIS 8.3 (ESRI, Redlands, California). We examined only breeding distributions because speciation occurs when breeding populations diverge from one another, regardless of wintering or

migratory distributions (Mayr 1942, 1963; Coyne and Orr 2004). Area and latitudinal calculations were made using ArcView 3.2, ArcGIS 8.3 and 9.1, and the Xtools extension.

We examined patterns of subspecific variation in the six most diverse families of nonpasserine and six most diverse families of passerine birds in the world (12 families total; Nonpasserines: Phasianidae, Picidae, Trochilidae, Psittacidae, Columbidae, Accipitridae; Passerines: Tyrannidae, Corvidae, Muscicapidae, Sylviidae, Passeridae, Fringillidae). Within each family, we examined the latitudinal distribution of subspecies within all species that have five or more subspecies per hemisphere. Examining species with five or more subspecies per hemisphere restricted our analysis to species that are actively differentiating and/or old, and provided sufficient variation within a species to examine latitudinal patterns in this differentiation. To address a potential bias of restricting our analysis in this way, we extended our analysis to include all species with subspecies in the two most diverse nonpasserine and passerine families (Trochilidae—331 species, and Fringillidae—1005 species, respectively).

For each species examined, we split the breeding distribution into low and high latitudes by dividing the latitudinal breadth within a hemisphere equally by two (Fig. 1). We then counted the number of subspecies that bred within low versus high latitude regions, and measured the area (km²) of the breeding range within the same regions. Subspecies distributions were assessed using an extensive literature provided in Supporting Appendix S2.

For species that overlapped the equator, we only examined subspecific patterns within the hemisphere(s) that held five or more subspecies. In each case, we cut the distribution at the equator, and examined the latitudinal distribution of the five or more subspecies in the breeding distribution that fell within the focal hemisphere, disregarding all subspecies and distributions in the other hemisphere (Fig. 1). If a species showed five or more subspecies within both hemispheres, we took the average number of subspecies and area of breeding distributions in low versus high latitudinal belts across both hemispheres for use in the overall analysis. Thus, each species is represented only once in our analysis. When we examined patterns in northern and southern hemispheres independently, we used data taken from the hemisphere under consideration.

To address the potential influence of our choice of taxonomic references, we examined the distribution of subspecies for a subset of our original sample (all six nonpasserine families, chosen a priori) following the alternative specific and subspecific taxonomy of del Hoyo et al. (1992–2002) that considered some subspecies in Dickinson (2003) to be full species. We also examined the distribution of subspecies for all six nonpasserine families excluding islands from the analysis to address the potential criticism that island taxa biased our results. We further repeated our analysis without species that overlapped the equator to address

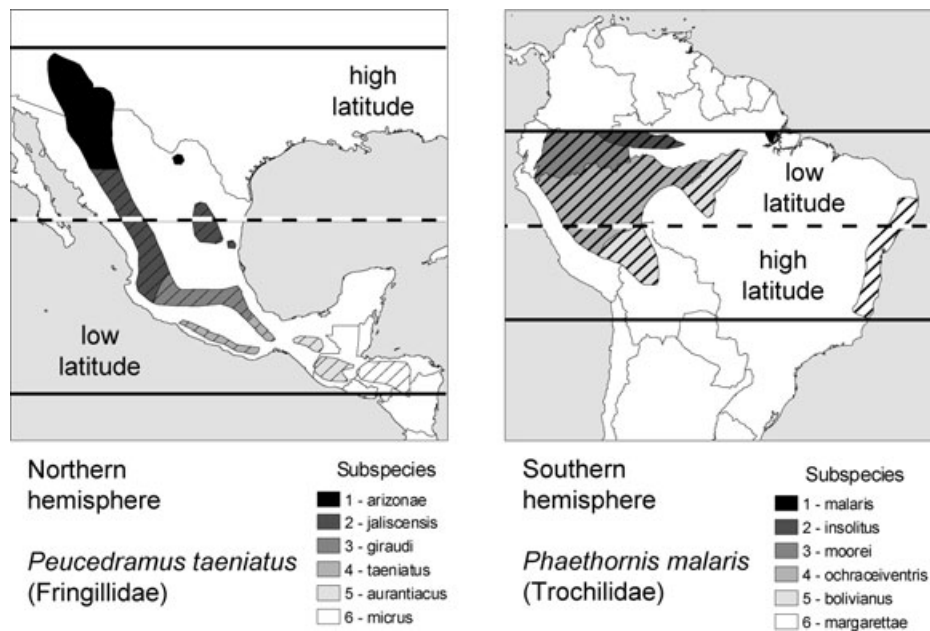


Figure 1. Two examples of the methodology, using the Olive Warbler (Fringillidae: *Peucedramus taeniatus*) and Great-billed Hermit (Trochilidae: *Phaethornis malaris*). We mapped breeding distributions of all focal species, and then divided distributions into regions of equal latitudinal breadth within a hemisphere (dashed lines, latitudinal midpoint in each species). We then counted the number of subspecies occurring at low versus high latitudes. In the case of the Olive Warbler and Great-billed Hermit, five and six subspecies occur at low latitudes and two and three subspecies at high latitudes, respectively.

any potential bias of our method for analyzing equatorial species. If subspecific density simply reflects biased taxonomy, we predicted that the highest density of subspecies should be found in areas that have received the most attention from taxonomists—the north temperate regions of Europe and North America. To address this potential bias, we repeated our analysis after excluding all species that occurred in regions of highest taxonomic effort (25–50°N in the Americas, 35–60°N in Europe).

Geographic variation in taxonomic effort could still cause bias when using subspecies densities as a measure of phenotypic evolution (Isaac et al. 2004; Agapow et al. 2004), particularly if greater taxonomic research leads to an increased likelihood of discovering cryptic species that were previously described as subspecies. We attempted to limit the effects of geographic variation in taxonomic effort, and the likelihood of discovering cryptic species, by examining the subspecies distributions within species, as taxonomic reviews are usually conducted by the same authors across all subspecies within a species. This methodology, however, does not address the potential influence of geographic variation in taxonomic effort within the distributions of species. We might expect a latitudinal bias in taxonomic effort within species to lead to a disproportionate number of cryptic species (previously recognized as subspecies) in equatorial or polar regions of species ranges. A review of the recently described bird species that were previously described as subspecies from the Americas north of the Panamanian border does not suggest such a latitudinal bias

(American Ornithologists' Union 1998; Banks et al. 2000, 2002, 2003, 2004, 2005, 2006, 2007).

STATISTICAL TESTS

We tested three hypotheses: (1) More subspecies occur at lower latitudes as compared with higher latitudes within species. (2) More subspecies at lower latitudes can be explained by variation in area of the breeding range at low versus high latitudes. (3) The latitudinal differences in subspecies within species vary geographically across the globe. We tested the first and second hypotheses simultaneously using the entire dataset (710 species, 6129 subspecies). We used a Linear Mixed-Effects Model fit by maximum likelihood with the $\ln(\text{number of subspecies in low latitude/number of subspecies in high latitude})$ as the dependent variable, $\ln(\text{area in low latitude/area in high latitude})$ as a fixed factor, and family as the grouping variable. Thus, the area term assesses the importance of differing area of the breeding range at high and low latitudes on the number of subspecies at high and low latitudes, whereas the model intercept tests the hypothesis that the number of subspecies differs between low and high latitudes independent of area. This statistical approach provides a paired framework within species, and thus controls for variation among species and for phylogeny (assuming species are monophyletic—we test this assumption below). We tested the third hypothesis, that the latitudinal differences in subspecies within species varied geographically across the globe, using a Linear Mixed-Effects Model

fit by maximum likelihood and using treatment contrasts, with the $\ln(\text{number of subspecies in low latitude}/\text{number of subspecies in high latitude})$ as the dependent variable, $\ln(\text{area in low latitude}/\text{area in high latitude})$ and “continental region” as fixed factors in a saturated model, and family as the grouping variable. The saturated model was run, and then simplified in a step-wise fashion, removing the most complicated factors that did not significantly improve the model (Crawley 2002). An improved model was identified by a lower AIC (Akaike Information Criterion) value, whereas the significance of the improvement was assessed using analysis of variance (ANOVA) ($\alpha = 0.01$ cutoff) (Crawley 2002). “Continental region” represented 14, 20° latitude-wide regions across the world (Americas: 0–20°S, 20–40°S; 0–20°N, 20–40°N, 40–60°N); Africa: 0–20°S, 20–40°S, 0–20°N; Australasia: 0–20°S, 20–40°S, 40–60°S; Eurasia: 0–20°N, 20–40°N, 40–60°N). We grouped all species whose centroid latitude fell within a given focal 20° latitude belt, and plotted geographical variation in the latitudinal differences in subspecies within species taken from the model intercepts for each region (controlling for variation in the area of breeding ranges). Centroid latitude is the area-weighted latitudinal midpoint of a species’ range and provides a better approximation of the latitudinal distribution of a species’ range than does the latitudinal midpoint (Cardillo et al. 2005).

