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CHAPTER 4

SUBSPECIES ORIGINATION AND EXTINCTION IN BIRDS

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Abstract.—Avian taxonomists have traditionally used subspecies to describe geographic variation in morphology, plumage, and song. A complementary evolutionary perspective is that subspecies are incipient species, representing the first stages of speciation. Here, I review the evidence that subspecies may capture early stages of the speciation process and consider what we have learned about factors that drive subspecies diversification. I apply variants on the birth–death model to species age and subspecies richness data from 1,100 bird species. Clade-wide estimates of species diversification rates correlate positively with subspecies origination (hereafter "subspeciation") rates but not subspecies richness; thus, the evidence for heritable factors promoting speciation and subspeciation is equivocal. Subspeciation rates are higher among insular than among continental species, although this result is highly sensitive to the definition of insularity. *A posteriori* simulations based on the maximum-likelihood constant-rate birth–death parameter estimates reveal model inadequacy. One possible explanation for such model inadequacy is non-homogeneity in diversification rate through time, and I find support for a model that invokes an exponential decline in subspeciation rates through time, with differing rates in continental and insular species. Finally, I discuss some alternative models of subspecies origination and how they might be assessed using population genetic information and geographic range maps.

Key words: birth–death, diversity-dependent, phylogenetic, speciation, subspecies.

Origen y Extinción de las Subespecies de Aves

Resumen.—Los taxónomos de aves tradicionalmente han utilizado a las subespecies para describir la variación geográfica en morfología, plumajes y cantos. Una perspectiva evolutiva complementaria es que las subespecies son especies incipientes, por lo cual representan las primeras etapas de la especiación. En este trabajo reviso la evidencia que indica que las subespecies podrían capturar las primeras etapas del proceso de especiación y considero lo que hemos aprendido acerca de los factores que impulsan la diversificación de las subespecies. Aplico variantes del modelo de nacimiento y muerte para analizar datos sobre la edad de las especies y sobre la riqueza de subespecies en 1100 especies de aves. Los estimados de las tasas de diversificación a través de los clados se correlacionan positivamente con la tasa de origen de las subespecies ("subespeciación"), pero no con la riqueza de subespecies. Por lo tanto, la evidencia de que existen factores heredables que promueven la especiación y la subespeciación es equívoca. Las tasas de subespeciación son mayores en especies insulares que en especies continentales, aunque este resultado es altamente sensible a la definición de insularidad. Simulaciones *a posteriori* basadas en los estimados de máxima verosimilitud de parámetros de nacimiento y muerte constante indican que el modelo es inadecuado. Una posible explicación para esto es la existencia de hetereogeneidad temporal en la tasa de diversificación. Encontré evidencia a favor de un modelo que involucra una disminución exponencial en las tasas de subespeciación en el

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tiempo, con tasas distintas en especies continentales y especies insulares. Finalmente, discuto algunos modelos alternos de subespeciación y cómo podrían evaluarse información de genética poblacional y mapas de distribución geográfica.

For over a century, the designation and utility of subspecies has been a tension point between taxonomists, who aim to describe patterns of geographic variation, and evolutionary biologists, who are interested in the processes of local adaptation and incipient speciation (Mayr 1982a). Mayr (1963:424) defined the subspecies as "an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species." Although this definition is precise in terms of geography, it is vague regarding the taxonomic differences required for subspecies delimitation, which has led to difficulties in the consistent application of the subspecies concept and may partially explain why this rank has drawn such strong criticism from taxonomists (Wilson and Brown 1953, Zink 2004, Rising 2007). The challenge for taxonomists is accentuated because different characters often show discordant divergence among populations, which means that the delimitation of subspecies may differ depending on the characters used (Wilson and Brown 1953). Avian subspecies were traditionally described on the basis of phenotypic characters, in particular morphology and plumage, but in recent years the advent of molecular tools has seen many cases in which neutral genetic information conflicts with subspecies taxonomy (Barrowclough 1980, Zink 2004). From an evolutionary perspective, however, discordance among different characters that are subject to different evolutionary forces is not surprising (Wilson and Brown 1953; de Queiroz 1998, 2005; Fraser and Bernatchez 2001; Winker 2009).

Here, I begin by discussing evidence that avian subspecies may represent the early stages of geographic speciation. I review comparative studies that have sought to explain variation in the numbers of subspecies across different species and highlight the variety of ways that subspeciation has been modeled and the assumptions that have been made. Then, as a case study, I examine the extent to which variants on the birth–death model (in which rates are allowed to differ among clades, between islands and continents, and through time) can explain patterns of subspecies richness using a large sample of bird species. I also test for a relationship between species and subspecies diversification. Finally, I examine the gaps in our knowledge regarding subspecies diversification and how they might be addressed. I focus on birds in the present study because the delimitation of subspecies in this group has received more attention than subspecies of any other taxon. A corollary of the disproportionate attention given to avian subspecies is that the findings of this study may not be extendable to other groups.

Review

Subspecies and Speciation

Ernst Mayr advocated the idea that subspecies could be incipient species (Mayr 1940, 1942b; O'Brien and Mayr 1991); indeed, he stated that "geographic speciation is thinkable only, if subspecies are incipient species" (Mayr 1942b:155). However, Mayr considered that only geographically isolated subspecies have the potential to become new species (Mayr 1942b, 1982a). Endler (1977) demonstrated that subspecies with abutting ranges are often strongly differentiated, and this finding, combined with evidence that ecological speciation can occur in the face of gene flow (reviewed in Rundle and Nosil 2005), suggests that incipient species status may reasonably be extended to contiguous parapatric subspecies. If subspecies are on the evolutionary trajectory toward being full species (whether or not they ever go on to attain full species status; Patten, this volume), we can reasonably expect them to show divergence in characters that are considered important in speciation (e.g., pre- and postzygotic reproductive isolation, ecological divergence, and genetic divergence).

Subspecies are often delimited on the basis of characters that may play a role in prezygotic reproductive isolation. For example, geographic variation in vocalizations (Slabbekoorn and Smith 2002, Dingle et al. 2008), plumage color, and plumage pattern (Mayr 1942b) may all render members of a population most attractive to members of the same population (Clayton 1990, Uy et al. 2009), and these same traits are routinely used to delimit subspecies.

