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BIOGEOGRAPHICAL BASIS OF RECENT PHENOTYPIC DIVERGENCE AMONG BIRDS: A GLOBAL STUDY OF SUBSPECIES RICHNESS

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Theory predicts that biogeographic factors should play a central role in promoting population divergence and speciation. Previous empirical studies into biogeography and diversification have been relatively restricted in terms of the geographical area, phylogenetic scope, and the range of biogeographic factors considered. Here we present a global analysis of allopatric phenotypic divergence (measured as subspecies richness) across more than 9600 bird species. The main aim of this study was to examine the extent to which biogeographical factors can explain patterns of phenotypic divergence. Analysis of the taxonomic distribution of subspecies among species suggests that subspecies formation and extinction have occurred at a considerably faster rate than has species formation. However, the observed distribution departs from the expectation under a random birth–death model of diversification. Across 19 phylogenetic trees, we find no significant linear relationship between species age and subspecies richness, implying that species age is a poor predictor of subspecies richness. Both subspecies richness and subspecies diversification rate are found to exhibit low phylogenetic signal, meaning that closely related species do not tend to possess similar numbers of subspecies. As predicted by theory, high subspecies richness was associated with large breeding range size, island dwelling, inhabitation of montane regions, habitat heterogeneity, and low latitude. Of these factors, breeding range size was the variable that explained the most variation. Unravelling whether species that have invaded previously glacial areas have more or fewer subspecies than expected proves to be complicated due to a covariation between the postglacial colonization, latitude, geographic range size, and subspecies richness. However, the effect of postglacial colonization on subspecies richness appears to be small. Mapping the distribution of species' subspecies richness globally reveals geographical patterns that correspond to many of the predictions of the statistical models, but may also reflect geographical variation in taxonomic practice. Overall, we demonstrate that biogeographic models can explain about 30% of the global variation in subspecies richness in birds.

KEY WORDS: Birds, divergence, extinction, islands, range size, subspecies.

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Identifying the extent to which different biogeographic conditions promote population divergence and speciation presents a considerable challenge for biologists (Mayr and Diamond 2001; Newton 2003). A suite of methods has been developed to test for correlates of speciation and divergence, typically employing data from either the fossil record (Jablonski and Roy 2003) or from the reconstruction of phylogenetic relationships among extant lineages (Isaac et al. 2003; Paradis 2005). Although these methods have provided many interesting insights into correlates of diversification, they are most often applied to the investigation of events in the distant past and thus require assumptions regarding models of trait evolution and ecological conditions over time. This condition is particularly difficult to satisfy for biogeographical factors, as there is no single accepted model of geographic range change over time (Gaston 2003; Losos and Glor 2003).

One way to avoid the problems associated with reconstructing ancient ranges and analyzing ancient patterns of speciation is to use contemporary patterns of phenotypic divergence to test the relative importance of various biogeographic factors. Here we use subspecies richness, defined as the number of subspecies recognized within a species, as an index of the extent of contemporary phenotypic divergence among populations of a particular species (Phillimore and Owens 2006). Although subspecies richness is not without its problems as an index of recent divergence (e.g., Patten and Unitt 2002; Zink 2004), it does possess useful properties: First, it is meaningful in the context of speciation because subspecies may represent a stepping-stone along a trajectory towards allopatric species (Darwin 1859; Miller 1956; O'Brien and Mayr 1991). Although introgression and extinction may curtail the trajectory from subspecies to full species (O'Brien and Mayr 1991), subspecies richness probably provides a proximate measure of the extent of phenotypic variation shown by a species. Second, in the case of taxonomically well-studied groups, such as birds, the number of subspecies per species has been described across all lineages and biogeographic regions (Clements 2000; Dickinson 2003). These properties of subspecies richness underpin why several previous studies have adopted this approach for studying recent diversification (Rensch 1933; McCall 1997; Møller and Cuervo 1998; Belliure et al. 2000; Mayr and Diamond 2001; Newton 2003; Sol et al. 2005).

But do subspecies tend to describe populations following different evolutionary trajectories? Subspecies have traditionally been defined on the basis of phenotypic discontinuities among geographically contiguous or disjunctive populations, meaning that they may offer insights into allopatric and parapatric, but not sympatric, divergence. The adaptive function of geographically distributed phenotypic differences, such as morphology (e.g., Benkman 1989), plumage (e.g., Mumme et al. 2006), and song (e.g., Patten et al. 2004), amongst avian subspecies has received empirical support. Furthermore, over 35% of avian subspecies included in a recent cross taxon analysis showed considerable phylogenetic differentiation at mitochondrial loci (Phillimore and Owens 2006). This latter finding contrasts with a number of earlier molecular studies that highlighted cases in which subspecies showed a poor congruence with phylogenetic clusters (Barrowclough 1980; Ball and Avise 1992; Burbrink et al. 2000; Zink 2004). Nevertheless, Phillimore and Owens' (2006) estimate of the proportion of avian subspecies that are evolutionarily divergent is likely to be conservative. This is because, even if recently divergent populations are reproductively isolated, insufficient time may have elapsed for reciprocal monophyly to be achieved (Hudson and Coyne 2002). In addition, Zink's (2004) criterion that subspecies should be reciprocally monophyletic is not an absolute requirement for studying diversification; evidence from both theoretical (Gavrilets 1999, 2004) and empirical studies (Postma and Van Noordwijk 2005) shows that trait divergence can persist in the face of gene flow. The available information therefore suggests that, at least in birds, many subspecies do describe lineages that are on divergent evolutionary trajectories.

It has been predicted that biogeographic factors may influence evolutionary divergence among populations in a number of (potentially nonindependent) ways. For instance, alternative models of allopatric divergence predict either a positive (Rosenzweig 1978, 1995) or negative (Gaston 1998; Gavrilets et al. 2000) relationship between land area and rate of divergence, or, as a result of these conflicting influences, medium-sized ranges corresponding to greatest opportunity for divergence (Rosenzweig 1995; Gaston 1998). Similarly, a positive relationship between island dwelling and rate of divergence is anticipated under allopatric models of diversification (Darwin 1859; Mayr 1982; Rosenzweig 1995) and mountain regions are invoked as promoters of divergence through allopatric divergence, associated with vicariance or dispersal (Janzen 1967), or via parapatric divergence between vegetation zonal transitions across altitudinal gradients (Terborgh 1971). Under ecological models of divergence, variation in habitat is predicted to promote divergence in allopatry or parapatry (Miller 1956; Endler 1977; Smith et al. 1997; Schluter 2000). Other biogeographic factors may also be associated with reduced levels of population divergence. For example, species that inhabit recently glaciated areas are assumed to have colonized these regions postglaciation (Pianka 1966; Hawkins and Porter 2003), meaning that there may not have been sufficient time for subspecies differentiation. Alternatively, species whose ranges have been bisected by glaciers may have experienced elevated opportunity for diversification in isolated refugial populations (Weir and Schluter 2004). Finally, one possible explanation for the observed latitudinal gradient in taxon richness (Wallace 1878; Pianka 1966), may be that diversification proceeds more rapidly at lower latitudes (Rohde 1992; Cardillo 1999; Cardillo et al. 2005).