Additional Linear Mixed-Effects models were run with $\ln(\text{number of subspecies in low latitude}/\text{number of subspecies in high latitude})$ as the dependent variable and family as the grouping variable to address potentially confounding factors. These additional tests involved (1) using an alternative subspecific taxonomy, (2) excluding island taxa, (3) excluding species that overlapped the equator, (4) excluding regions of highest taxonomic effort, and (5) examining all species with the Trochilidae and Fringillidae.

Overall, we performed three statistical tests of hypotheses, and used a sequential Bonferroni correction to control for multiple tests on nonindependent data (Rice 1989). Further corrections for additional tests (i.e., the five performed to address potentially confounding factors) were not warranted, because these additional tests did not inflate Type I error.

PHYLOGENETIC DATA

Taxonomies used in this analysis are generally consistent with phylogenetic evidence based on molecular data (i.e., species are usually monophyletic; see Monroe and Sibley [1993] and Dickinson [2003] for citations and detailed discussion); however, there are very few cases in which molecular data are available for all subspecies within a species and their potential sister species, allowing a test for monophyly. If the species are not monophyletic, then subspecific divergence only describes part of the historical divergence of the lineage. Paraphyly, however, may lead to an underestimation or overestimation of the latitudinal bias in

phenotypic differentiation, depending on where the paraphyletic species sits latitudinally. To address the issue of monophyly, we found all published molecular phylogenies based on mtDNA for our 710 focal species, where the majority of subspecies (>75%) and potential sister species were represented. We used published phylogenies to (1) test for the prevalence of paraphyly among focal species, and (2) examine how the inclusion of paraphyletic taxa changed the latitudinal patterns of phenotypic divergence within the lineage.

Results

Of the 710 focal species examined, 65.6% had more subspecies at lower latitudes, 14.4% showed equal number of subspecies at low and high latitudes, and 20.0% had more subspecies at higher latitudes. Overall, a significantly greater number of subspecies occurred in low latitude (5.95 subspecies/species, 75.9%), as compared with high latitude (4.14 subspecies/species, 56.1%), portions of a species’ range (Table 1). This pattern was consistent across all 12 families of birds (Fig. 2), across both hemispheres, and across six continents (Fig. 3A), despite varying latitudinal patterns in area of the breeding range across continents (Fig. 3B). Area was a strong predictor of subspecies richness within species (Tables 1 and 2), but because area of the breeding range was not consistently greater at lower or higher latitudes within species (Fig. 3B), the inclusion of breeding range area had no significant effect on the pattern of greater subspecies at lower latitudes—this pattern remained almost identical when area was included in the model compared to the same model with area removed (Fig. 3C).

The latitudinal differences in subspecies within species varied significantly across continental regions of the world (Table 2; Fig. 4). All regions showed a significantly greater number of subspecies at lower latitudes with the exception of tropical America (0–20°N), southern Africa (20–40°S), and New Zealand (40–60°S) (Fig. 4). In general, differences were strongest in the extra-tropical regions of the northern hemisphere. Among southern

Table 1. Results of a linear mixed-effects model testing the importance of latitude (high or low) and differential area of breeding range in determining the number of subspecies within species.

	Value ²	SE	df	<i>t</i> -value	<i>P</i> -value
Latitude ¹	0.390	0.051	697	7.7	<0.0001
Area ²	0.101	0.024	697	4.2	<0.0001

¹Latitude tests the central hypothesis that the number of subspecies differs between low and high latitudes within species (a test of the intercept differences in this model). A value greater than zero indicates more subspecies at lower latitudes.

²Both the number of subspecies (dependent variable) and area of the breeding range (fixed factor) were calculated as $\ln(\text{low latitude value}/\text{high latitude value})$.

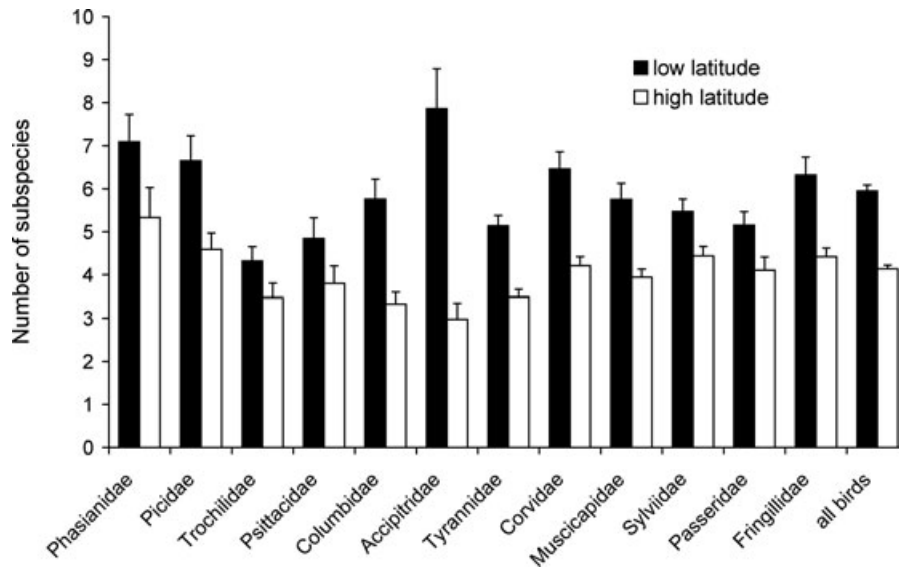


Figure 2. Number of subspecies per species (mean+SE) in low versus high latitude portions of the breeding range in species with five or more subspecies per hemisphere across 12 diverse nonpasserine and passerine avian families. Sample sizes are as follows (species [subspecies]): Phasianidae (33 [300]), Picidae (41 [371]), Trochilidae (22 [156]), Psittacidae (25 [173]), Columbidae (38 [283]), Accipitridae (21 [203]), Tyrannidae (65 [533]), Corvidae (117 [1087]), Muscicapidae (63 [583]), Sylviidae (94 [727]), Passeridae (49 [381]), Fringillidae (142 [1333]), all birds (710 [6129]).

hemisphere continents, South America showed the strongest latitudinal patterns (Fig. 4).

The overall differences in subspecies within species between low and high latitudes persisted when we used an alternative taxonomy (del Hoyo et al. 1992–2002; nonpasserines, $t = 4.79$, $df = 164$, $P < 0.0001$, $N = 170$ species), and when all islands were excluded from analyses (nonpasserines, $t = 4.62$, $df = 105$, $P < 0.0001$, $N = 111$ species). The pattern also persisted when we excluded species with distributions that overlapped the equator ($t = 8.05$, $df = 344$, $P < 0.0001$, $N = 356$ species) and species that occur within areas of highest taxonomic effort (temperate North America and Europe) ($t = 3.97$, $df = 478$, $P < 0.0001$, $N = 490$ species). The pattern was not restricted to species with five or more subspecies. Species of Trochilidae and Fringillidae with any subspecific differentiation showed significantly more subspecies at lower latitudes ($t = 3.60$, $df = 673$, $P = 0.0003$, $N = 675$ species).

Molecular phylogenetic data representing >75% of subspecies within a species, in addition to potential sister species, were available for only 26 of the 710 species examined in our study (Table 3). In 23 of these species, at least some of the subspecies did not show reciprocal monophyly at the mtDNA locus examined, and breaks in mtDNA did not necessarily correspond with subspecific designations. In total, seven species (27%) were paraphyletic, with sister species more recently diverged than some subspecies (Table 3). Incorporating paraphyletic species within the analysis did not change results for these seven species. Using the original taxonomy (Dickinson 2003), three of seven species

showed a greater number of subspecies at lower latitudes, whereas three of seven species showed a greater number of taxa (subspecies and species) at lower latitudes when we examined monophyletic lineages (i.e., incorporating paraphyletic taxa). Across the seven species, paraphyletic taxa occurred only at lower latitudes in one species, at both lower and higher latitudes in five species, and only at higher latitudes in one species.