I am aware of no reports of postzygotic incompatibities (measured as F_1 hybrid fertility and viability) arising between avian subspecies, which is not surprising given that even among full species these barriers are often weak (Price and Bouvier

2002). However, Bensch et al. (1999) suggested that when subspecies follow different migratory routes, hybrids between these forms might have reduced recruitment. In addition, a study of sympatric red and black color morphs of Gouldian Finch (*Erythrura gouldiae*) found that the progeny of between-color-morph crosses suffered greater inviability than those of within-morph crosses (Pryke and Griffith 2009).

Selection drives ecological speciation (Rundle and Nosil 2005). For subspecies to represent the initial stages of ecological speciation, phenotypic differences between them ought to be the result of selection and have a genetic basis. Common garden studies have revealed cases in which differences between subspecies in morphology, life history, phenology, and song-based mate preferences have a genetic component (Price 2008: table 3.1). However, some geographic differences between subspecies, such as carotenoid-based plumage in House Finches (*Carpodacus mexicanus*; Hill 1993) and morphology in Red-winged Blackbirds (*Agelaius phoeniceus*; James 1983), reflect environmental effects. Unfortunately, there are too few common garden and reciprocal transplant experiments on avian subspecies to draw general conclusions regarding the genetic and environmental contributions to phenotypic variation. Field studies have highlighted cases in which divergence between subspecies in bill morphology (Benkman 1993a) and plumage and behavior (Mumme et al. 2006) has an adaptive function and is presumably the result of selection. Further evidence that selection plays an important role in geographic variation comes from a meta-analysis across many taxa (including but not restricted to birds), which found that phenotypic divergence between populations tends to exceed the null expectation under genetic drift (Leinonen et al. 2008).

Because (1) a long period of no (or little) gene flow is required for neutral genes to coalesce (Hudson and Coyne 2002) and (2) under selection, populations may diverge in the face of gene flow, monophyly of subspecies should not be necessary for their delimitation (Patten, this volume). It has been pointed out elsewhere (e.g., Winker 2009) that the divergence between species may take place along two axes, one phenotypic, the other genetic, and the divergence along each axis need not be correlated. The observation that more than a third of subspecies are monophyletic on a mitochondrial DNA (mtDNA) tree (i.e., members of a subspecies are more closely related to one another than to members of another subspecies) and that monophyly is greater among insular subspecies (Phillimore and Owens 2006) is consistent with geographically isolated populations being on independent evolutionary trajectories, as envisaged by Mayr (1942b).

Darwin (1859) predicted that speciose genera should generally subtend species that possess more varieties. A positive correlation between species richness and subspecies richness would be consistent with heritable or shared factors promoting diversification at both taxonomic levels. Haskell and Adhikari (2009) reported a positive correlation between the number of species in avian genera and the average number of subspecies subtended by each species. However, species and genera both vary in age, which means that variation in species and subspecies richness may reflect variation in genus and species age rather than variation in rates of diversification.

Comparative Studies

Numerous interspecific comparative studies have examined variation in the numbers of subspecies per species (subspecies richness), as a proxy for either phenotypic diversification or incipient speciation (e.g., Belliure et al. 2000, Phillimore et al. 2007, Seddon et al. 2008). Such studies make a multitude of assumptions; perhaps the most important is that different taxonomists consistently delimit subspecies across taxa, regions, and environments (but see Fitzpatrick, this volume). Any systematic departure from consistent subspecies delimitation has the potential to confound comparative analyses. A second important assumption is that the focal statistical models adequately capture the process of subspecies diversification, a subject to which I will return.

There is a long history of comparative research addressing variation in subspecies richness. Rensch (1960:23) noted that migratory passerines tend to have fewer subspecies than sedentary forms. In another classic work, Diamond et al. (1976) defined species as "great speciator[s]" if they are represented by five or more subspecies or allospecies in the Solomon Islands, and they found that the great speciators are predominantly short-distance colonists. In cuckoos, subspecies richness is highest among virulent parasitic species with multiple hosts, which implies a role for coevolution in cuckoo subspeciation (Krüger et al. 2009). In other studies, which vary in taxonomic and geographic scope, subspecies richness has been found to be elevated in species that have larger geographic range sizes (Belliure et al. 2000, Phillimore et al. 2007), in species that inhabit montane areas (Mayr and Diamond 2001) and understory rainforest habitats (Burney and Brumfield 2009), and in species that exhibit a greater degree of insularity (Phillimore et al. 2007), shorter natal dispersal distances (Belliure et al. 2000, Newton 2003), greater plumage ornamentation (Møller and Cuervo 1998), more pronounced plumage dichromatism (Seddon et al. 2008), higher song pitch (Seddon et al. 2008), more complex song (Seddon et al. 2008), smaller body size (Seddon et al. 2008), or larger relative brain size (Sol et al. 2005). Strikingly, even those cross-species studies that considered multiple predictors leave more than half of the variation in subspecies richness unexplained (e.g., Belliure et al. 2000, Phillimore et al. 2007).

On observing that a single authority often described the subspecies of a single species, Martin and Tewksbury (2008) went some way toward addressing the problem of inconsistent taxonomy by making intraspecific comparisons. They found that when they bisected species' latitudinal ranges at the latitudinal midpoint, 65.6% of 710 species with more than five subspecies had a greater number of subspecies at low latitudes than at high latitudes. For comparison, 20.0% of species had more subspecies at high latitudes. High-latitude subspecies also tend to have larger geographic ranges than low-latitude subspecies (Rapoport 1982: table 5.6). An additional reason that Martin and Tewksbury (2008) gave for focusing on intraspecific comparisons was that, if speciation occurs in peripheral isolates, recently formed sister species will tend to differ substantially in both range size and subspecies richness. Consistent with this argument is the observation that subspecies richness has a weak phylogenetic signal; that is, closely related species do not tend to have similar numbers of subspecies (Sol et al. 2005, Phillimore et al. 2007).

Modeling Diversification of Subspecies

Although subspecies richness has been the focus of several comparative studies, the underlying processes have received surprisingly little attention. Some studies make no mention of a model and simply compare predictors of subspecies richness (e.g., Belliure et al. 2000). Studies that tried to model a particular subspeciation process have tended to make conflicting assumptions. For example, Phillimore et al. (2007) modeled subspeciation variously as a pure birth, birth–death, or Poisson process, with the consequence that in some analyses they assumed that subspecies extinction was absent (pure birth and Poisson models), and in others they assumed that all species were of equal age (Poisson and birth–death models).