The overall aim of this study was to use a new global dataset of subspecies richness and geographic information on all known extant bird species (Orme et al. 2005) to examine the role of a range of biogeographic factors in promoting contemporary divergence among subspecies. Here we will: (1) examine statistical properties of the subspecies per species frequency distribution; (2) use phylogenetic information to test whether subspecies richness is predicted by a species' age; (3) quantify the phylogenetic/taxonomic signal of subspecies richness in living birds; (4) use single and multipredictor comparative methods to test for biogeographic correlates of subspecies richness; (5) map the distribution of the average subspecies richness per species across space.

Materials and Methods

DATA COLLECTION

The number of subspecies per bird species was obtained from a standard ornithological checklist (Clements 2000). We used this source for subspecies richness because it includes all currently recognized subspecies, whereas the standard avian taxonomy (Sibley and Monroe 1990, 1993) only includes those subspecies "groups" that have been at some earlier time recognized as species. The subspecies-richness information is available in online Appendices S1a and S1b. Geographical information on the breeding ranges of all species was obtained from a global dataset of all known bird species based on presence–absence in an equal area grid at a resolution approximately equivalent to 1° latitude $\times$ 1° longitude (Orme et al. 2005). The terrestrial land area within the cells in which each species was present was summed to provide an estimate of the extent of a species' breeding range in km^2. The breeding range was divided into island and continental area, where island grid cells were those that contained no continental landmass. Continental cells were those containing continental landmass, so in some cases they also contained islands. A species was classified as island dwelling if more than 20% of its breeding range was found in island cells. Data on global biomes (Olson et al. 2001) were used to assign biome data to each cell. Habitat heterogeneity was then scored for each species as the number of biomes that coincided with 5% or more of the total number of grid cells occupied by that species. The 5% cutoff was chosen to minimize the degree to which the habitat generalism score would be inflated by grid cells in which multiple biomes exist without actually being coincident with the species' underlying geographic range. For each grid cell the maximum elevation was obtained from the GTOPO30 dataset (http://lpdaac.usgs.gov/gtopo30/gtopo30.asp). Then the proportion of a species' grid cells that included a maximum altitude of greater than 2500 m in elevation (corresponding to "UN Mountain Watch" category 3) was used to quantify the extent to which a species was mountain dwelling. Information on land areas that have been glaciated at some time during the last 21,000 years was obtained from Peltier (1993). Species that exhibited $> 20\%$ breeding range overlap with recently ice-covered regions were classified as inhabiting recently glaciated areas. The latitudinal centroid and latitudinal extent of each species breeding range was calculated from the underlying geographic information systems (GIS) shape files. All GIS mapping and manipulations were conducted using ArcInfo (ESRI). The taxonomy used for the collection of range data (Orme et al. 2005) was that of Sibley and Monroe (1990, 1993). Where the species nomenclature of Clements' (2000) checklist differed from this, subspecies were reconciled with the species identified by Sibley and Monroe (1990, 1993) on the basis of synonymy.

DISTRIBUTION OF SUBSPECIES WITHIN SPECIES

Yule (1925) observed that the frequency distribution of species within genera adhered to a power law. Power law behavior has since been reported at several taxonomic levels and in many different groups (Burlando 1990, 1993). We apply the birth–death model of Reed and Hughes (2002) to estimate two parameters relating to subspecies birth rate ($\tilde{\lambda} = \lambda/\rho$) and extinction rate ($\tilde{\mu} = \mu/\rho$). Where λ = a subspecies formation parameter relating to the probability that a subspecies will split, μ = an extinction parameter relating to the probability that a subspecies will go extinct, and ρ = a speciation parameter relating to the probability that a new species will form. This model assumed constant rates for subspecies birth and death and species formation. As we include a parameter for species formation, as well as parameters for the birth and death of subspecies, we do not assume that all species are of equal age. However, we do not take into account the actual ages of species, instead, we assume that the ages of species are exponentially distributed with the parameter ρ. The two parameters, $\tilde{\lambda}$ and $\tilde{\mu}$, were estimated and their standard errors calculated following a maximum-likelihood procedure described in Reed and Hughes (2002). We compared the performance of this model to the simpler Yule model ($\tilde{\mu} = 0$) via a likelihood ratio test.

The probability mass function, corresponding to the probabilities of species containing different numbers of subspecies, was obtained using $\tilde{\lambda}$ and $\tilde{\mu}$ parameter estimates (for further details of how this was calculated see Reed and Hughes 2002). The predicted frequency distribution of subspecies richness was then calculated as the total number of species multiplied by the probability mass function. We compared the observed frequency distribution of subspecies richness against the predicted distribution under the null birth–death model using a chi-square goodness-of-fit test. To ensure that the expected frequency was ≥ 5 in all cases (a requirement of the chi-square goodness-of-fit test) some of the frequencies for larger subspecies-richness values were pooled.

SPECIES AGE AND SUBSPECIES RICHNESS

Under an exponential model of diversification a linear relationship between taxon age and the logarithm of subtaxon richness is anticipated (Yule 1925). We tested whether such a relationship between species age and subspecies richness is supported within 19 ($\geq$ 90% complete) ultrametric species-level phylogenies that represent numerous geographic regions and different orders of birds. In total these phylogenies include 352 species subtending 883 subspecies. The phylogenetic completeness criterion was important because missing taxa may artificially elevate the age estimated for their sister taxa. Nonultrametric trees that had been reconstructed using models of DNA evolution were made ultrametric using penalized likelihood (Sanderson 2002) implemented in the APE R library (Paradis et al. 2004; Paradis 2006). Relative species ages were estimated as the lengths of the terminal branches subtending species from molecular phylogenies. The degree to which species age predicts subspecies richness (ln transformed) was then assessed using a generalized least squares (GLS) phylogenetic comparative approach. A GLS approach permitted estimation of the relationship between two traits, while simultaneously estimating the maximum-likelihood phylogenetic branch length transformation under a Brownian motion model of trait evolution (Grafen 1989; Martins and Hansen 1997; Pagel 1999). Except where stated otherwise all analyses were conducted in the R programming environment (R Development Core Team 2004).

Effect size estimates obtained for the correlation across each phylogeny (Pearson's r) were standardized as Fisher's Z_r (eq. 1).

$$Z_r = 0.5[\ln(1 + r) - \ln(1 - r)] \quad (1)$$

The standard error of Z_r was calculated as $(n - 3)$, where n is equal to the test sample size, and was used as an inverse weighting in the meta-analysis. We estimated the Q statistic, a test for homogeneity of variance across the correlations estimated for each of the phylogenies, and used this to determine whether a fixed or random effect approach to calculating mean effect size should be preferred (Cooper and Hedges 1994). The null hypothesis, that there is no relationship between species age and subspecies richness, was tested using the weighted mean Z statistic (with df = 1).

PHYLOGENETIC SIGNAL OF SUBSPECIES RICHNESS

We tested the degree to which closely related species share similar subspecies numbers in two ways. First, in the absence of a completely resolved species-level phylogenetic tree across all bird species, our first approach was to analyze the variance components of subspecies richness at three taxonomic levels (Harvey and Clutton-Brock 1985). A nested generalized linear mixed model (GLMM) with quasi-Poisson distributed errors was used to examine the variance components partitioned within taxonomic levels for subspecies richness (S). Analysis was conducted on the number of subspecies divisions that had taken place within a species ($S - 1$), under the assumption that this process follows a Poisson distribution. A high proportion of the total variation in subspecies richness partitioned among the higher taxonomic levels would suggest that closely related species possess similar numbers of subspecies. Conversely, a low proportion would suggest that subspecies richness is more randomly distributed with respect to taxonomy. GLMMs were implemented using the MASS package (Venables and Ripley 2002).