Evidence suggests that subspecies are precursors to species and provide an index of divergence relevant to diversification (Supporting Appendix S1). This evidence includes a positive relationship between the observed maximum number of subspecies per species within a genus and the number of species within that genus (after controlling for the null expectation), suggesting that genera that have differentiated significantly in the past are continuing to show significant differentiation at the subspecies level (Supporting Figure S1; $F = 281$, $df = 1$, $P < 0.0001$; $N = 2150$ genera, 9674 species, 21,479 subspecies, following the taxonomy of Dickinson 2003).

Discussion

LATITUDINAL DIFFERENCES IN SUBSPECIFIC DIVERSIFICATION WITHIN SPECIES

Within focal species of birds, more subspecies occur at lower as compared with higher latitudes across 12 families, six continental regions, and both hemispheres, regardless of variation in area of the breeding range (Table 1; Figs. 2 and 3). This general result persisted when we used an alternative taxonomy, and when

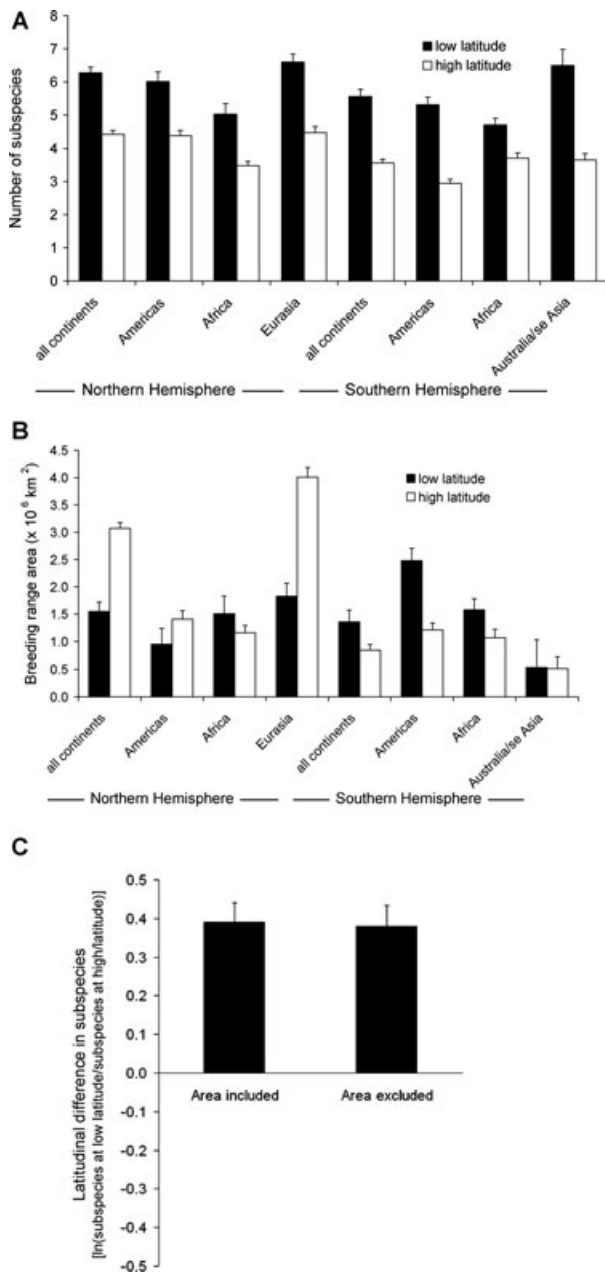


Figure 3. (A) Number of subspecies per species (mean±SE) in low versus high latitude portions of the breeding range in species with five or more subspecies per hemisphere across continental regions in each hemisphere. (B) Area of the breeding range (mean±SE) for these same species in low versus high latitude portions of the breeding range across the same continental regions in each hemisphere. Sample sizes for (A) and (B) are as follows (species [subspecies]): Northern Hemisphere: all continents (503 [4107]), Americas (223 [1825]), Africa (37 [220]), Eurasia (224 [1873]); Southern Hemisphere: all continents (276 [2023]), Americas (82 [518]), Africa (71 [461]), Australasia (107 [907]). (C) Latitudinal difference in the number of subspecies within species when area was included in the model (effect of latitude, $t=7.7$, $P<0.0001$), and when area was excluded from the model ($t=7.1$, $P<0.0001$). A value greater than zero indicates more subspecies at lower latitudes.

we excluded island taxa, equatorial species, and regions of high taxonomic effort. The overall result suggests that subspecific diversification within species is greater at lower latitudes across most regions of the earth (Figs. 3A and 4). These results correspond well to studies of diversification rates in birds that found higher rates of diversification in tropical as compared with temperate clades (Cardillo 1999; Cardillo et al. 2005; Ricklefs 2005, 2006; see also Hawkins et al. 2006, 2007; Diniz-Filho et al. 2007; Supporting Appendix S1).

A recent study of the global patterns of subspecific variation across species of birds found more subspecies per species at lower latitudes within the southern, but not northern, hemispheres (Phillimore et al. 2007), inconsistent with our results showing more subspecies within species across both hemispheres. The difference in results is likely due to variation in across-species versus within-species patterns of subspecies densities. Phillimore et al. (2007) examined data on the number of subspecies per species, but not the location of those subspecies within the range of the species. Using this methodology, species with broad distributions that include both the tropics and high latitudes (e.g., *Dendroica petechia*; Browning 1994) dampen latitudinal trends in subspecies richness. High speciation rates in the tropics (Jablonski 1993; Jablonski et al. 2006; but see Weir and Schluter 2007) could also obscure patterns at the species level by increasing variance in the number of subspecies per species, if peripheral subspecies commonly split off to form new monotypic species (Funk and Omland 2003). This peripheral isolate pattern of speciation could leave the basal sister species with many subspecies, and the derived sister species monotypic. Phillimore et al. (2007) found no relationship between the age of species and the number of subspecies, and an overall low phylogenetic signal, both of which are consistent with a peripheral isolate model of speciation creating high variance in the number of subspecies per species within lineages.

Table 2. Factors contributing to a linear mixed-effects model to explain latitudinal differences in the number of subspecies within species. Statistics and P -values are from sequential model simplification moving from most complex to least complex terms. See Figure 4 for illustrations of the continental regions and their intercepts.

	ΔAIC^1	L.Ratio	P -value
area ²	11.8	13.8	0.0002
Continental region	61.8	87.8	<0.0001
Area × continental region	-3.4	22.6	0.047

¹A positive change in AIC when the factor was dropped from the model indicates a significant contribution of the factor to the model.

²Both the number of subspecies (dependent variable) and area of the range (fixed factor) were calculated as $\ln(\text{low latitude value}/\text{high latitude value})$.