Analyses at the species level and above routinely use the birth–death model and variants thereof to estimate parameters of interest (Ricklefs 2007). Under the birth–death model, at each point in time, every lineage has a constant probability of splitting into two species and a different constant probability of going extinct (Kendall 1948). Here, I will limit my focus to the application of birth–death models to subspecies diversification.

Most previous comparative studies that focused on subspecies did not account for variation in the age of species. Sol et al. (2005) proposed that species age could be ignored on the basis of weak correlations between species age and ln subspecies richness. However, a high constant rate of extinction erodes the correlation between clade age and ln clade richness even if lineages arise at a constant rate (Paradis 2004, Ricklefs 2006). If the birth-death model provides a reasonable approximation of subspecies origination and extinction then species ages should not be ignored in rate estimation.

Temporal variation in diversification rates can also erode the relationship between clade size and richness (Ricklefs 2006). There is growing evidence that speciation and extinction have not been constant through time and that species diversification may in fact be diversity dependent, slowing toward the present (Ricklefs 2006, Weir 2006, McPeek 2008, Phillimore and Price 2008, Rabosky and Lovette 2008, Rabosky 2009b). It is plausible that a similar process could also govern subspecies diversification; as a species' geographic range is subdivided among a greater number of subspecies, subspeciation rates may decline or subspecies extinction rates may increase, or both. If this were the case, and most species are at their subspecies-richness carrying capacity, then addressing correlates of subspecies richness (i.e., carrying capacity) is more appropriate than addressing correlates of subspecies diversification or origination (Rabosky 2009a).

Case Study

The aims of the following study are to (1) examine whether a constant-rate birth–death model can account for the observed co-distribution of species ages and subspecies richness, (2) estimate subspeciation and subspecies extinction rates under a birth–death model, (3) examine the link between species diversification and subspecies diversification, (4) test whether subspecies diversification differs between insular and continental species, and (5) estimate the likelihood of the data under two temporally non-homogeneous models.

METHODS

Species ages.—I estimated species ages from the Bayesian posterior distributions of 44 mtDNA-based, species-level phylogenies (Appendix), all of which included >70% of the species recognized in their clades (Phillimore and Price 2008). These phylogenies had been constructed using a relaxed-clock approach in BEAST (Drummond et al. 2006, Drummond and Rambaut 2007), with the assumption that the nucleotide substitution rate of mitochondrial protein-coding genes has a mean of 1% per million years and is lognormally distributed across branches (for more details, see Phillimore and Price 2008). I adopted the species limits recommended by the original authors of the phylogenetic studies. I estimated the age of each species (i.e., the stem age for the intraspecific clade) as the median time to most recent common ancestor across the posterior distribution of 2,000 trees. Note, however, that estimating time to the most recent common ancestor from gene trees will overestimate the age of species to a degree that depends on the extent of ancestral genetic variation (Edwards and Beerli 2000).

Subspecies richness, insularity, and body-mass data.—I obtained subspecies richness information for the species with phylogenetic data from Phillimore et al. (2007: appendix S1B). This data set was compiled by reconciling information in Clements (2000) with Sibley and Monroe's (1990, 1993) taxonomy. Where species limits in the phylogeny differed from those in the data set, I split or lumped subspecies accordingly, with phylogenetic information taking primacy.

Because species-level phylogenetic studies are biased toward larger clades (Ricklefs 2007; Phillimore and Price 2008, 2009), it is possible that the species ages estimated in the present study are a nonrandom sample of all birds. To test whether the subspecies richness of birds in the study departed from a random sample, I compared the number of sampled species that have 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, or >10 subspecies to the expected numbers from the global data using a chi-square goodness-of-fit test.

The number of insular subspecies per species was obtained from Clements (2000). A subspecies was deemed insular if its range was limited to islands in the United Nations Islands Directory (see Acknowledgments). For each species, I then calculated the proportion of subspecies that were restricted to islands. If more than one subspecies was found on a single island, this was counted as a single case, because I was interested in inter-island rather than intra-island subspecies divergence. For example, five subspecies are described for *Aegotheles bennetti*, all of which are restricted to islands; however, four subspecies inhabit a single island, New Guinea, giving an insularity score of 2/5 = 0.4. If the proportion of insular subspecies was ≥0.3, I classed the species as having numerous insular subspecies. If the proportion was <0.3, I classed the species as continental. I then examined the sensitivity of results to this definition of insularity by repeating all analyses, replacing 0.3 with (1) 0.5 and (2) 0.8.

Statistical analysis.—If subspeciation follows an exponential pure birth process (Equation 1), a positive linear relationship between species age (t) and ln subspecies richness (N), of slope λ (the subspeciation rate) is expected. I examined the evidence for this using linear regression.

$$N(t) = e^{\lambda t} \tag{1}$$

If some subspecies suffer extinction, a constant-rate birth–death model (Kendall 1948, Harvey et al. 1994, Nee et al. 1994),

$$N(t) = \frac{\lambda e^{(\lambda-\mu)t} - \mu}{\lambda - \mu} \tag{2}$$

where μ represents a constant rate of stochastic lineage extinction, is more appropriate than the pure birth model. A constant rate of speciation and extinction can lead to nonlinear relationships between species age and subspecies richness, because extinction will have had more time to prune the lineages descended from old species (Harvey et al. 1994, Paradis 2004, Ricklefs 2006). If subspecies extinction rates approach subspeciation rates, $\ln(N)/t$ will give a biased estimate of the subspecies diversification rate ($r = \lambda - \mu$; Ricklefs 2006).

Given a subspeciation rate (λ) and subspecies extinction rate (μ), I estimated the likelihood ($l_i = P(n|t)$) of observing n subspecies in species i of age t following Equation 3 and Equation 4 (Bokma 2003; Ricklefs 2007, 2009), where the relative extinction rate $\varepsilon = \mu/\lambda$.

$$E(n) = e^{\lambda(1-\varepsilon)t} = e^{(\lambda-\mu)t} \tag{3}$$

$$P(n|t) = (1-\varepsilon)\frac{[E(n)-1]^{n-1}}{[E(n)-\varepsilon]^{n}} \tag{4}$$

The maximum-likelihood values of λ and ε for a distribution of species ages and their subspecies richness were those that maximized the sum of log likelihoods ($\ln L = \Sigma\ln(l_i)$). I identified the maximum-likelihood values for λ and ε by iterating through values of ε in the range 0–0.99999 in steps of 1^{-5} and using the optimize function (Brent 1973) in R (R Development Core Team 2008) to identify the maximum-likelihood value of λ for each value of ε. The maximum-likelihood values of λ and ε combined were those that corresponded to maximum ln*L* across these iterations. Approximate 95% and 99% confidence intervals (CIs) were calculated as those values of λ and ε for which $\ln L(\max) - \ln L(\lambda,\varepsilon) = 2.996$ and 4.605, respectively. Because incomplete species sampling could bias inferences by inflating species ages, I repeated parameter estimation including only phylogenies in which >90% of recognized species were included.