Using a second approach we examined the strength of phylogenetic signal across the 19 species-level avian phylogenies. The phylogenetic signal for both subspecies richness, ln(S), and subspecies diversification rate under a pure birth model of diversification, ln(S)/t (where t = species age), were estimated via a GLS approach (Grafen 1989; Martins and Hansen 1997; Pagel 1999), implemented in the R environment. The influence of phylogeny on each of these variables was modeled by incorporating the phylogenetic covariance matrix in a GLS model. The phylogenetic covariance structure was multiplied by a phylogenetic signal value, in the range 0 (no phylogenetic autocorrelation) to 1 (maximum phylogenetic autocorrelation), and the log-likelihood was recorded; from the resulting likelihood surface a maximum-likelihood phylogenetic signal value was obtained (Pagel 1999). The strength of the phylogenetic signal in subspecies richness and subspecies diversification rate within different clades was assessed by summing the log-likelihoods across each phylogenetic signal value. The log-likelihood distribution is asymptotically chi-squared, allowing approximate confidence intervals for the maximum-likelihood phylogenetic signal value to be calculated using likelihood ratio tests (with degrees of freedom equal to the difference in the number of parameters, in this case 1) (Edwards 1972).

BIOGEOGRAPHIC CORRELATES OF SUBSPECIES RICHNESS

To control for any phylogenetic nonindependence in the covariance between subspecies richness and the explanatory variables, taxonomy was incorporated as a series of nested random effects at the level of order, family, and genus. This nested design was implemented in a GLMM, which is the taxonomic analogue of the phylogenetic mixed model (Lynch 1991; Housworth et al. 2004). We used a quasi-Poisson error structure because, in the absence of a robust mixed modelling method for negative binomial errors, this was the most appropriate method for analyzing count data. Again, $S - 1$ (where S = subspecies richness) was the response variable. Simulations demonstrated that neither type-I error rates nor parameter estimates were biased using this approach.

Putative biogeographic predictors of subspecies richness were first analyzed individually in GLMM models, treating each factor as a fixed effect. In the case of breeding range size, a quadratic term was added to the simple linear model to test whether a mid-optimum range size coincided with maximum subspecies richness (Gaston 1998); the difference between the residual deviance of this model and the more simple range size model was compared and the significance tested on the basis of likelihood ratios. To examine whether a latitudinal gradient in subspecies richness existed in each hemisphere and whether the sign of the slope differed in each hemisphere, a more complex model was used. This model included hemisphere as a factor and allowed for an interaction term between hemisphere and latitudinal centroid. The latitudinal centroid for wide-ranging species may be less informative as regards diversification at that particular latitude; consequently, only species with a latitudinal extent of $< 20^\circ$ were included.

Biogeographic terms were considered in conjunction with each other in two different models to facilitate an examination of the relative contributions made by each variable in explaining variation in subspecies richness. The first multipredictor model included breeding range size, island dwelling, mountain dwelling, habitat heterogeneity, and recent glacial overlap data for more than 9500 species. The second multipredictor model was conducted on the species with a restricted latitudinal extent ($< 20^\circ$) and included the aforementioned variables, with the addition of latitudinal centroid, hemisphere, and the interaction between the two. Model fit was estimated as the proportion of the residual variance explained by the covariates, excluding the variance partitioned among taxonomic random effects. This measure of model fit is expected to behave well if the random effects are independent of the fixed effects.

As breeding range size showed strong right skew, a power transformation (0.2) was used to normalize it. Due to the nonorthogonal nature of the data, the potential problem of colinearity among explanatory variables was assessed using variance inflation factors (Fox and Monette 1992). None of the variables possessed a variance inflation factor greater than 10, which we cautiously interpreted as an indication that colinearity did not pose a problem with these analyses (Myers 1990).

MAPPING SUBSPECIES RICHNESS

To illustrate the distribution of subspecies globally, one would ideally obtain range distribution maps for each individual subspecies. Unfortunately, we do not possess data at such a resolution. However, data on the range distributions of all extant avian species are available (Orme et al. 2005). Using these data we were able to plot the average subspecies richness (mean of the natural logarithm) of those species found in each grid cell with a resolution approximately equivalent to 1° latitude $\times$ 1° longitude (an ASCII file containing these data is available in Appendix S2). Subspecies-rich areas of the resulting subspecies richness map should thus be interpreted as areas that harbor species that tend to be subspecies rich, but it does not mean that subspecies diversification has necessarily proceeded more rapidly in these cells.

Finally, we mapped the global distribution of the median residual values for the species found in each grid cell. Residuals were obtained from the model that included breeding range size, island dwelling, mountain dwelling, habitat heterogeneity, and glacial overlap as terms. Mapping the residuals allowed us to informally test whether the data were independent after conditioning on the predictor variables, and whether any residual variation may be explained by other geographically distributed variables. Interpretation of apparent peaks must be interpreted cautiously as such features may arise due to either spatial autocorrelation of the variables tested here or due to artificial spatial autocorrelation because the same species appears in several cells and these cells tend to be aggregated.

Mapping was conducted using the open source GIS tool GRASS (available from http://grass.itc.it/). Mapping the residuals allowed us to informally test whether the data were independent after conditioning on the predictor variables, and whether any residual variation may be explained by other geographically distributed variables.

Results

DISTRIBUTION OF SUBSPECIES WITHIN SPECIES

Reconciling the subspecies recognized by Clements (2000) with the taxonomic nomenclature presented in Sibley and Monroe (1990) resulted in 27,503 subspecies distributed amongst 9657 species. The median number of subspecies per species was two (treating monotypic species as having a single subspecies). The golden whistler (*Pachycephala pectoralis*) possessed the maximum number of subspecies per species with 64. At the other extreme of the frequency distribution, 4360 species were monotypic.

A logarithmic frequency plot of subspecies richness showed substantial departure from linear power law behavior (Fig. 1). The maximum-likelihood values for $\tilde{\lambda}$ (relating to the ratio of subspecies formation to species formation) and $\tilde{\mu}$ (relating to the ratio of subspecies extinction to species formation) were estimated at 32.57 ($\pm$ 19.64) and 38.16 ($\pm$ 23.42), respectively, indicating that subspecies formation and extinction takes place at a much faster rate than species formation. However, it should be noted that the parameters $\tilde{\lambda}$ and $\tilde{\mu}$ were tightly correlated ($r = 0.99$). The Reed–Hughes (2002) birth–death model was significantly better than the Yule pure birth model of diversification (1925) when applied to these subspecies data (likelihood ratio = 858.9, df = 1, $P < 0.001$). Despite the good fit of the Reed–Hughes model to the observed distribution (Fig. 1), there was a significant difference between the observed and the expected distributions