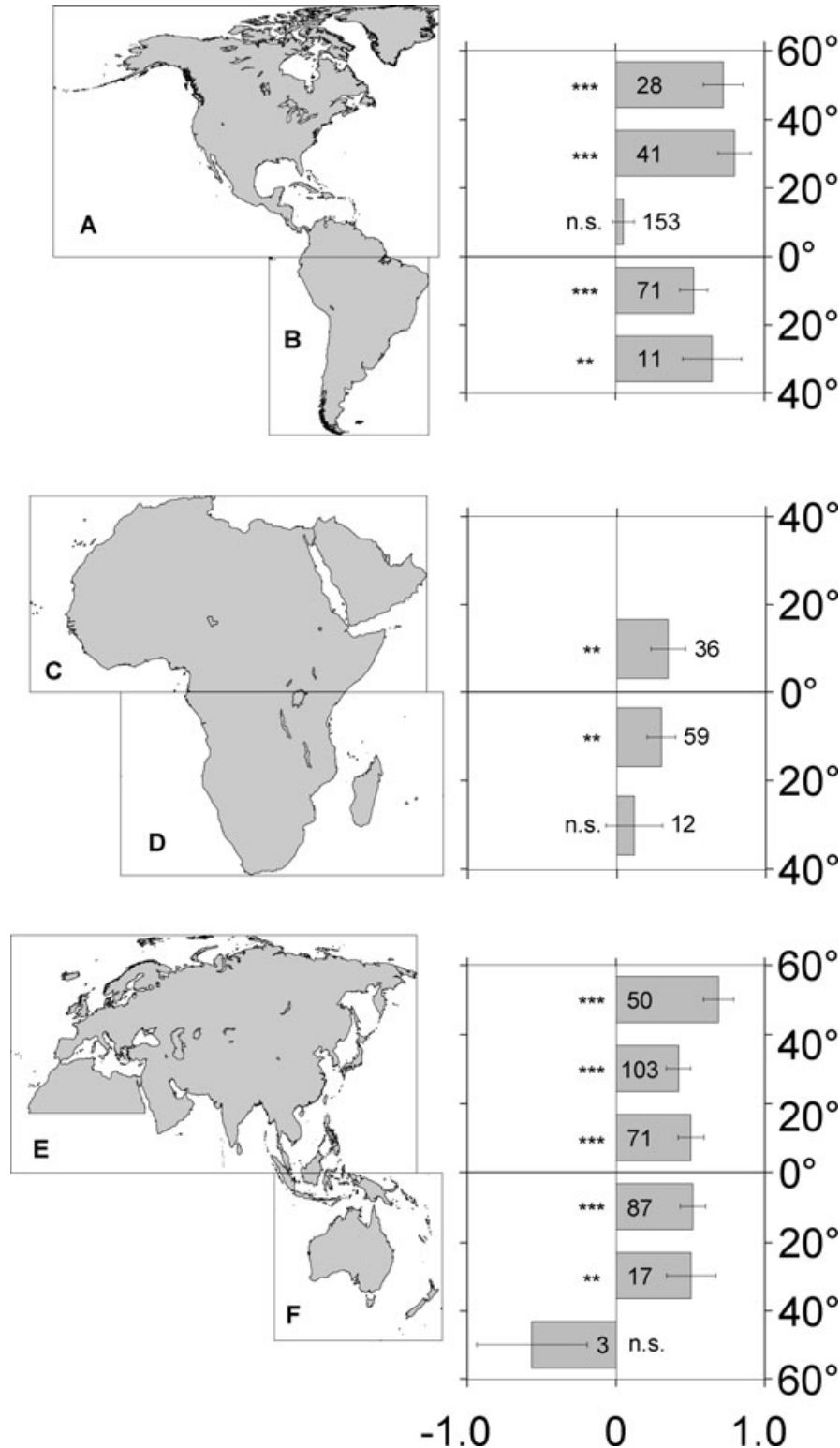


Figure 4. Difference in the number of subspecies between low and high latitude belts within species [$\ln(\text{subspecies at low latitude}/\text{subspecies at high latitude})$; mean \pm SE] across six continental regions. Asterisks signify statistically significant differences from zero (n.s.=not significantly different; ** $P < 0.01$; *** $P < 0.0001$). Species were grouped within regions based on the centroid latitude of their breeding range within a focal hemisphere. The relative difference in subspecies represents the intercepts for each region from a linear mixed-effects model that statistically controlled for variation in the area of breeding range. Values to the right of zero are consistent with the prediction that more subspecies occur at lower latitudes within species. Numbers associated with bars are sample sizes.

Table 3. Focal species for which molecular (mtDNA) data were available for the majority of subspecies and potential sister species, allowing tests of mtDNA monophyly.

Family	Genus	Species	Total subspecies	Subspecies low latitude	Subspecies high latitude	Subspecies monophyletic	Species monophyletic	All subspecies monophyletic	% subspecies with genetic data	References
Phasianidae	<i>Meleagris</i>	<i>gallopavo</i>	6	6	3	no	yes	no	83	Mock et al. 2002
Phasianidae	<i>Tetrao</i>	<i>urogallus</i>	9	8	6	no	yes	no	100	Duriez et al. 2007
Accipitridae	<i>Milvus</i>	<i>migrans</i>	7	7	2	no	no	no	86	Johnson et al. 2005
Accipitridae	<i>Buteo</i>	<i>buteo</i>	11	11	5	no	no	no	91	Kruckenhauser et al. 2004
Accipitridae	<i>Spizaetus</i>	<i>cirrhatius</i>	6	5	2	no	yes	no	100	Gamauf et al. 2005
Tyrannidae	<i>Schiffornis</i>	<i>turdina</i>	13	8	3	no	yes	no	77	Nyári 2007
Tyrannidae	<i>Lepidothrix</i>	<i>coronata</i>	8	4.5	3.5	no	yes	no	88	Cheviron et al. 2005
Corvidae	<i>Cyanopica</i>	<i>cyana</i>	8	7	6	no	yes	no	100	Fok et al. 2002
Corvidae	<i>Gymnorhina</i>	<i>tibicen</i>	9	4	7	no	yes	no	89	Toon et al. 2003, 2007
Corvidae	<i>Artamus</i>	<i>cinereus</i>	5	4	3	no	yes	no	80	Joseph et al. 2006; Joseph and Wilke 2007
Muscicapidae	<i>Myadestes</i>	<i>genibarbis</i>	6	4	2	yes	yes	yes	83	Miller et al. 2007
Muscicapidae	<i>Catharus</i>	<i>ustulatus</i>	6	4	4	no	yes	no	83	Ruegg and Smith 2002
Muscicapidae	<i>Enicurus</i>	<i>leschenaulti</i>	6	4	2	yes	yes	yes	83	Moyle et al. 2005
Sylviidae	<i>Iduna</i>	<i>pallida</i>	6	5	5	no	no	no	83	Ottosson et al. 2005
Sylviidae	<i>Phylloscopus</i>	<i>collybita</i>	6	6	3	no	yes	no	83	Helbig et al. 1996
Sylviidae	<i>Phylloscopus</i>	<i>reguloides</i>	7	4	5	yes	yes	yes	100	Olsson et al. 2005
Sylviidae	<i>Alcippe</i>	<i>morrisonia</i>	7	5	6	no	no	no	86	Pasquet et al. 2006; Zou et al. 2007
Sylviidae	<i>Chamaea</i>	<i>fasciata</i>	5	3	5	no	yes	no	100	Burns and Barhoum 2006
Passeridae	<i>Motacilla</i>	<i>flava</i>	17	10	15	no	no	no	82	Ödeen and Björklund 2003; Pavlova et al. 2003
Fringillidae	<i>Carpodacus</i>	<i>erythrinus</i>	5	5	3	no	yes	no	80	Arnaiz-Villena et al. 2001; Pavlova et al. 2005
Fringillidae	<i>Passerella</i>	<i>iliaca</i>	15	7	12	no	yes	no	80	Zink 1994; Zink and Weckstein 2003
Fringillidae	<i>Zonotrichia</i>	<i>leucophrys</i>	5	5	2	no	no	no	100	Weckstein et al. 2001
Fringillidae	<i>Spizella</i>	<i>passerina</i>	5	5	2	no	yes	no	100	Carson and Spicer 2003; Milá et al. 2006
Fringillidae	<i>Buarremon</i>	<i>brunneinuchus</i>	10	3	8	no	no	no	90	Cadena et al. 2007
Fringillidae	<i>Buarremon</i>	<i>torquatus</i>	14	2.5	6.5	no	yes	no	93	Cadena et al. 2007
Fringillidae	<i>Certhidea</i>	<i>olivacea</i>	8	2	5	no	yes	no	100	Tomms et al. 2005

Given that subspecific differentiation is a likely precursor to the majority of speciation events in birds (Mayr 1942, 1963; Price 2008), a greater density of subspecies at lower latitudes suggests a greater opportunity for future speciation at lower latitudes within species, all else being equal. Other factors that influence the likelihood of future speciation, however, may also vary latitudinally, including the degree of phenotypic differentiation of subspecies, gene flow among subspecies, transition times to speciation, strength and patterns of selection, the relative importance of genetic drift, and the likelihood of subspecific extinction. Data are not presently available to address latitudinal variation in all of these factors. Nonetheless, the degree of phenotypic differentiation varies significantly among subspecies (e.g., *Coereba flaveola*; Seutin et al. 1994), with some subspecies differentiated to the verge of allopatric sister species, and others barely distinguishable from each other. The degree of differentiation also varies latitudinally in some species (e.g., *D. petechia*; Browning 1994); however, we presently know of no data that address a general latitudinal pattern.

Data are available on latitudinal variation in genetic variation among populations within species (Martin and McKay 2004; Eo et al. 2008). These data suggest greater evolutionary independence of low latitude populations. In addition, the correspondence between subspecific differentiation and differentiation in genes believed to evolve by drift is also stronger in lower latitude species (see Phillimore and Owens 2006; cf Zink 2004), supporting the idea that subspecies at lower latitude may exhibit greater evolutionary independence. Given that gene flow impedes population differentiation, greater evolutionary independence of low latitude populations could potentially explain a greater number of subspecies occurring at lower latitudes, and may predispose subspecies to future divergence and speciation.