I estimated λ and ε for each phylogeny. Approximate 95% CIs for λ were calculated by fixing ε at its maximum-likelihood value and finding the values of λ that satisfied $\ln L(\max) - \ln L(\lambda,\varepsilon) = 1.92$. A similar procedure was followed to estimate confidence intervals for ε. I tested whether there was any evidence for heterogeneity in rates among clades using a likelihood ratio statistic, *T*, calculated as follows (Bokma 2003):

$$T = 2(\ln L_1 + \ln L_2 + \cdots + \ln L_{44} - \ln L_0) \tag{5}$$

The values $\ln L_{1-44}$ represent the maximum log likelihoods for each of the 44 phylogenies, and $\ln L_0$ denotes the global estimate across all trees. *T* should be approximately chi-square-distributed, with degrees of freedom equal to the difference in number of parameters between the null and alternative hypothesis, in this case $(44 \times 2) - 2 = 86$.

For each of the 44 phylogenies, I estimated the diversification rate among species as follows (Magallón and Sanderson 2001):

$$\hat{r} = [\ln(n) - \ln(2)]/t \tag{6}$$

where t was the median crown-group age for the phylogeny and n was the number of extant species. Using regression, I then examined the degree to which $\hat{r}$ predicted variation in (1) the mean ln transformed subspecies richness for clades and (2) clade subspeciation (λ) estimates.

Islands are often thought to be promoters of species and subspecies diversification (Mayr and Diamond 2001, Phillimore et al. 2007, Moyle et al. 2009). I tested whether estimates of λ and ε differ between a continental and island setting by estimating the ln*L*(max) separately for (1) species classed as continental and (2) species classed as insular, and then calculating *T* (Equation 5). I used a likelihood ratio test with 2 degrees of freedom to compare the multiple-rate versus fixed-rate models. I also explored the sensitivity of estimates to different definitions of insularity.

To assess the fit of the maximum-likelihood birth–death model to the data, I conducted simulations using the relevant parameter estimates for continental and insular taxa. I used a modified version of the "birthdeath.tree" function in the GEIGER R library (Harmon et al. 2008) to simulate branching and extinction of lineages starting with a single lineage and running the simulation for a fixed duration, after which the numbers of extant tips were counted. If all lineages were extinct before the simulation was completed, the simulation was repeated until ≥1 extant lineages resulted. The distribution of simulation durations followed the distribution of species ages. I conducted 1,000 replicates, each consisting of a separate simulation yielding extant subspecies for each species age observation. For each replicate, I calculated the mean ln('subspecies' richness) in each of the following species age classes (in millions of years): 0–0.9, 1–1.9, 2–2.9, 3–3.9, 4–4.9, 5–5.9, 6–6.9, 7–7.9, 8–8.9, and ≥9. I then calculated the 0.025 and 0.975 quantiles for each of these expected mean subspecies richness values and compared the observed and expected distributions. Good model fit would correspond to a case in which most of the observed data lie within the expected quantiles.

I then assessed the likelihood of the data under a model describing an exponential decline in subspeciation (and subspecies extinction) rate from an initial level λ_0, during the time since species origination (t). This was implemented by replacing r ($\lambda - \mu$ in Equation 3) with r_t, which corresponds to diversification rate at time t; thus (Rabosky 2009b):

$$r_t = \lambda_0 e^{-zt}(1-\varepsilon) \tag{7}$$

I identified the maximum-likelihood values of λ_0, z, and ε after calculating the likelihood of all combinations of parameters described by $\lambda_0 = 0.5 - 2$ (in units of 0.01), $z = 0 - 1$ (in units of 0.01), and $\varepsilon = 0.5 - 0.999$ (in units of 0.001). I assessed support for the exponential-decline model by comparing the ln$L$(max) to the likelihood of the best model satisfying $z = 0$ (constant rate of diversification) via a likelihood ratio test with a single degree of freedom. I also fitted the exponential decline model separately for continental and insular species.

If subspeciation is diversity dependent, one of the main determinants of subspeciation and subspecies diversification rates is likely the size of species' geographic ranges. Therefore, I replaced λ_0 with species' geographic range sizes (A) and a slope (c) and intercept (d) and replaced r ($\lambda - \mu$ in Equation 3) with $r_{\mathrm{i,t}}$ (corresponding to the diversification rate of species i at time t), thus:

$$r_{i,t} = (d + c\log(A_i))e^{-zt}(1-\varepsilon) \qquad (8)$$

Equation 8 is similar to equation 7 in Rabosky (2009b) but with the addition of an intercept (d). The model allows geographic range to influence the initial rate of subspeciation (and subspecies diversification). An assumption of this model is that species' geographic ranges have been constant through time (Rabosky 2009b).

Breeding-season geographic ranges (km^2) of 1,038 of the species included here were obtained from Phillimore et al. (2007)—these data were extracted from ARCGIS global distribution data (Orme et al. 2005, 2006). The maximum-likelihood values of d, c, z, and ε were identified after calculating the likelihood of the data under all combinations of parameters described by $d = -1 - 2$ (in units of 0.01), $c = -1 - 1$ (in units of 0.01), $z = 0 - 1$ (in units of 0.01), and $\varepsilon = 0.5 - 0.99$ (in units of 0.01). A model in which $c = 0$ corresponds to the initial subspeciation rate being unaffected by breeding-range size, which means that d is then the same as λ_0 in Equation 7. To assess whether geographic range size influences the rate of diversification, I used a likelihood ratio test to compare ln$L$(max) with the log likelihood of the most likely model satisfying $c = 0$. I also tested the support for this geographic-range model separately for continental and insular species.

None of the interspecific comparisons accounted for phylogenetic autocorrelation. However, given that subspecies richness appears to have little phylogenetic signal (Sol et al. 2005, Phillimore et al. 2007), this is unlikely to be a major source of statistical bias. All analyses were conducted in R.