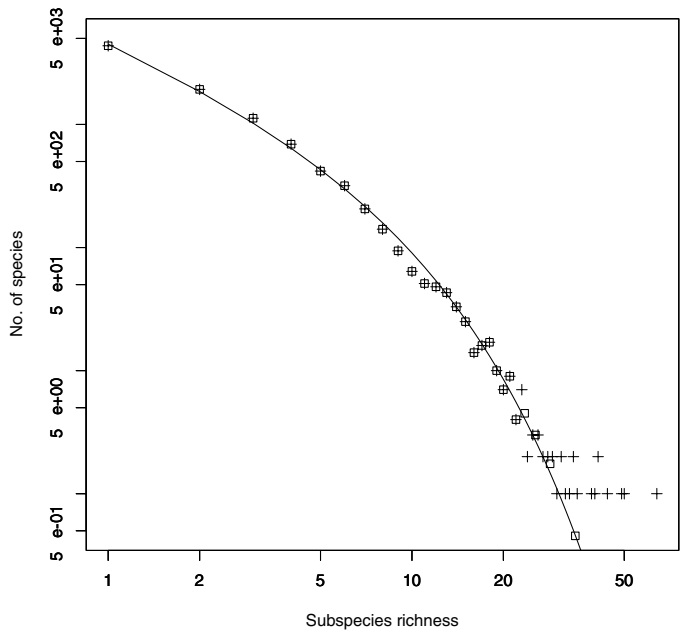

Figure 1. Logarithmic frequency plot of the subspecies richness of 9657 bird species. The curve is the predicted relationship estimated under maximum likelihood using the Reed–Hughes model (Reed and Hughes 2002). Crosses represent the observed data. Squares represent the data grouped at higher levels of subspecies richness (groups are 23–24, 25–26, 27–30, 31–64).

($\chi^2 = 66.5$, df = 23, $P < 0.001$). The lack of fit was most extreme at high values of subspecies richness in which the predicted relationship underestimated the number of extreme subspecies-rich clades. However, this is not surprising, given that we were trying to fit a two-parameter model to > 9500 species.

SPECIES AGE AND SUBSPECIES RICHNESS

A positive relationship was detected between species age and subspecies richness in 12 of the 19 tests (Table 1). However, this relationship was only found to be significant in two of the cases. Analyzed across the phylogenies, the effect sizes showed no significant departure from homogeneity of variance ($Q = 22.72$, df = 18, $P = 0.20$). Consequently, a fixed effects model was used for meta-analysis. The mean effect size described a weak positive relationship between species age and subspecies richness (mean weighted $Z_r = 0.04$, $r = 0.02$), which was not significantly different from zero ($Z = 0.63$, df =1, $P = 0.53$).

PHYLOGENETIC SIGNAL OF SUBSPECIES RICHNESS

Variance components analysis of taxonomic levels using generalized linear modeling (GLMM) with Poisson errors revealed that only 5% of the variance in subspecies richness is located among higher taxonomic levels, with the remaining 95% of variance partitioned among species. This result was in broad agreement with a similar test restricted to passerine birds (Sol et al. 2005), although the previous study reported a lower proportion of the variance distributed among species (75%).

The maximum-likelihood phylogenetic signal value was zero for 14 of 19 and 12 of 19 cases for the individual phylogenetic analyses of subspecies richness and subspecies diversification rate, respectively (Table 1). The pooled maximum-likelihood phylogenetic signal value was zero for both subspecies richness (approximate 95% confidence interval of 0.00–0.05) and subspecies diversification rate (approximate 95% confidence interval of 0.00–0.07). Thus taxonomic and phylogenetic approaches agree that subspecies richness and diversification rate generally exhibit a very low phylogenetic signal.

BIOGEOGRAPHIC CORRELATES OF SUBSPECIES RICHNESS

The breeding range size of a species explained a sizeable proportion of the variation in subspecies richness (Table 2 and Fig. 2). However, a linear relationship is significantly better supported than a quadratic relationship (likelihood ratio = 33.24, df = 1, $P < 0.001$). When analyzed in isolation, island-dwelling species were found to possess significantly fewer subspecies on average than their continental counterparts (Table 2). Insular species, however, tend to have smaller geographic ranges and the influence of the range size was found to mask the influence of insularity. In fact, for a given geographic range size, an island-dwelling species is predicted to be more subspecies rich than a continental species (Fig. 2). A weak negative correlation was identified between the proportion of a species' range classified as montane and its subspecies richness (Table 2, Fig. 2). After controlling for range size, however, we found a significant positive relationship between mountain dwelling and subspecies richness (slope = 0.35, SE = 0.06, $P < 0.001$). Habitat heterogeneity correlated positively with subspecies richness (Table 2, Fig. 2), explaining more than 10% of the variance in subspecies richness globally. Inclusion of breeding range size in the model reduced the slope of this relationship, although the term remained significant (slope = 0.23, SE = 0.05, $P < 0.001$). Species that inhabit recently glaciated regions tend to posses a significantly greater number of subspecies (Table 2) than those that do not, but this pattern was reversed when breeding range size was included (Fig. 2), reflecting the fact that these recolonizing species often have large range sizes.

The analysis of latitudinal variation in subspecies richness revealed a significant relationship in the southern hemisphere, with low latitude species being more subspecies rich (Table 2, Fig. 2). No such tendency was revealed in the Northern hemisphere.

The inclusion of breeding range size, island dwelling, mountain dwelling, habitat heterogeneity, and glacial dwelling in the same model accounted for 32% of the variation in global subspecies richness (Table 3A). All terms were significant predictors of subspecies richness. Large breeding ranges, insularity,

Table 1. Summary statistics for phylogenies, species age, and subspecies richness for phylogenies used in analyses.

Taxa	Order	Distribution	Tips sampled	Tips total[4]	Slope (± SE)	r	P value	Phylogenetic signal ln(S)	Phylogenetic signal ln(S)/t	Reference
Cracidae (*Crax*, *Mitu*, *Pauxi* & *Nothocrax*)	Craciformes	Neotropics	14	14	−1.83 (9.50)	−.48	.08	.00 (.00–1.00)	.29 (.00–1.00)	Pereira and Baker (2004)
Tetraoninae[1] (*Bonasa*, *Centrocercus*, *Dendragapus*, *Lagopus*, *Tetrao*, *Tympanuchus*)	Galliformes	Nearctic, Palaearctic	17	17	.86 (1.26)	.17	.51	.00 (.00–.83)	.00 (.00–.59)	Dimcheff et al. (2002)
Anas[2]	Anseriformes	Afrotropics, Australasia, Indo-Malaysia, Nearctic, Neotropics, Oceania, Palaearctic	30	30[L1S3]	.20 (.47)	.08	.67	.00 (.00–.31)	.00 (.00–.30)	Johnson and Sorenson (1999)
Pteroglossus[3] (*Pteroglossus*, *Baillonius*)	Piciformes	Neotropics	14	14	6.71 (16.57)	.12	.69	.00 (.00–.54)	.00 (.00–.47)	Eberhard and Bermingham (2005)
Amazona[2]	Psittaciformes	Neotropics	28	31	−.02 (.06)	−.08	.68	.00 (.00–.43)	.18 (.00–.59)	Russello and Amato (2004)
Gruidae[2]	Gruiformes	Afrotropics, Australasia, Nearctic, Neotropics, Palaearctic	15	15	3.29 (1.26)	.59	.02	.00 (.00–.58)	.00 (.00–.58)	Krajewski and Fetzner (1994)
Tringa[1] (Tringa, Catoptrophorus)	Ciconiiformes	Afrotropics, Nearctic, Neotropics, Palaearctic	15	16	−.19 (.74)	−.07	.80	.00 (.00–.74)	.00 (.00–.70)	Pereira and Baker (2005)
Laridae[1]	Ciconiiformes	Afrotropics, Australasia, Indo-Malaysia, Nearctic, Neotropics, Oceania, Palaearctic	53	50[S3]	−.39 (.32)	−.16	.24	.00 (.00–.30)	1.00 (.99–1.00)	Pons et al. (2005)
Alcinae[2]	Ciconiiformes	Nearctic, Palaearctic	23	23	.30 (.69)	.09	.67	.32 (.00–.78)	.00 (.00–.43)	Friesen et al. (1996)
Spheniscidae[1]	Ciconiiformes	Antarctica, Australasia, Neotropics	17	17	1.48 (.66)	.50	.04	.00 (.00–.60)	.00 (.00–.40)	Baker et al. (2006)
Empidonax[3]	Passeriformes	Nearctic, Neotropics	16	16	−.72 (.47)	−.38	.15	.00 (.00–.44)	.00 (.00–.42)	Johnson and Cicero (2002)
Geositta/*Geobates*[3]	Passeriformes	Neotropics	11	11	−.01 (.02)	.12	.72	.94 (.12–1.00)	.87 (.01–1.00)	Cheviron et al. (2005)
Cinclodes[3]	Passeriformes	Neotropics	14	13[S1]	−17.53 (18.01)	−.28	.35	.00 (.00–.77)	.00 (.00–.79)	Chesser (2004)
Xiphorhynchus[3]	Passeriformes	Neotropics	11	13[L2]	.00 (.00)	.02	.94	.00 (.00–.90)	.05 (.00–1.00)	Aleixo (2004)
Cinclus[1]	Passeriformes	Nearctic, Neotropics, Palaearctic	5	5	2.04 (1.21)	.70	.19	.34 (.00–1.00)	.00 (.00–.82)	Voelker (2002)