Transition (or lag) time to speciation is the time between initial divergence of populations and the evolution of reproductive isolation that defines a biological speciation event (Coyne and Orr 2004). Transition time to speciation appears to be longer for tropical populations (Chek et al. 2003; Weir and Schluter 2007), and thus could bias estimates of speciation rates over latitude based solely on subspecies densities. In other words, the influence of more subspecies at lower latitudes on speciation rates could potentially be offset by the longer time required for reproductive isolation to evolve among low latitude subspecies. Reconciling these opposing influences on latitudinal variation in speciation rates will require more detailed intraspecific phylogenetic information than is presently available.

The strength and patterns of selection, the relative importance of genetic drift, and the likelihood of subspecific extinction may also vary latitudinally, but at present we have little comparative evidence to address these patterns. The strength and patterns of selection have long been thought to vary latitudinally (e.g.,

Darwin 1859, pp. 69, 78; Wallace 1878; see Mittelbach et al. 2007), but we know of no data to explicitly test this hypothesis. Greater evolutionary independence of populations at lower latitudes within species (Martin and McKay 2004; Eo et al. 2008) may suggest smaller effective population sizes and a greater potential for drift at lower latitudes (see also Fedorov 1966); however, population bottlenecks at higher latitudes during glacial expansions and retractions make drift a likely influence at higher latitudes as well (Bernatchez and Wilson 1998; Hewitt 2000; Hughes and Hughes 2007). Similarly, subspecific extinction could be greater at higher latitudes (e.g., species-level model, Weir and Schluter 2007; genus-level fossil data, Jablonski et al. 2006); however, small population and range sizes of lower latitude subspecies could increase rates of extinction at lower latitudes (Hansen 1980; Jablonski et al. 1985 and references within; see also Soulé 1986), consistent with other evidence (e.g., order-level fossil data, Martin et al. 2007). Overall, a greater number of subspecies at lower latitudes within species presents a greater potential for future speciation; however, other factors such as transition times to speciation or variation in selection could alter any relationship between the number of subspecies and speciation rate.

SUBSPECIFIC AGE AND PARAPHYLY

The majority of subspecies did not show reciprocal monophyly at the mtDNA locus (see also Zink 2004; Phillimore and Owens 2006). This is consistent with subspecific differences evolving quickly in response to selection, and differences in mtDNA among populations evolving slowly by genetic drift (Hudson and Coyne 2002). A total of 19 of 26 species examined in this study were monophyletic at the mtDNA locus. If the mtDNA phylogenies are congruent with species-level phylogenies (Nichols 2001), then these subspecies shared a more recent common ancestor with each other than with any other species. For these monophyletic species, subspecies differentiation provides a good approximation of phenotypic differentiation within the lineage. For the seven paraphyletic species, some subspecies were equally or more closely related to another species compared to other subspecies within the species. Paraphyly means that subspecific diversification describes only part of the evolutionary diversification of these lineages, and thus focusing on subspecies could potentially bias latitudinal patterns of differentiation in either direction. When we examined subspecific and specific differentiation of the monophyletic lineages (i.e., incorporating paraphyletic taxa into the analysis), we found no difference in the results—the same number of species (3/7) had more subspecies at lower latitudes regardless of whether we controlled for paraphyly or not. Thus the limited data available provide no evidence that paraphyly influences the general latitudinal patterns in subspecies densities.

AREA

Area has long been known to have a significant influence on patterns of richness (Brown 1995; Rosenzweig 1995; Kalmar and Currie 2006, 2007), and has been advocated as the major cause of latitudinal variation in richness within the “area hypothesis” (Terborgh 1973; Rosenzweig 1992, 1995, 2003). Although we found evidence for a strong, positive relationship between area of the breeding range and number of subspecies (see also Graves 1985), this relationship had no effect on latitudinal differences in subspecies richness within species (Fig. 3C). More subspecies are consistently found in the low latitude sections of the range (Fig. 3A), and area of breeding range did not consistently vary with latitude within species (Fig. 3B). Given that the mechanism by which area is thought to influence both subspecific differentiation and speciation is the same (i.e., through the increase in geographic barriers with increasing area; Rosenzweig 1995), these results suggest that increased area is not a cause of latitudinal variation in avian richness, at least through a speciation mechanism (see also Rohde 1997; Cardillo 1999; Ruggiero 1999; Chown and Gaston 2000; Fine 2001; Hawkins and Porter 2001; Macpherson 2002; Fine and Ree 2006; Willig and Bloch 2006; Mittelbach et al. 2007).

LATITUDINAL DIFFERENCES IN SUBSPECIFIC DIVERSIFICATION AROUND THE WORLD

The latitudinal differences in subspecies within species varied significantly across the world. Although more subspecies were found in low latitude regions within species in most regions, this relationship was not significant in tropical America just north of the equator and southern Africa, and not present in New Zealand (Fig. 4). Tropical America north of the equator (0–20°N) includes many regions of high diversification (e.g., the Lesser Antilles and Central America) that approach the upper limits of this region (20°N), and thus we should expect little latitudinal variation in subspecific diversification within this area. Similarly, the Cape region of southern Africa is famous for its high rates of population differentiation and speciation (e.g., Latimer et al. 2005), consistent with the lack of a significant latitudinal pattern in subspecific diversification there (Fig. 4). In the case of high latitude Australasia (40–60°S), only three species were represented, and all were island taxa occurring in New Zealand and nearby islands (Psittacidae: *Cyanoramphus novaeseelandiae*, Sylviidae: *Megalurus punctatus*, Passeridae: *Anthus novaeseelandiae*). In these cases, the lack of relationship between latitude and subspecies density reflects the overwhelming influence of island isolation on subspecific diversification, with high latitude island populations (e.g., Macquarie, Antipodes Is.) equally likely to differentiate as compared with lower latitude island populations (e.g., Norfolk, Kermadec Is.).

CAUSES OF THE LATITUDINAL DIVERSITY GRADIENT

The general correspondence between the strength of latitudinal differences in subspecies density within species (Fig. 4) and published data on variation in the latitudinal gradient in species richness [on a regional (e.g., > 40,000 km²) scale; Hawkins et al. 2003b; Orme et al. 2005] suggests either causal relationships between the two factors, or covariation due to common influences. We suggest that subspecific differentiation provides an index of evolutionary diversification relevant to speciation (see Supporting Appendix S1), and that covariation between the latitudinal gradient in species richness and subspecific differentiation reflects the importance of population differentiation and speciation in creating high regional diversity. This regional diversity provides the pool of species that may subsequently expand into sympatry (Ricklefs 1987, 2007), thus allowing local richness to increase in response to other factors. A number of studies suggest that these other factors are dominated by available energy that may limit the number of species that can coexist locally across the globe (Wright et al. 1993; Hawkins et al. 2003a,b; Currie et al. 2004; Kalmar and Currie 2007).

If subspecies density does provide an index of rates of speciation, then our results support evolutionary hypotheses for the latitudinal diversity gradient that invoke higher tropical speciation rates. These hypotheses include differential effects of Milankovitch (glacial) cycles over latitude (Dynesius and Jansson 2000), reduced tropical seasonality of temperature (Janzen 1967; Ghalambor et al. 2006), warmer temperatures causing faster rates of tropical evolution (Rohde 1992; Allen et al. 2002), and a greater importance of biotic versus abiotic selective pressures in the tropics (Dobzhansky 1950; Fischer 1960; Schemske 2002; see Mittelbach et al. 2007 for broader discussion). Testing among these hypotheses will require a spatially explicit dataset that incorporates causal factors instead of using latitude as a surrogate variable (Rahbek and Graves 2001; Hawkins and Diniz-Filho 2004).

An alternative explanation for more subspecies at lower latitudes within species of birds is that greater densities of subspecies may reflect lower rates of speciation, consistent with recent work on birds and mammals. Weir and Schluter (2007) found younger sister species at higher latitudes, after controlling for latitudinal differences in transition times to speciation—a result consistent with greater speciation rates and greater extinction rates of species at higher latitudes. This conclusion was based on several assumptions, including the assumption that latitudinal variation in maximal population divergence within species approximates transition times to speciation, and the assumption that latitudinal variation in species-level taxonomies does not overly bias ages of sister species (Weir and Schluter 2007). If these assumptions hold and speciation rates are greater at higher latitudes in birds and mammals, then densities of subspecies may be negatively

related to rates of speciation. Such a situation could arise if subspecies are transient at higher latitudes, becoming sister species more rapidly and frequently than at lower latitudes, whereas tropical subspecies accumulate over time, taking longer to evolve reproductive isolation and thus become full species. Faster transition times to speciation are indeed evident at higher latitudes (Chek et al. 2003; Weir and Schluter 2007); however, it is unclear whether this difference could explain the latitudinal variation in subspecies within species observed here. Looking across the seven paraphyletic taxa in our analysis that involved 11 sister species, sister species were not more common at higher or lower latitudes (seven spanned both high and low latitudes, two were restricted to high latitudes, two were restricted to low latitudes)—a pattern that does not lend support for a positive or negative correlation between latitude and speciation rates.