Results

Global birth–death model.—Species age estimates (median = 3.17 MY, 2.5% quantile = 0.17 MY, 97.5% quantile = 10.61 MY) were obtained for 1,100 species from 44 different phylogenies. The median subspecies richness across sampled species was 2 (min = 1, max = 50), and in total there were 3,353 subspecies. Species included in this study were a random sample of all bird species with respect to subspecies richness ($\chi^2 = 7.43$, df = 10, $P = 0.68$).

There was a significant positive linear correlation between species age and subspecies richness ($b = 0.044 \pm 0.008$, $P < 0.001$); however, species age explained only 2.5% of the variance in subspecies richness (Fig. 1A). When a birth–death model was fitted to the same data, subspecies extinction was estimated to have occurred at a rate essentially equal to the subspeciation rate ($\lambda = 0.740$, $\varepsilon = 0.9999$, ln$L = -2{,}244.16$; Fig. 1A, B), and the likelihood of the data was substantially higher under this model than under a pure birth model ($\lambda = 0.298$, ln$L = -2{,}510.10$). Restricting the data to 27 phylogenies with good species sampling (≥90% complete at the species level) led to very little change in maximum-likelihood estimates of subspeciation and subspecies extinction ($\lambda = 0.744$, $\varepsilon = 0.99999$, ln$L = -1.083.57$).

Heterogeneity in subspeciation rate.—Maximum-likelihood estimates of λ and ε for different phylogenies revealed considerable heterogeneity in λ rates, from 0.06 in storks (Ciconiidae) to 2.02 in *Cinclodes*, but very little variation in ε, with 42 of 44 phylogenies returning a value of 0.99999 and 35 of 44 returning ε estimates that differed significantly from zero (Appendix). The sum of the maximum-likelihood estimates was −2,122.91, and the likelihood ratio compared with the global model was −121.25, which strongly supports the alternative hypothesis that λ and ε vary among clades ($T = 242.51$, df = 86, $P < 0.001$).

Species versus subspecies diversification.—Clade-wide species diversification rates did not predict variation in average subspecies richness ($a = 0.80 \pm 0.13$, $b = -0.47 \pm 0.49$, $R^2 = 0.02$; Fig. 2A), but these clade-wide rates were a strong positive predictor of variation in subspeciation rate estimates ($a = 0.19 \pm 0.18$, $b = 2.06 \pm 0.67$, $R^2 = 0.18$; Fig. 2B).

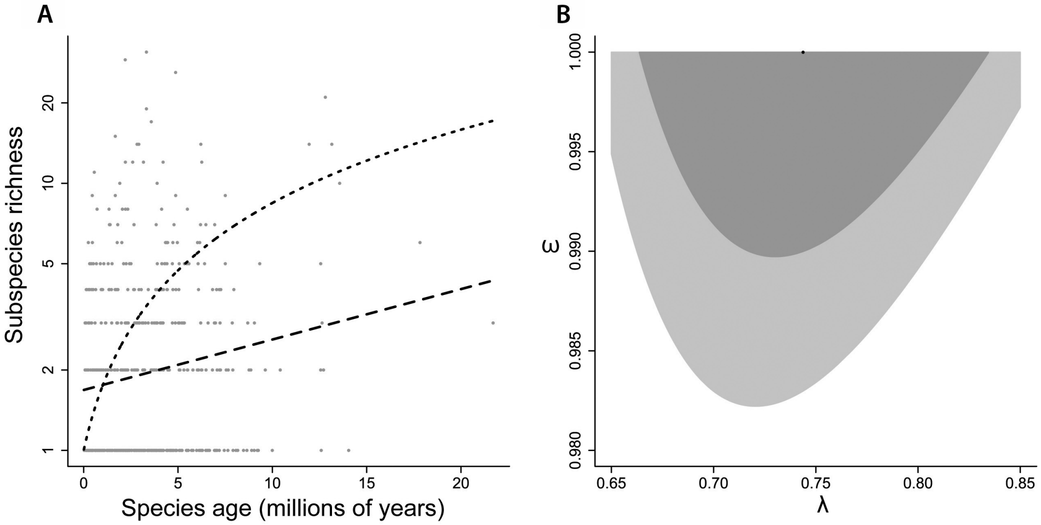

FIG. 1. (A) Species age versus subspecies richness for 1,100 species. The dashed line ($a = 0.564 \pm 0.039$, $b = 0.044 \pm 0.008$) is from a linear regression of ln(N) on t. The dotted line is fitted using the maximum-likelihood estimate for λ and ε, which are 0.740 and 0.99999, respectively. (B) A contour plot showing the maximum-likelihood values of λ and ε and the corresponding approximate 95% and 99% confidence intervals (ln$L$(max) = ln$L(\lambda,\varepsilon)$ = 1.92 and 3.32, respectively).

Continental versus insular species.—The subspeciation rate among the 212 insular species (λ = 1.029, 95% CI: 0.869–1.224; ε = 0.99999, 95% CI: 0.969–0.99999; ln$L$ = −451.19) exceeded that of their 888 continental counterparts (λ = 0.672, 95% CI: 0.615–0.735; ε = 0.99999, 95% CI = 0.993–0.99999; ln$L$ = −1,783.34), despite appearing superficially similar (Fig. 3A, B). This difference in rates between the two models was highly significant (T = 19.25, df = 2, $P < 0.001$).

When applied to the distribution of continental and insular species ages and subspecies richness,