Continued.

Table 1. Continued.

Taxa	Order	Distribution	Tips sampled	Tips total[4]	Slope (± SE)	r	P value	Phylogenetic signal ln(S)	Phylogenetic signal ln(S)/t	Reference
Catharus[1]	Passeriformes	Nearctic, Neotropics	12	12^{S1}	1.13 (.79)	.41	.18	.27 (.00–.97)	.00 (.00–.52)	Outlaw et al. (2003)
Tachycineta[3]	Passeriformes	Nearctic, Neotropics	9	8^{S1}	.00 (.00)	.22	.58	1.00 (.00–1.00)	1.00 (.00–1.00)	Whittingham et al. (2002)
Sylvia[2]	Passeriformes	Afrotropics, Palaearctic	24	25^{S1}	.38 (.34)	.23	.27	.00 (.00–.60)	.00 (.00–.57)	Böhning-Gaese et al. (2003)
Icterus[2]	Passeriformes	Nearctic, Neotropics	25	25^{L1S2}	.15 (.65)	.05	.82	.00 (.00–.77)	.80 (.00–.94)	Omland et al. (1999)

[1] Phylogenetic trees were made ultrametric using a penalized-likelihood approach (Sanderson 2002) implemented in the APE R library (Paradis et al. 2004). The optimal smoothing parameter was identified via minimization of D^2 (see Paradis 2006 for details).

[2] Phylogenetic trees supplied by Price (2007), details of the tree reconstruction methods and rate smoothing approaches therein.

[3] Phylogenetic trees obtained from Weir (2006), methods described therein.

[4] Tips total was the number of species as recognized by Sibley and Monroe (1990, 1993) in the smallest monophyletic clade that was ≥90% complete.

In the tips total column the superscript denotes whether the phylogenetic taxa were split (superscript S) or lumped (superscript L) relative to the Sibley and Monroe data and the number of occasions on which this was conducted. This means that it is possible for a phylogenetic taxa that has been split to have more tips (tips sampled) than were recognized by Sibley and Monroe (tips total).

mountain dwelling, inhabitation of multiple biomes, and absence from lands that were glaciated within the last 21,000 years ago all appear to predispose species to elevated subspecies richness. Interestingly, in this model, mountain dwelling and overlap with recently glaciated areas each showed the opposite relationship with subspecies richness to those estimated in the single-predictor models. The robustness of these findings was corroborated by qualitatively similar results obtained using a generalized linear model with a negative-binomial error structure (without fitting the nested taxonomic random effects).

A latitudinal gradient of subspecies richness in both hemispheres received strong statistical support when other biogeographic variables were included in the model (Table 3B). The gradient between latitude and subspecies richness was found to be significantly different in each hemisphere. All of the other biogeographic variables were significant in this model and the majority of biogeographic traits showed similar coefficients in this model to those in the global model (Table 3A). The exception to this rule is glacial overlap, which in the latitudinal model was found to be positively associated with subspecies richness, meaning that species inhabiting recently glaciated regions have significantly more subspecies than those inhabiting regions that have been ice-free in recent times. There remains the possibility that the reversal of the direction of this effect could reflect colinearity between latitude and glacial overlap. However, the highest variance inflation factor reported for these variables was 7.04, falling below the commonly used threshold of 10 (Myers 1990), and suggesting that colinearity may not be the explanation. Again this model was able to explain approximately 27% of the variation in subspecies richness.

GLOBAL DISTRIBUTION OF SUBSPECIES RICHNESS

Geographical heterogeneity in the distribution of subspecies richness per species is illustrated in Figure 3A. Care must be taken in interpreting this map, as high values areas are not "hot spots" of subspecies richness per se, rather they are areas that correspond to species that on average possess higher numbers of subspecies across their range. The high-value areas correspond partially to areas of large average range size, such as the Palaearctic and North Africa (Orme et al. 2006). Conversely, the subspecies-poor areas show some agreement with regions of small geographic range size, such as the Neotropical Andes. Regions with very distinct avifaunas tend towards lower average subspecies richness, as can be seen in the cases of Australia, New Zealand, and Madagascar. Remote islands and archipelagos (e.g., Hawaii), also tend to harbor relatively subspecies-poor species. However, island groups in close proximity to one another and a mainland source (e.g., within Melanesian archipelagos) were found to harbor species that were, on average, subspecies rich. The low subspecies richness of Afrotropical and Neotropical species countered by the

Table 2. Biogeographical correlates of subspecies richness, controlling for taxonomic effects. Univariable models (A) included only a single term, and bivariable models included two terms and, in the case of latitude, an interaction term. Coefficients were derived from a generalized linear mixed model (GLMM) with nested taxonomic levels fitted as random effects and quasi-Poisson error structure. Coefficient values are on the log scale.

	Variable	Intercept	Intercept 2 or slope	*P* value	*n*	Model fit[2]	Log-likelihood
(A) Univariable models							
	Breeding range	−1.82 (.12)	.12 (2.6×10^{-3})	<.001	9593	.249	−18,231.58
	Island dwelling	.48 (.08)	.30 (.04)[1]	<.001	9593	.003	−18,329.75
	Mountain dwelling	.48 (.09)	−.25 (.06)	<.001	9593	.012	−18,285.6
	Habitat heterogeneity	−1.08 (.11)	1.19 (.04)	<.001	9593	.121	−18,224.98
	Glacial overlap	.91 (.11)	.40 (.06)[1]	<.001	9593	.000	−18,353.8
(B) Bivariable models							
1.	Breeding range	1.86 (.15)	.13 (.01)	<.001			
	Breeding range quadratic		-1.1×10^{-4} (3.1×10^{-4})	.73	9593	.247	−18,248.20
2.	Latitude (Northern Hemisphere)	1.08 (.12)	-4.1×10^{-4} (1.5×10^{-3})	.78			
	Latitude (Southern Hemisphere)	1.09 (.06)	.017 (.00)	<.001	3647	.015	−5832.366

[1]The second intercept corresponds to island dwelling (vs. continental dwelling) and no glacial overlap (vs. glacial overlap) in the island dwelling and glacial overlap factors.