Further considering the results of Weir and Schluter (2007), we may expect that greater extinction rates of bird and mammal species at higher latitudes would also be reflected in subspecies, given that factors leading to more frequent extinctions of species should similarly cause more frequent extinctions of populations and subspecies. Higher rates of subspecies extinctions at higher latitudes, however, would eliminate potential incipient species before they evolve reproductive isolation, thus reducing speciation rates at higher latitudes inconsistent with some of their conclusions (Weir and Schluter 2007). More detailed phylogenetic information for populations within species and closely related species may be required before we can decipher true relationships between subspecies densities and speciation rates across latitudes.

ACKNOWLEDGMENTS

We thank F. Bonier, E. Dossett, J. Knox, H. Montag, S. Ozaki for help with map drawing, K. Bennett and P. Hurvitz for GIS scripting, and F. Bonier, T. Bradshaw, J.A.F. Diniz-Filho, W.C. Funk, C. Ghalambor, D. Haak, R. Huey, B. Kerr, D. Levey, N. Machnicki, T. Martin, J. McKay, S. Rohwer, K. Rowell, D. Schemske, K. Sheldon, B. Swalla, and T. Daniel and the MathBio, EvoSyst, and Tewksbury laboratory groups for comments at various stages. PRM thanks G. Adams, C. del Agua, B. Di Labio, R. Dobbs, R. Gelis, H. Greeney, J. Martin, L. Martin, R. Robertson, L. Robertson, and M. Vargas, and acknowledges support from the Natural Sciences and Engineering Research Council of Canada, Sigma Xi, an Ed Harrison Memorial Scholarship from the Western Foundation of Vertebrate Zoology, and a Baillie Family Endowment.

LITERATURE CITED

- Agapow, P.-M., O. R. P. Bininda-Emonds, K. A. Crandall, J. L. Gittleman, G. M. Mace, J. C. Marshall, and A. Purvis. 2004. The impact of species concept on biodiversity studies. *Q. Rev. Biol.* 79:161–179.
- Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297:1545–1548.
- American Ornithologists' Union. 1998. Check-list of North American Birds. 7th edn. American Ornithologists' Union, Washington, D.C.
- Arnaiz-Villena, A., J. Guillén, V. Ruiz-del-Valle, E. Lowy, J. Zamora, P. Varela, D. Stefani, and L. M. Allende. 2001. Phylogeography of cross-bills, bullfinches, grosbeaks, and rosefinches. *Cell. Mol. Life Sci.* 58:1159–1166.
- Banks, R. C., C. Cicero, J. L. Dunn, A. W. Kratter, H. Ouellet, P. C. Rasmussen, J. V. Remsen, Jr., J. D. Rising, and D. F. Stotz. 2000. Forty-second supplement to the American Ornithologists' Union *Check-list of North American Birds*. *Auk* 117:847–858.
- Banks, R. C., C. Cicero, J. L. Dunn, A. W. Kratter, P. C. Rasmussen, J. V. Remsen, Jr., J. D. Rising, and D. F. Stotz. 2002. Forty-third supplement to the American Ornithologists' Union *Check-list of North American Birds*. *Auk* 119:897–906.
- . 2003. Forty-fourth supplement to the American Ornithologists' Union *Check-list of North American Birds*. *Auk* 120:923–931.
- . 2004. Forty-fifth supplement to the American Ornithologists' Union *Check-list of North American Birds*. *Auk* 121:985–995.
- . 2005. Forty-sixth supplement to the American Ornithologists' Union *Check-list of North American Birds*. *Auk* 122:1026–1031.
- . 2006. Forty-seventh supplement to the American Ornithologists' Union *Check-list of North American Birds*. *Auk* 123:926–936.
- Banks, R. C., R. T. Chesser, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, P. C. Rasmussen, J. V. Remsen, Jr., J. D. Rising, and D. F. Stotz. 2007. Forty-eighth supplement to the American Ornithologists' Union *Check-list of North American Birds*. *Auk* 124:1109–1115.
- Belliure, J., G. Sorci, A. P. Møller, and J. Clobert. 2000. Dispersal distance predicts subspecies richness in birds. *J. Evol. Biol.* 13:480–487.
- Bernatchez, L., and C. C. Wilson. 1998. Comparative phylogeography of Nearctic and Palearctic fishes. *Mol. Ecol.* 7:431–452.
- Brown, J. H. 1995. *Macroecology*. Univ. of Chicago Press, Chicago, IL.
- Browning, R. 1994. A taxonomic review of *Dendroica petechia* (Yellow Warbler) (Aves: Parulinae). *Proc. Biol. Soc. Wash.* 107:27–51.
- Burns, K. J., and D. N. Barhoum. 2006. Population-level history of the wren tit (*Chamaea fasciata*): implications for comparative phylogeography in the California Floristic Province. *Mol. Phylogenet. Evol.* 38:117–129.
- Cadena, C. D., J. Klicka, and R. E. Ricklefs. 2007. Evolutionary differentiation in the Neotropical montane region: molecular phylogenetics and phylogeography of *Buarremon* brush-finches (Aves, Emberizidae). *Mol. Phylogenet. Evol.* 44:993–1016.
- Cardillo, M. 1999. Latitude and rates of diversification in birds and butterflies. *Proc. R. Soc. Lond. B* 266:1221–1225.
- Cardillo, M., C. D. L. Orme, and I. P. F. Owens. 2005. Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology* 86:2278–2287.
- Carson, R. J., and G. S. Spicer. 2003. A phylogenetic analysis of the emberizid sparrows based on three mitochondrial genes. *Mol. Phylogenet. Evol.* 29:43–57.
- Chek, A. A., J. D. Austin, and S. C. Loughheed. 2003. Why is there a tropical-temperate disparity in the genetic diversity and taxonomy of species? *Evol. Ecol. Res.* 5:69–77.
- Cheviron, Z. A., S. J. Hackett, and A. P. Capparella. 2005. Complex evolutionary history of a Neotropical lowland forest bird (*Lepidothrix coronata*) and its implications for historical hypotheses of the origin of Neotropical avian diversity. *Mol. Phylogenet. Evol.* 36:338–357.
- Chown, S. L., and K. J. Gaston. 2000. Areas, cradles and museums: the latitudinal gradient in species richness. *Trends Ecol. Evol.* 15:311–315.
- Coyne, J., and H. A. Orr. 2004. *Speciation*. Sinauer Associates, Sunderland, MA.
- Crawley, M. J. 2002. *Statistical computing: an introduction to data analysis using S-plus*. John Wiley & Sons Ltd. New York, New York.
- Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J.-F. Guégan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, et al.