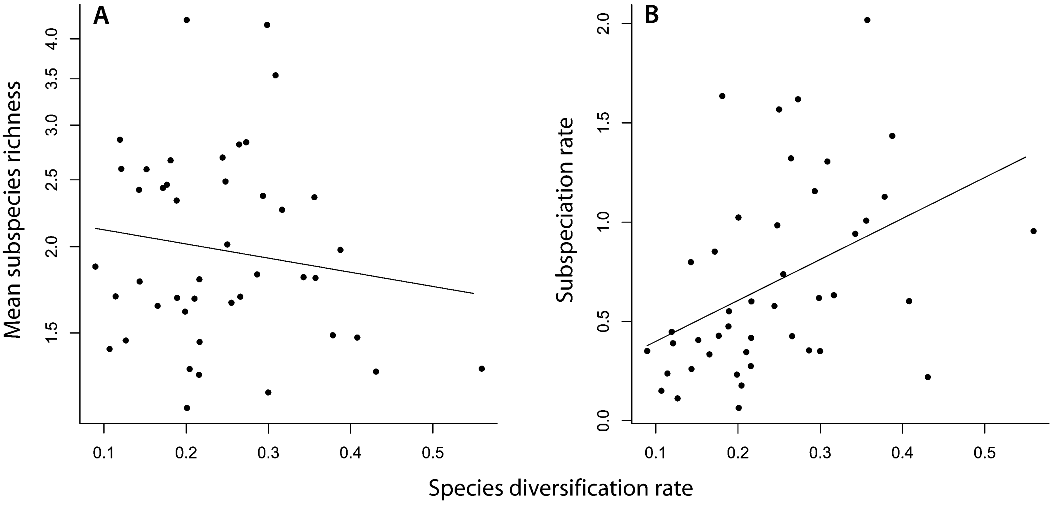

FIG. 2. (A) The linear regression of back-transformed mean ln(subspecies richness) on clade species diversification rate (see Equation 6), $a = 0.80 \pm 0.13$, $b = -0.47 \pm 0.49$, $R^2 = 0.02$. (B) The linear regression of subspeciation rate (λ; see Appendix) on species diversification rates (r), $a = 0.19 \pm 0.18$, $b = 2.06 \pm 0.67$, $R^2 = 0.18$.

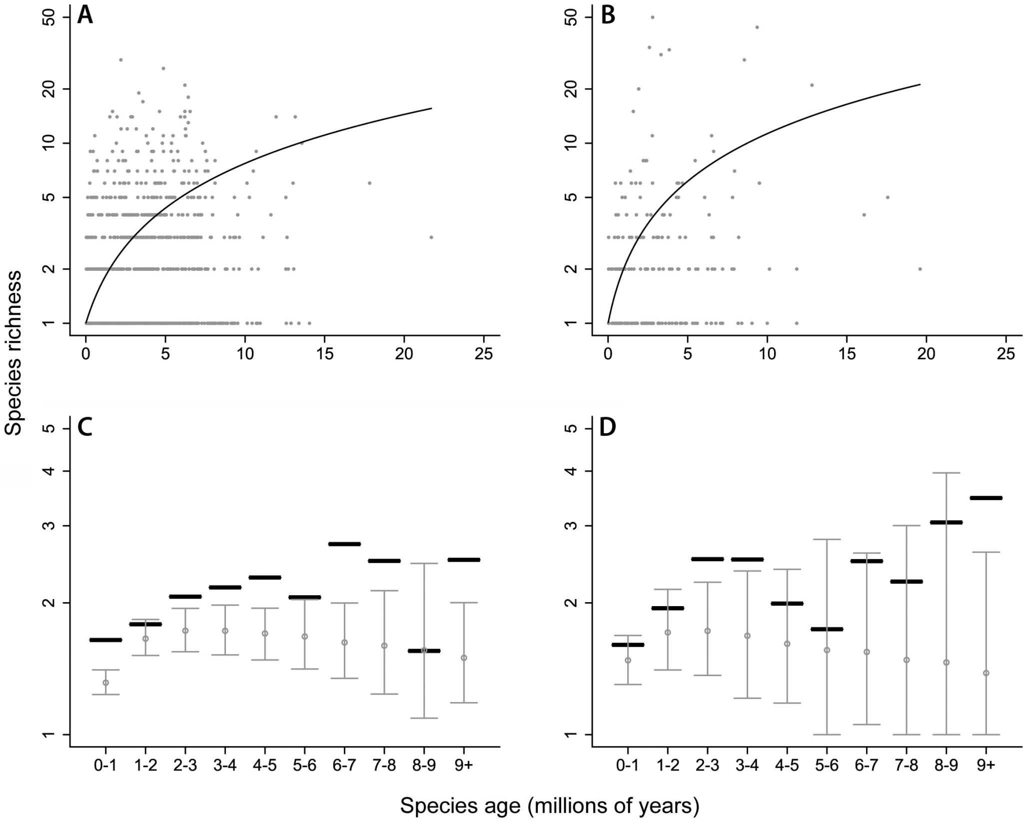

FIG. 3. Plots A and B show the observed relationship between species age and subspecies richness in continental (solid line fitted using λ = 0.67, ε = 0.99999) and insular species (solid line fitted using λ = 1.03, ε = 0.99999), respectively. Plots C and D show the average subspecies richness observed (black lines) and expected (gray 95% confidence interval; see text) in different age classes on continents and islands, respectively.

the birth–death model again received greater support than the pure birth model. However, there was a poor fit between the observed distribution and that expected given the maximum-likelihood parameter estimates (Fig. 3C, D). The average subspecies richness observed in each age class consistently exceeded the median that was expected and, in many cases, lay outside the 95% CIs.

Subspeciation rate estimates proved very sensitive to the definition of insularity. Defining insularity at a 0.5 cut-off (see above) resulted in a substantial reduction in the subspeciation rate estimated for insular species (number of species = 185; λ = 0.673, 95% CI: 0.552–0.823; ε = 0.99999, 95% CI: 0.980–0.99999; ln$L$ = −335.25) to below that of continental species (number of species = 915; λ = 0.753, 95% CI: 0.691–0.821; ε = 0.99999, 95% CI: 0.994–0.99999; ln$L$ = −1,908.40). The difference in rates between the two groups was nonsignificant (T = 1.01, df = 2, P = 0.60). A more stringent definition of insularity (≥80% of subspecies must be island endemics) led to a considerable decrease in the estimated subspeciation rate for insular taxa (number of species = 141; λ = 0.416, 95% CI: 0.318–0.543; ε = 0.99999, 95% CI: 0.999–0.99999; ln$L$ = −200.61), as compared with continental taxa (number of species = 959; λ = 0.783, 95% CI: 0.720–0.851; ε = 0.99999, 95% CI: 0.995–0.99999; ln$L$ = −2,033.69). In this instance, a model that allowed rates to differ between the two groups was preferred to the null (T = 19.72, df = 2, P < 0.001).

Diversity-dependent subspeciation.—A model of exponentially declining subspeciation (Equation 7) performed significantly better than the best constant-rate model (λ_0 = 1.53, z = 0.19, ε = 0.999, ln$L$ = −2,142.01, likelihood ratio = 205.04, df = 1,

$P < 0.001$). When this model was applied separately to insular and continental species (using the 0.3 cut-off; see above), the exponential-decline model was preferred to the constant-rate model in both cases (continental species: $\lambda_0 = 1.54$, $z = 0.21$, $\varepsilon = 0.999$, $\ln L = -1{,}691.91$, likelihood ratio = 184.27, df = 1, $P < 0.001$; insular species: $\lambda_0 = 1.61$, $z = 0.13$, $\varepsilon = 0.999$, $\ln L = -438.95$, likelihood ratio = 24.65, df = 1, $P < 0.001$), and parameters differed significantly between the two ($T = 22.3$, df = 3, $P < 0.001$).