[2]Model fit estimated as the proportion of the total residual variance (i.e., not distributed among taxonomic random effects) that can be explained by the inclusion of a term.

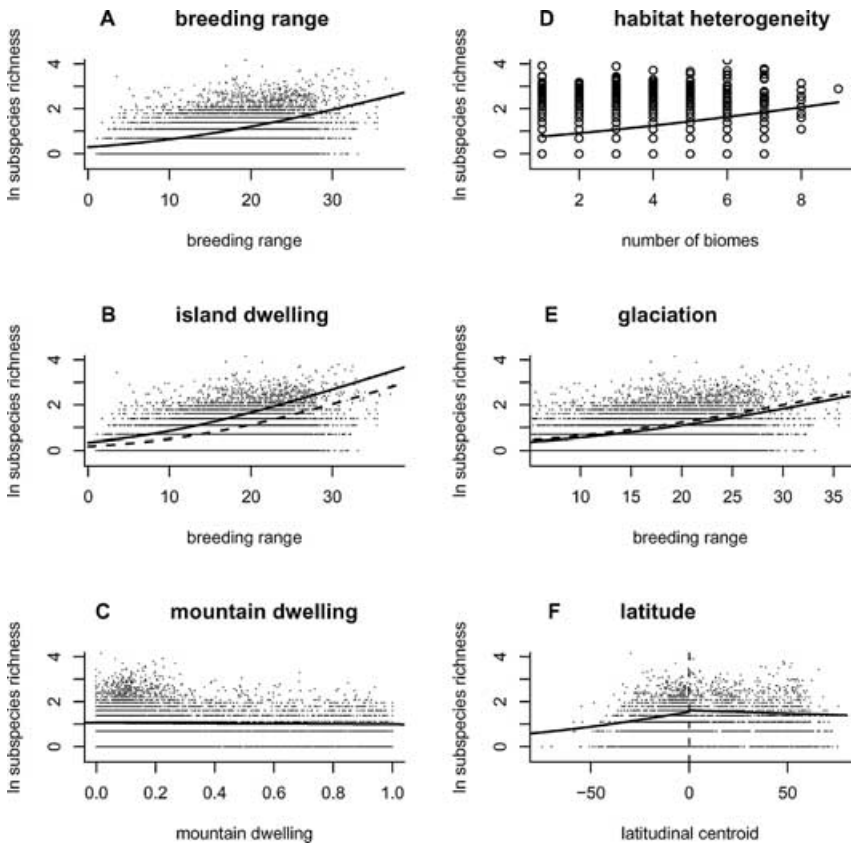

Figure 2. Relationships between the subspecies richness and a series of biogeographic variables. Plots show the underlying data and predicted fits from a generalized linear model with Poisson errors. Breeding range was normalized by scaling to the power 0.2. In the island-dwelling plot the dashed and solid lines represent the relationships between breeding range and subspecies richness for strictly continental and island dwellers, respectively. In the glaciation plot the dashed and solid lines represent the predicted relationships between breeding range and subspecies richness species that have ranges that were classified as no glacial overlap and glacial overlap, respectively (see Methods). The latitude plot shows the predicted latitudinal centroid (in degrees) versus subspecies relationship for each hemisphere based upon a reduced dataset of species with a latitudinal extent of $<20°$.

high subspecies richness of Europe and the western United States raises the possibility that taxonomic practices may differ between regions. It is possible that the Afrotropics and Neotropics may harbor more subspecies-poor species due to a reduction in the average range size, or due to populations having completed speciation rather than remaining at the subspecies stage. Nonetheless, a historically lower intensity of taxonomic study conducted on intraspecific variation in the Afrotropics and Neotropics compared with Europe and the western United States represents a likely explanation that may contribute to the observed geographic pattern.

After fitting multiple biogeographic terms to try to explain subspecies richness (Table 3A), geographic variation in the residuals from this model is still evident (Fig. 3B). Most islands appear as areas of high residual values, suggesting that our binary island-dwelling term may not adequately account for the relationship between islands and subspecies richness. The Andes mountain chain is also notably subspecies rich, which indicates that this region possesses more subspecies-rich species than predicted by the model. The large "hot spot" in the southwest Nearctic is, however, harder to explain. We tentatively suggest that this may reflect either a tendency for taxonomists to describe more subspecies in this region or the influence of a further ecological or biogeographic predictor of subspecies richness that was not considered in this study. A latitudinal gradient in the residuals is also apparent, with species that possess higher residuals found close to the equator.

Discussion

BIOGEOGRAPHIC CORRELATES OF SUBSPECIES RICHNESS

Our results support theoretical predictions that biogeographic factors play an important role in population divergence. The phylogenetic signal of subspecies richness was found to be very weak, indicating that closely related species often have very different numbers of subspecies. This finding is consistent with similar findings on passerine subspecies richness (Sol et al. 2005) and species richness conducted on avian families (Ricklefs 2004; Phillimore et al. 2006). The implication of low phylogenetic signal is that strong predictors of interspecific variation in subspecies richness are likely to be either phylogenetically plastic, or extrinsic factors independent of phylogeny (e.g., biogeographical), rather than highly conserved traits such as body size. When we tested the relative contribution of a variety of biogeographic factors in explaining variation in subspecies richness, breeding range size was found to be the most important factor, explaining approximately 20% of the variance in subspecies richness. Species with geographic ranges encompassing multiple biomes were also found to possess significantly more subspecies, even after range size was controlled for. Subspecies richness was also positively correlated with insularity, mountains, and regions that have been under ice sheets within the past 21,000 years. Interestingly, we also identified a weak but significant latitudinal gradient in subspecies richness that was not attributable to covariance with other latitudinally distributed features such as range size (Orme et al. 2006). Taken together, these results demonstrate that pluralities of biogeographic barriers and conditions are associated with the divergence and persistence of subspecies over time.

It is perhaps unsurprising that breeding range size is the strongest predictor of subspecies richness. Several previous studies have identified a significant relationship between total geographic area and various levels of taxon richness (Gaston 1998; Owens et al. 1999; Belliure et al. 2000; Bennett and Owens 2002). Indeed, Darwin (1859) noted that more widespread plant species tend to possess more varieties. However, there has been some debate on the direction of this relationship. Analyses that consider range size as the sum across the members of a clade have tended to find a positive trend, whereas those that consider the range sizes averaged across members of a clade have tended to find the opposite (Jablonski and Roy 2003). One of the proposed explanations for the negative relationship sometimes observed between diversification rate and range size is that another trait (such as abundance or dispersal), which promotes range spread, may also act to ameliorate the opportunity for phenotypic divergence (Jablonski and Roy 2003). Here, however, we were not only able to reject a negative relationship between range size and subspecies richness, but were also able to reject the hypothesis that subspecies richness is maximized at an intermediate range size (Gaston 1998). The demonstration here of a positive correlation between the total continental range size of species and subspecies richness agrees with both allopatric and parapatric models of divergence. Alternatively, larger geographic range size could lead to elevated subspecies richness by reducing the likelihood of population extinction (Hansen 1978).