2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett.* 7:1121–1134.
- Darwin, C. R. 1859. The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, UK.
- del Hoyo, J., A. Elliott, and J. Sargatal. (eds.) 1992. Handbook of the birds of the world. Volume 1. Ostrich to Ducks. Lynx Edicions, Barcelona, Spain.
- . (eds.) 1994. Handbook of the birds of the world. Volume 2. New world vultures to Guinea-fowl. Lynx Edicions, Barcelona, Spain.
- . (eds.) 1996. Handbook of the birds of the world. Volume 3. Hoatzin to Auks. Lynx Edicions, Barcelona, Spain.
- . (eds.) 1997. Handbook of the birds of the world. Volume 4. Sandgrouse to Cuckoos. Lynx Edicions, Barcelona, Spain.
- . (eds.) 1999. Handbook of the birds of the world. Volume 5. Barn-Owls to Hummingbirds. Lynx Edicions, Barcelona, Spain.
- . (eds.) 2001. Handbook of the birds of the world. Volume 6. Mousebirds to Hornbills. Lynx Edicions, Barcelona, Spain.
- . (eds.) 2002. Handbook of the birds of the world. Volume 7. Jacamars to Woodpeckers. Lynx Edicions, Barcelona, Spain.
- Dickinson, E. C., ed. 2003. The Howard and Moore complete checklist of the birds of the world. 3rd edn. Princeton Univ. Press, Princeton, NJ.
- Diniz-Filho, J. A. F., T. F. L. V. B. Rangel, L. M. Bini, and B. A. Hawkins. 2007. Macroevolutionary dynamics in environmental space and the latitudinal diversity gradient in New World birds. *Proc. R. Soc. Lond. B* 274:43–52.
- Dobzhansky, T. 1950. Evolution in the tropics. *Am. Sci.* 38:209–221.
- Duriez, O., J.-M. Sachet, E. Ménoni, N. Pidancier, C. Miquel, and P. Taberlet. 2007. Phylogeography of the capercaillie in Eurasia: what is the conservation status in the Pyrenees and Cantabrian Mountains? *Conserv. Genet.* 8:513–526.
- Dynesius, M., and R. Jansson. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl. Acad. Sci. USA* 97:9115–9120.
- Eo, S. H., J. P. Wares, and J. P. Carroll. 2008. Population divergence in plant species reflects latitudinal biodiversity gradients. *Biol. Lett.* doi:10.1098/rsbl.2008.0109.
- Fedorov, A. A. 1966. The structure of tropical rain forest and speciation in the humid tropics. *J. Ecol.* 54:1–11.
- Fine, P. V. A. 2001. An evaluation of the geographic area hypothesis using the latitudinal gradient in North American tree diversity. *Evol. Ecol. Res.* 3:413–428.
- Fine, P. V. A., and R. H. Ree. 2006. Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *Am. Nat.* 168:796–804.
- Fischer, A. G. 1960. Latitudinal variation in organic diversity. *Evolution* 14:64–81.
- Fok, K. W., C. M. Wade, and D. T. Parkin. 2002. Inferring the phylogeny of disjunct populations of the azure-winged magpie *Cyanopica cyanus* from mitochondrial control region sequences. *Proc. R. Soc. Lond. B* 269:1671–1679.
- Funk, D. J., and K. E. Omland. 2003. Species-level parphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annu. Rev. Ecol. Syst.* 34:397–423.
- Gamauf, A., J.-O. Gjershaug, N. Røv, K. Kvaløy, and E. Haring. 2005. Species or subspecies? The dilemma of taxonomic ranking of some south-east Asian hawk-eagles (genus *Spizaetus*). *Bird Conserv. Int.* 15:99–117.
- Ghalambor, C., R. B. Huey, P. R. Martin, J. J. Tewksbury, and G. Wang. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol.* 46:5–17.
- Graves, G. R. 1985. Elevational correlates of speciation and intraspecific geographic variation in plumage in Andean forest birds. *Auk* 102:556–579.
- Hansen, T. A. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology* 6:193–207.
- Hawkins, B. A. and J. A. F. Diniz-Filho. 2004. 'Latitude' and geographic patterns in species richness. *Ecography* 27:268–272.
- Hawkins, B. A., and E. E. Porter. 2001. Area and the latitudinal diversity gradient for terrestrial birds. *Ecol. Lett.* 4:595–601.
- Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, et al. 2003a. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117.
- Hawkins, B. A., E. E. Porter, and J. A. F. Diniz-Filho. 2003b. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology* 84:1608–1623.
- Hawkins, B. A., J. A. F. Diniz-Filho, C. A. Jaramillo, and S. A. Soeller. 2006. Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *J. Biogeogr.* 33:770–780.
- Hawkins, B. A., J. A. F. Diniz-Filho, C. A. Jaramillo, and S. A. Soeller. 2007. Climate, niche conservatism, and the global bird diversity gradient. *Am. Nat.* 170:S16–S27.
- Helbig, A. J., J. Martens, I. Seibold, F. Henning, B. Schlotzler, and M. Wink. 1996. Phylogeny and species limits in the Palearctic chiffchaff *Phylloscopus collybita* complex: mitochondrial genetic differentiation and bioacoustic evidence. *Ibis* 138:650–666.
- Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405:907–913.
- Hudson, R. R., and J. A. Coyne. 2002. Mathematical consequences of the genealogical species concept. *Evolution* 56:1557–1565.
- Hughes, A. L., and M. A. K. Hughes. 2007. Coding sequence polymorphism in avian mitochondrial genomes reflects population histories. *Mol. Ecol.* 16:1369–1376.
- Isaac, N. J. B., J. Mallet, and G. M. Mace. 2004. Taxonomic inflation: its influence on macroecology and conservation. *Trends Ecol. Evol.* 19:464–469.
- Jablonski, D. 1993. The tropics as a source of evolutionary novelty through geological time. *Nature* 364:142–144.
- Jablonski, D., K. W. Flessa, and J. W. Valentine. 1985. Biogeography and paleobiology. *Paleobiology* 11:75–90.
- Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102–106.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101:233–249.
- Johnson, J. A., R. T. Watson, and D. P. Mindell. 2005. Prioritizing species conservation: does the Cape Verde kite exist? *Proc. R. Soc. Lond. B* 272:1365–1371.
- Joseph, L., and T. Wilke. 2007. Lack of phylogenetic structure in three widespread Australian birds reinforces emerging challenges in Australian historical biogeography. *J. Biogeogr.* 34:612–624.
- Joseph, L., T. Wilke, J. T. Have, and R. T. Chesser. 2006. Implications of mitochondrial DNA polyphyly in two ecologically undifferentiated but morphologically distinct migratory birds, the masked and white-browed woodswallows *Artamus* spp. of inland Australia. *J. Avian Biol.* 37:625–636.
- Kalmar, A., and D. J. Currie. 2006. A global model of island biogeography. *Global Ecol. Biogeogr.* 15:72–81.
- . 2007. A unified model of avian species richness on islands and continents. *Ecology* 88:1309–1321.
- Kruckenhauser, L., E. Haring, W. Pinsker, M. J. Reising, H. Winkler, M. Wink, and A. Gamauf. 2004. Genetic vs. morphological differentiation of Old World buzzards (genus *Buteo*, Accipitridae). *Zoologica Scripta.* 33:197–211.
- Latimer, A. M., J. A. Silander, Jr., and R. M. Cowling. 2005. Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hot spot. *Science* 309:1722–1725.