In the maximum-likelihood range-size model (Equation 8), the initial rate of subspeciation was correlated with geographic range size and subspeciation rates declined exponentially thereafter ($d = -0.38$, $c = 0.14$, $z = 0.20$, $\varepsilon = 0.99$, $\ln L = -1{,}995.24$). The data were significantly more likely under this model than one positing no relationship between geographic range size and initial rate of subspeciation ($d = 1.58$, $z = 0.19$, $\varepsilon = 0.99$, $\ln L = -2{,}059.80$, likelihood ratio = 129.12, df = 1, $P < 0.001$). However, when assessed separately across 841 continental species and 197 insular species with range-size information, the slope (c) between geographic range size and initial subspeciation rate did not differ significantly from zero in either case (continental species: $d = 1.36$, $c = 0.01$, $z = 0.22$, $\varepsilon = 0.99$, $\ln L = -1{,}547.95$, likelihood ratio = 0.30, df = 1, $P = 0.32$; insular species: $d = 1.41$, $c = 0.03$, $z = 0.19$, $\varepsilon = 0.99$, $\ln L = -401.68$, likelihood ratio = 0.21, df = 1, $P = 0.65$). The difference in rates between the two settings was significant ($T = 91.22$, df = 4, $P < 0.001$), but the sum of continental and insular log likelihoods did not differ significantly between the maximum-likelihood model and models with c fixed at zero (total $\ln L = -1{,}949.75$, likelihood ratio = 0.22, df = 2, $P = 0.89$).

Discussion

Species diversification rate was not correlated with subspecies richness. By contrast, diversification rates were positively correlated with subspeciation rates, agreeing with a recent study that correlated species richness with subspecies richness in birds (Haskell and Adhikari 2009). If species and subspecies origination and extinction both followed constant-rate birth–death processes, the observed correlation would be consistent with shared factors promoting speciation and subspeciation. However, I found evidence that subspeciation has slowed over time, rather than being constant. This could lead to estimates of subspeciation being higher for younger species (i.e., species originating from clades with rapid diversification rates) than for older species (Rabosky 2009a). Although it remains to be established whether species are at their subspecies carrying capacity, if this were the case then comparative analyses focusing on subspecies richness (the carrying capacity) would be more informative than analyses focusing on subspeciation or diversification rates (Rabosky 2009a).

Subspecies extinction rates approached subspeciation rates in all the models considered in the present study. Extinction of a subspecies may arise because of the extirpation of a population, but it may also arise if the phenotypic differences between two populations collapse (O'Brien and Mayr 1991). A corollary of high subspeciation and subspecies extinction-rate estimates is that many contemporary subspecies should have arisen relatively recently (Nee et al. 1994).

The estimated subspeciation and subspecies extinction rates in the present study were higher among insular than among continental species. Although these results were highly sensitive to definitions of insularity, they persisted under the exponential subspeciation-rate-decline models. An earlier study on biogeographic predictors of subspecies richness also identified insularity as a factor promoting higher levels of subspecies richness (Phillimore et al. 2007). There are several potential explanations for this result. A reduction in gene flow between island populations may facilitate greater phenotypic divergence, either by drift or by selection. In addition, ecological conditions may vary more across islands than across continental regions, making divergence via selection more likely on islands (Price 2008). Alternatively, taxonomic practice may differ between continental and insular species. For instance, Pratt (this volume) suggests that 20th-century taxonomists, such as Mayr and Amadon, tended to relegate what in essence were good insular species to subspecies and lumped these together as polytypic species. If this practice was widespread, the ratio of subspecies to species for insular taxa will have been overestimated in this study.

Subspecies diversification models.—Constant-rate pure birth and birth–death models of subspeciation and extinction are unable to account for the subspecies richness observed across species of different age. Both models describe subspeciation as an exponential process, with each lineage equally likely to subspeciate at each moment in time; this seems unlikely in reality. Both subspeciation-rate-decline models were preferred to the constant-rate models. These models may correspond to a scenario in which the probability of subspecies formation is a function of geographic range size, with larger geographic ranges more prone to subdivision (Rosenzweig 1978) and species' geographic range sizes changing little through time. As subspecies subdivide the geographic range among themselves, the probability that each of these subspecies ranges will themselves be subdivided further is expected to decline.

Although I found greatest support for models invoking exponentially declining subspeciation rates, I considered only two of a wide range of possible temporally non-homogeneous models. Diversification rates may, in fact, decline linearly (Rabosky 2009b) or be dependent on the number of lineages present at a particular time. Perhaps even time-varying birth–death processes do not capture the true subspecies diversification process. For instance, multiple subspecies may already exist at the time of speciation, or one subspecies with a large range may be the parent of many peripheral isolate subspecies (Rapoport 1982).

Comparative analyses that address the topology and temporal dynamics of species-level molecular phylogenies have shed light on modes of speciation (Barraclough and Nee 2001). Unfortunately, below the species level, ongoing gene flow, historical introgression, and incomplete lineage sorting are more pronounced, and these factors may reduce the efficacy of subspecies-level phylogenies for reconstructing patterns of divergence. In this context, population genetic approaches to identifying hierarchical structure may offer greater promise, particularly where some gene flow is likely to have occurred.

In addition to phylogenetic–taxonomic approaches, the support for different subspecies diversification models can be assessed from the geographic distributions of subspecies. Rapoport (1982) found that there were more North American mammalian subspecies at the periphery of species' ranges than predicted under a simple null model and that peripheral subspecies tended to have smaller geographic ranges; both findings suggest a peripheral-isolates model of subspeciation. In recent years, however, most work on geographic ranges has been conducted at the species level, and subspecies distributions have been overlooked.