The strong positive correlation between habitat heterogeneity and subspecies richness argues for adaptation to local ecological conditions playing a role in promoting subspecies richness. Such a relationship is predicted under both parapatric "ecotone" and allopatric models of diversification (Smith et al. 1997; Schluter 2000), although we cannot distinguish between the two in the present study. Alternatively, it is possible that taxa possessing greater tolerance to different environmental conditions may be better able to survive periods of climatic change (Brown 1971).

That island species possess more subspecies than their continental counterparts, after controlling for geographic range size, is consistent with the findings of Mayr and Diamond (2001) and follows the predictions of allopatric divergence via dispersal and peripatric divergence (Mayr 1963). The role of island dwelling in promoting subspecies richness is well illustrated by considering the five bird species with the highest number of described

Table 3. Maximal generalized linear mixed models (GLMMs) of global biogeographic correlates of subspecies divergence events, controlling for taxonomy. Models implemented with a quasi-Poisson error structure. Model (A) $n = 9599$, model fit = 0.32. Random effect variance components: order = 0.18 (0.07–0.42), family = 0.12 (0.07–0.21), genus = 0.14 (0.12–0.18), species = 3.06 (2.97–3.15). Model (B) $n = 3645$, model fit = 0.27. Random effect variance components: order = 0.24 (0.10–0.58), family = 0.12 (0.07–0.22), genus = 0.17 (0.13–0.21), species = 2.62 (2.49–2.77). Coefficient values are on the log scale.

Variable	Model (A) full global dataset			Model (B) restricted latitude dataset		
	Coefficient	Standard error	*P* value	Coefficient	Standard error	*P* value
Intercept	−3.38	.15	<.001	−2.14	.20	<.001
Breeding range	.14	3.0×10^{-3}	<.001	.11	5.6×10^{-3}	<.001
Island dwelling[1]	1.08	.05	<.001	1.08	.06	<.001
Mountain dwelling	.48	.06	<.001	.77	.10	<.001
Habitat heterogeneity	.47	.05	<.001	.62	.07	<.001
Glacial overlap[1]	.24	.06	<.001	−.19	.07	<.01
Latitude				−.02	1.8×10^{-3}	<.001
Hemisphere				−.04	.06	.51
Latitude × Hemisphere				.03	3.9×10^{-3}	<.001

[1]In the case of factors the coefficient represents the difference between the intercept and the second factor level. For the island-dwelling factor the second factor level is island (whereas the main intercept refers to continent dwelling). For the glacial overlap factor the second factor level is no overlap (while the main intercept refers to glacial overlap).

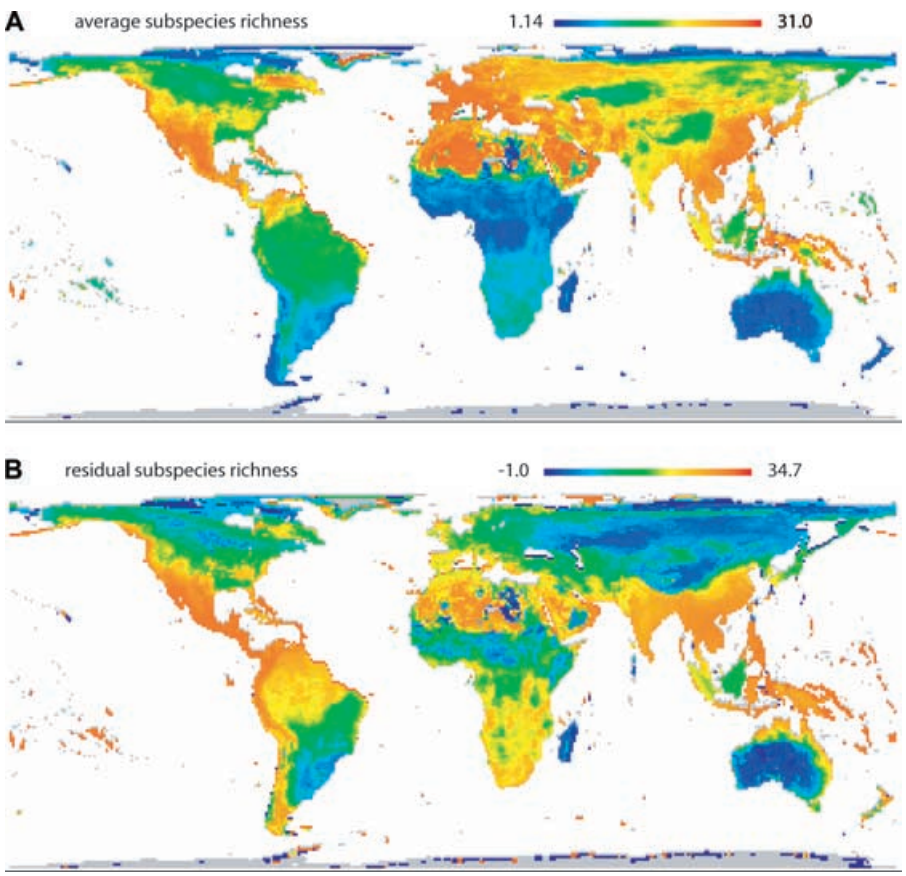

Figure 3. Geographical distribution of variation in subspecies richness across species. (A) The global distribution of average subspecies richness. Colors represent 10% quantiles in the mean of the ln-transformed subspecies richness of species within a given 1° grid cell. (B) The global distribution of the average residual values from the global model (Table 3A). Colors represent 10% quantiles in the median of the residual values of species within a given 1° grid cell. Parameter estimates for the global model from which residuals were derived are reported in Table 3A. Both maps are projected on an equal-area Behrmann grid.

subspecies: the golden whistler (*P. pectoralis*–64 subspecies), island thrush (*Turdus poliocephalus*–50 subspecies), collared kingfisher (*Todirhamphus chloris*–49 subspecies), winter wren (*Troglodytes troglodytes*–44 subspecies), and bananaquit (*Coereba flaveloa*–41 subspecies). All of these species inhabit numerous islands with between 45% and 100% of their subspecies being insular (Clements 2000). Given the apparent propensity for subspecies-rich taxa to be island dwelling, it seems somewhat surprising that the variance explained by island dwelling in our models was quite low. Interestingly, the mapping of subspecies richness seems to indicate that not all islands are equal in terms of generating subspecies-rich species (Fig. 3). High subspecies richness is most strongly promoted where multiple islands lie within close proximity to large landmasses, rather than on the most remote islands. Moreover, we recognize that our measure of island dwelling (a two-level categorical variable) is unlikely to satisfactorily encapsulate the role played by islands in population divergence. For instance, only two of the aforementioned subspecies-rich species would be classified as island dwelling using our criterion (*T. poliocephalus* and *T. chloris*), as the remaining three species possess ranges that encompass a considerable proportion of continental as well as island landmass. Thus, we predict that the effect of island dwelling on subspecies richness described here is an underestimate of the role islands play in the divergence of avian subspecies. Moreover, insular taxa are unlikely to be more diverse due to reduced extinction. Indeed, there is ample evidence to suggest elevated extinction risk of island-dwelling forms (Manne et al. 1999). We suggest that a quantification of the number of islands inhabited by species may offer a promising avenue for further exploration of the relationship between island dwelling and diversification.