- Macpherson, E. 2002. Large-scale species-richness gradients in the Atlantic Ocean. *Proc. R. Soc. Lond. B* 269:1715–1720.
- Martin, P. R., and J. K. McKay. 2004. Latitudinal variation in genetic divergence of populations and the potential for future speciation. *Evolution* 58:938–945.
- Martin, P. R., F. Bonier, and J. J. Tewksbury. 2007. Revisiting Jablonski (1993): cladogenesis and range expansion explain latitudinal variation in taxonomic richness. *J. Evol. Biol.* 20:930–936.
- Mayr, E. 1942. *Systematics and the origin of species*. Columbia Univ. Press, New York, New York.
- . 1963. *Animal species and evolution*. Harvard Univ. Press, Cambridge, MA.
- Mayr, E., and J. Diamond. 2001. *The birds of the Northern Melanesia: speciation, ecology and biogeography*. Oxford Univ. Press, Oxford, UK.
- Milá, B., T. B. Smith, and R. K. Wayne. 2006. Postglacial population expansion drives the evolution of long-distance migration in a songbird. *Evolution* 60:2403–2409.
- Miller, M. J., E. Bermingham, and R. E. Ricklefs. 2007. Historical biogeography of the New World Solitaires (*Myadestes* spp.). *Auk* 124:868–885.
- Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* 10:315–331.
- Mock, K. E., T. C. Theimer, O. E. Rhodes, Jr., D. L. Greenberg, and P. Keim. 2002. Genetic variation across the historical range of the wild turkey (*Meleagris gallopavo*). *Mol. Ecol.* 11:643–657.
- Møller, A. P., and J. J. Cuervo. 1998. Speciation and feather ornamentation in birds. *Evolution* 52:859–869.
- Monroe, B. L., Jr., and C. G. Sibley. 1993. *A world checklist of birds*. Yale Univ. Press, New Haven, CT.
- Moyle, R. G., M. Schilthuizen, M. A. Rahman, and F. H. Sheldon. 2005. Molecular phylogenetic analysis of the white-crowned fork-tail *Enicurus leschenaulti* in Borneo. *J. Avian Biol.* 36:96–101.
- Newton, I. 2003. *Speciation and biogeography of birds*. Academic Press, Oxford, UK.
- Nichols, R. 2001. Gene trees and species trees are not the same. *Trends Ecol. Evol.* 16:358–364.
- Nyári, Á. S. 2007. Phylogenetic patterns, molecular and vocal differentiation, and species limits in *Schiffornis turdina* (Aves). *Mol. Phylogenet. Evol.* 44:154–164.
- Ödeen, A., and M. Björklund. 2003. Dynamics in the evolution of sexual traits: losses and gains, radiation and convergence in yellow wagtails (*Motacilla flava*). *Mol. Ecol.* 12:2113–2130.
- Olsson, U., P. Alström, P. G. P. Ericson, and P. Sundberg. 2005. Non-monophyletic taxa and cryptic species—evidence from a molecular phylogeny of leaf-warblers (*Phylloscopus*, Aves). *Mol. Phylogenet. Evol.* 36:261–276.
- Orme, C. D. L., R. G. Davies, M. Burgess, F. Eigenbrod, N. Pickup, V. A. Olson, A. J. Webster, T.-S. Ding, P. C. Rasmussen, R. S. Ridgely, et al. 2005. Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436:1016–1019.
- Otsson, U., S. Bensch, L. Svensson, and J. Waldenström. 2005. Differentiation and phylogeny of the olivaceous warbler *Hippolais pallida* species complex. *J. Ornithol.* 146:127–136.
- Pasquet, E., E. Bourdon, M. V. Kalyakin, and A. Cibois. 2006. The fulvettas (*Alcippe*, Timaliidae, Aves): a polyphyletic group. *Zool. Scripta* 35:559–566.
- Pavlova, A., R. M. Zink, S. V. Drovetski, Y. Red'kin, and S. Rohwer. 2003. Phylogeographic patterns in *Motacilla flava* and *Motacilla citreola*: species limits and population history. *Auk* 120:744–758.
- Pavlova, A., R. M. Zink, and S. Rohwer. 2005. Evolutionary history, population genetics, and gene flow in the common rosefinch (*Carpodacus erythrinus*). *Mol. Phylogenet. Evol.* 36:669–681.
- Phillimore, A. B., and I. P. F. Owens. 2006. Are subspecies useful in evolutionary and conservation biology? *Proc. R. Soc. Lond. B* 273:1049–1053.
- Phillimore, A. B., C. D. L. Orme, R. G. Davies, J. D. Hadfield, W. J. Reed, K. J. Gaston, R. P. Freckleton, and I. P. F. Owens. 2007. Biogeographical basis of recent phenotypic divergence among birds: a global study of subspecies richness. *Evolution* 61:942–957.
- Price, T. 2008. *Speciation in birds*. Roberts and Company, Greenwood Village, CO.
- Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proc. Natl. Acad. Sci. USA* 98:4534–4539.
- Rensch, B. 1933. *Zoologische Systematik und Artbildungsprobleme*. Verhandlungen der Deutschen Zoologischen Gesellschaft Zoologischer Anzeiger (Supplement) 6:19–83.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:167–171.
- . 2005. Phylogenetic perspectives on patterns of regional and local species richness. Pp. 16–40 in E. Bermingham, C. Dick, and C. Moritz, eds. *Tropical rainforests. Past, present, and future*. Univ. of Chicago Press, Chicago, IL.
- . 2006. Global variation in the diversification rate of passerine birds. *Ecology* 87:2468–2478.
- . 2007. History and diversity: explorations at the intersection of ecology and evolution. *Am. Nat.* 170:S56–S70.
- Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65:514–527.
- . 1997. The larger area of the tropics does not explain latitudinal gradients in species diversity. *Oikos* 79:169–172.
- Rosenzweig, M. L. 1992. Species diversity gradients: we know more and less than we thought. *J. Mammal.* 73:715–730.
- . 1995. *Species diversity in space and time*. Cambridge Univ. Press, Cambridge, UK.
- . 2003. How to reject the area hypothesis of latitudinal gradients. Pp. 87–106 in T. M. Blackburn and K. J. Gaston, eds. *Macroecology: concepts and consequences*. Blackwell Publishing, Oxford, UK.
- Ruegg, K. C., and T. B. Smith. 2002. Not as the crow flies: a historical explanation for circuitous migration in Swainson's Thrush (*Catharus ustulatus*). *Proc. R. Soc. Lond. B* 269:1375–1381.
- Ruggiero, A. 1999. Spatial patterns in the diversity of mammal species: a test of the geographic area hypothesis in South America. *Ecoscience* 6:338–354.
- Schemske, D. W. 2002. Ecological and evolutionary perspectives on the origins of tropical diversity. Pp. 163–173 in R. L. Chazdon, and T. C. Whitmore, eds. *Foundations of tropical forest biology*. Univ. of Chicago Press, Chicago, IL.
- Seutin, G., N. K. Klein, R. E. Ricklefs, and E. Bermingham. 1994. Historical biogeography of the Bananaquit (*Coereba flaveola*) in the Caribbean region: a mitochondrial DNA assessment. *Evolution* 48:1041–1061.
- Sol, D., D. G. Stirling, and L. Lefebvre. 2005. Behavioral drive or behavioral inhibition in evolution: subspecific diversification in Holarctic passerines. *Evolution* 59:2669–2677.
- Soulé, M. E. 1986. *Conservation biology: the science of scarcity and diversity*. Sinauer, Sunderland, MA.
- Terborgh, J. 1973. On the notion of favourableness in plant ecology. *Am. Nat.* 107:481–501.
- Tonniss, B., P. R. Grant, R. Grant, and K. Petren. 2005. Habitat selection and ecological speciation in Galápagos warbler finches (*Certhidea olivacea* and *Certhicea fusca*). *Proc. R. Soc. Lond. B* 272:819–826.

- Toon, A., J. Hughes, A. Baker, and P. Mather. 2003. Discordance between morphology and genetic structure among three plumage forms of the Australian Magpie. *Emu* 103:337–343.
- Toon, A., P. B. Mather, A. M. Baker, K. L. Durrant, and J. M. Hughes. 2007. Pleistocene refugia in an arid landscape: analysis of a widely distributed Australian passerine. *Mol. Ecol.* 16:2525–2541.
- Wallace, A. R. 1878. *Tropical nature and other essays*. Macmillan, New York, New York.
- Weckstein, J. D., R. M. Zink, R. C. Blackwell-Rago, and D. A. Nelson. 2001. Anomalous variation in mitochondrial genomes of White-crowned (*Zonotrichia leucophrys*) and Golden-crowned (*Z. atricapilla*) sparrows: pseudogenes, hybridization, or incomplete lineage sorting? *Auk* 118:231–236.
- Weir, J. T., and D. Schluter. 2007. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* 315:1574–1576.
- Willig, M. R., and C. P. Bloch. 2006. Latitudinal gradients of species richness: a test of the geographic area hypothesis at two ecological scales. *Oikos* 112:163–173.
- Wright, D. H., D. J. Currie, and B. A. Maurer. 1993. Energy supply and patterns of species richness on local and regional scales. Pp. 66–74. *in* R. E. Ricklefs, D. Schluter, eds. *Species diversity in ecological communities: historical and geographical perspectives*. Univ. of Chicago Press, Chicago, IL.
- Zink, R. M. 1994. The geography of mitochondrial DNA variation, population structure, hybridization, and species limits in the Fox Sparrow (*Passerella iliaca*). *Evolution* 48:96–111.
- . 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. *Proc. R. Soc. Lond. B* 271:561–564.
- Zink, R. M., and J. D. Weckstein. 2003. Recent evolutionary history of the Fox Sparrows (Genus: *Passerella*). *Auk* 120:522–527.
- Zou, F., H. C. Lim, B. D. Marks, R. G. Moyle, and F. H. Sheldon. 2007. Molecular phylogenetic analysis of the Gray-cheeked Fulvetta (*Alcippe morrisonia*) of China and Indochina: a case of remarkable genetic divergence in a “species.” *Mol. Phylogenet. Evol.* 44:165–174.

Associate Editor: A. Mooers

Supporting Information

The following supporting information is available for this article:

Appendix S1. Evidence that subspecies are precursors to species and provide an index of divergence relevant to diversification.

Appendix S2. References consulted for information on distribution of species and subspecies of birds.

This material is available as part of the online article from:

<http://www.blackwell-synergy.com/doi/abs/10.1111/j.1558-5646.2008.00489.x>

(This link will take you to the article abstract).

Please note: Wiley Blackwell Publishing is not responsible for the content or functionality of any supporting informations supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.