After controlling for breeding range size, mountain dwelling was also identified as an important biogeographic correlate of subspecies richness. This finding agrees with previous studies that have identified relationships between mountains and interspecific divergence within particular biogeographic regions (Remsen 1984; Graves 1985; Ripley and Beehler 1990; Fjeldså 1994; Roy et al. 1997; Hughes and Eastwood 2006). However, as far as we are aware, this is the first study to provide comparative evidence linking mountain dwelling to an increase in intraspecific divergence on a global scale. This result is consistent with the view of mountain regions as engines of divergence (Fjeldså 1994; Roy et al. 1997). Moreover, if one also takes into account evidence that montane bird species tend to be younger than lowland species (Fjeldså 1994; Roy et al. 1997; Weir 2006), this suggests a contemporary, as well as historical, effect of mountains on phenotypic divergence. As Figure 3B shows, all mountain ranges may not be equal in terms of promoting subspecies richness, with the Andes being particularly subspecies rich (after controlling for multiple biogeographic variables).

The relationship between colonization of recently glaciated areas and subspecies richness was the most equivocal of the patterns reported here. This study revealed nonindependence between the colonization of recently glaciated regions and both range size and latitude. Examined on its own, inhabitation of recently glaciated regions was found to elevate subspecies richness, but once geographic range size was included in the model, this trend was reversed. When the latitudinal centroid of species was then included, the effect of glacial overlap on subspecies richness reverted to being positive. Disentangling the underlying influence of glacial region colonization on subspecies richness is thus extremely challenging. We do find, however, that after taking other biogeographic factors into account, recently glaciated areas, when compared to areas that were not glaciated, do not have very different subspecies richness.

A significant latitudinal gradient in subspecies richness, in both hemispheres, emerged from these data once variation in breeding range size had been accounted for. However, this gradient was only able to explain approximately 2% of the total variation in subspecies richness. The trend could be caused by latitudinal gradients in any of: (1) subspecies diversification rate (Rohde 1992); (2) subspecies extinction rate (Rosenzweig 1978); or (3) species age, with older species inhabiting lower latitudes (Pianka 1966; Farrell and Mitter 1993; Ricklefs and Schluter 1993). Unfortunately, our identification of the latitudinal subspecies richness trend does not permit us to go beyond speculation concerning potential proximate causes.

Of course, the possibility remains that some of the factors that we have identified as being important may simply reflect geographical variation in the allocation of taxonomic ranks. A potential lack of consistency in the delimitation of subspecies remains an area of concern (Patten and Unitt 2002) and may contribute to differences in subspecies richness between regions that different taxonomists have traditionally worked in. However, we do not believe that the results presented here can be explained purely on the basis of taxonomic biases. Another interesting human bias that may affect our results is a potential preference of taxonomists to create groups that are neither too small nor too large (Scotland and Sanderson 2004). However, the birth–death model that we used suggests that there are more subspecies-rich taxa than expected by chance, meaning that we have no evidence for human bias generating an inflation of species of intermediate subspecies richness. Indeed, if such a bias does exist it might be expected to add noise to the signal of any effect of biogeography on divergence.

In this study we have considered biogeographic factors in isolation from species' biological and ecological traits, and in doing so we may have missed causative factors that predict both biogoegraphy and diversification and generate an autocorrelation between them (Harvey and Pagel 1992). For example, there are

a priori reasons to predict that body size may influence diversification rate (e.g., Martin and Palumbi 1992) and there is evidence that body size varies with biogeographical variables (e.g., Mayr 1956; Brown and Maurer 1987; Clegg and Owens 2002), thus such relationships with body size may lead to autocorrelation between biogeography and diversification. However, body size is relatively highly conserved between closely related species (Phillimore et al. 2006), making it an unlikely candidate for explaining a phylogenetically labile trait such as subspecies diversification rate (Sol et al. 2005). Other ecological traits may covary with biogeography and diversification in a similar way. An obvious candidate for this is dispersal distance, which has been shown to covary negatively with subspecies richness (Belliure et al. 2000) and also correlates with geographic range size, although different studies have identified different signs to the relationship (Paradis et al. 1998; Böhning-Gaese et al. 2006). Dissecting how species traits and biogeography covary and the effect of this on diversification represents an interesting avenue to explore in the future.

HOW DOES SUBSPECIES RICHNESS RELATE TO DIVERSIFICATION?

Although some authors have proposed that assuming species are of equal age enables interpretation of subspecies richness as an index of diversification rate (e.g., Belliure et al. 2000; Sol et al. 2005), we argue that such an interpretation is untenable. We know that species differ in their age (e.g., Klicka and Zink 1997; Johnson and Cicero 2004) and therefore the time available for the formation of subspecies will differ among species. Furthermore, we found that a birth–death model (Reed and Hughes 2002) of diversification was significantly better supported than a pure birth model (Yule 1925). Because of this we discuss how the subspecies richness correlates we observe may be explained by variation in extinction rate or species age, as well as diversification rate.

The lack of correlation between species age and subspecies richness poses an important question (see also Sol et al. 2005), what form does the species age versus subspecies diversification relationship take? Understanding this dynamic more thoroughly is a priority if subspecies richness is to be employed as a proxy for contemporary diversification. However, what we can currently say is that the available data suggest that diversification does not take place at a constant rate and that extinction must also be considered.

If subspecies are potentially incipient species, we can ask how our inferences regarding subspecies richness correspond to findings reported by studies conducted at higher taxonomic levels. Although, the low phylogenetic signal of diversification rate among subspecies (Sol et al. 2005) agrees with inferences drawn at the higher taxonomic levels in birds (Ricklefs 2004; Phillimore et al. 2006), there were several differences in the correlations identified at different taxonomic levels. For example, studies conducted above the species level have found that dispersal covaries positively with diversification (Owens et al. 1999; Bennett and Owens 2002; Phillimore et al. 2006), whereas a study conducted on subspecies richness reported the opposite relationship (Belliure et al. 2000). Additionally, although island dwelling is a strong predictor of subspecies richness (this study), it was not found to predict the species richness of avian families (Phillimore et al. 2006). These discrepancies may reflect a difference in the processes that generate subspecies diversification as compared to speciation.

SUMMARY

In conclusion, our results suggest that on a global scale the relationship between biogeography and contemporary population divergence is complex. Rather than supporting a single biogeographic factor, our analyses suggest that several factors are intimately linked to phenotypic divergence. It remains to be seen whether certain intrinsic biological traits, such as dispersal distance and relative brain size, that have been shown to relate to subspecies diversification in birds (Belliure et al. 2000; Sol et al. 2005), interact with the biogeographic routes to diversification explored here. Furthermore, although correlates of diversification have been studied in both birds and several other groups (e.g., Stuart-Fox and Owens 2003; Isaac et al. 2005; Paradis 2005; Phillimore et al. 2006), we know of no large-scale nonavian study that has addressed correlates of intraspecific diversification, and we recommend this as an avenue for future research.

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Supplementary Material

The following supplementary material is available for this article:

Appendix S1a. Details regarding the data in appendix S1b.
Appendix S1b.
Appendix S2.

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