Model inadequacy.—*A posteriori* simulations of subspecies diversification given the maximum-likelihood birth–death parameters generated consistently fewer subspecies than were actually observed (Fig. 3C, D), which implies that the maximum-likelihood model is inadequate. Two possible explanations are that subspeciation rates vary across subspecies because of one or more unaccounted-for variables and that subspeciation rates vary through time (Rabosky 2009b), both of which appear to be true of these subspecies data. Recent work by Rabosky (2010) demonstrates that if the rate of diversification (r) varies across lineages, then, even in the absence of extinction ($\varepsilon = 0$), application of a likelihood model to clade ages versus richness data will often lead to estimates of ε that approach 1. Rabosky also found that the likelihood surface around the maximum-likelihood estimate of ε can be very steep, yet this feature is not recovered when data are simulated using the estimated parameters. Across all analyses in the present study, I found that estimates of ε were close to 1 and estimated with an apparently high degree of confidence; therefore, I recommend caution in interpreting these high extinction-rate estimates.

Subspecies and evolutionary potential.—Appropriately delimited subspecies may be indicators of future evolutionary potential and speciation hotspots (Fraser and Bernatchez 2001, Winker et al. 2007). If we accept that, like species, subspecies may diverge along two somewhat independent axes, a genetic and a phenotypic axis, this may facilitate greater consistency and agreement among taxonomists (Winker 2009). A sound understanding of the processes that govern the origination and extinction of subspecies will be invaluable in the practical conservation of evolutionary potential. This study is the first to provide evidence that subspecies diversification rates may vary through time.

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APPENDIX. Parameters estimated for individual phylogenies. For details regarding the phylogenies used, see Phillimore and Price (2009). The maximum-likelihood value of λ was estimated following Equation 4.

Clade	Number of species in phylogeny	Median species age (millions of years)	Median subspecies richness	λ (approximate 95% CI)	ε (approximate 95% CI)[a]	$\ln L$ (max)
Acanthiza	13	4.150	2.0	0.47 (0.24–0.97)	1.00 (0.49–1.00)	−24.93
Aegotheles	9	4.434	2.0	0.26 (0.10–0.66)	1.00 (0.00–1.00)	−13.78
Albatross	14	1.032	1.0	0.60 (0.25–1.40)	1.00 (0.00–1.00)	−17.49
Alcinae	22	3.156	2.0	0.42 (0.23–0.77)	1.00 (0.54–1.00)	−34.99
Alectoris	7	2.921	3.0	0.85 (0.37–2.18)	1.00 (0.58–1.00)	−16.01
Amazona	28	1.362	1.0	0.60 (0.32–1.30)	1.00 (0.71–1.00)	−44.03
Anas	45	0.656	1.0	1.13 (0.64–1.99)	1.00 (0.91–1.00)	−79.67
Anthus	37	5.142	3.0	0.58 (0.40–0.86)	1.00 (0.75–1.00)	−79.99
Caciques and oropendolas	17	3.238	2.0	0.35 (0.18–0.70)	1.00 (0.42–1.00)	−26.96
Catharus	12	5.188	4.5	1.02 (0.55–2.07)	1.00 (0.79–1.00)	−29.68
Cinclodes	13	0.868	2.0	2.02 (0.96–4.35)	1.00 (0.77–1.00)	−24.14
Cracidae	14	2.298	1.0	0.22 (0.08–0.56)	1.00 (0.00–1.00)	−13.50
Cranes	15	2.091	1.0	0.18 (0.08–0.32)	0.00 (0.00–1.00)	−14.15
Dendroica, Parula, Seiurus and *Vermivora*	40	2.467	1.0	0.94 (0.64–1.41)	1.00 (0.91–1.00)	−83.78
Empidonax	17	2.249	1.0	0.55 (0.27–1.14)	1.00 (0.67–1.00)	−27.32
Ficedula	27	4.560	1.0	0.33 (0.20–0.57)	1.00 (0.66–1.00)	−45.68
Geositta	11	5.497	1.0	0.15 (0.06–0.36)	1.00 (0.00–1.00)	−14.59
Grackles and allies	36	3.203	2.0	1.01 (0.67–1.55)	1.00 (0.92–1.00)	−84.84
Grouse, turkeys, partridges and tragopans	53	2.665	2.0	1.64 (1.19–2.30)	1.00 (0.97–1.00)	−131.25
Hemispingus	12	5.300	1.0	0.24 (0.10–0.57)	1.00 (0.21–1.00)	−15.30
Icterus	28	2.540	2.5	1.16 (0.72–1.91)	1.00 (0.91–1.00)	−65.66
Laridae	52	0.616	1.0	0.95 (0.57–1.58)	1.00 (0.76–1.00)	−66.98
Meliphaga	12	5.288	2.5	0.39 (0.20–0.81)	1.00 (0.51–1.00)	−23.95
Myiarchus	19	1.507	2.0	1.57 (0.87–2.90)	1.00 (0.88–1.00)	−39.90
Myioborus	12	1.956	1.5	1.43 (0.68–3.18)	1.00 (0.74–1.00)	−24.40
Parus	42	3.967	4.0	1.31 (0.94–1.86)	1.00 (0.95–1.00)	−115.93
Penguins	18	1.390	1.0	0.27 (0.11–0.63)	1.00 (0.00–1.00)	−18.99
Phylloscopus and *Seicercus*	59	4.310	1.0	0.43 (0.30–0.62)	1.00 (0.89–1.00)	−113.43
Pteroglossus	13	1.338	1.0	0.74 (0.32–1.69)	1.00 (0.44–1.00)	−18.59
Puffinus	24	1.464	1.0	0.35 (0.17–0.70)	1.00 (0.00–1.00)	−24.42
Ramphastos	8	2.494	2.0	0.34 (0.11–1.02)	1.00 (0.11–1.00)	−11.53
Sterinae	34	2.583	2.5	0.80 (0.52–1.25)	1.00 (0.93–1.00)	−73.60
Storks	16	4.069	1.0	0.06 (0.02–0.18)	1.00 (0.00–1.00)	−11.63
Swallows	31	3.902	1.0	0.23 (0.14–0.39)	1.00 (0.29–1.00)	−41.05
Sylvia	23	4.725	3.0	0.41 (0.24–0.69)	1.00 (0.75–1.00)	−44.97
Tangara	42	3.768	2.0	0.63 (0.43–0.94)	1.00 (0.85–1.00)	−83.63
Tauraco	13	1.974	2.0	0.35 (0.15–0.83)	1.00 (0.63–1.00)	−19.10
Thamnophilus	30	3.064	3.0	1.32 (0.86–2.08)	1.00 (0.91–1.00)	−72.56
Toxostoma	10	4.361	2.0	0.43 (0.20–1.98)	1.00 (0.30–1.00)	−18.05
Tringa	12	7.073	1.0	0.11 (0.05–0.27)	1.00 (0.00–1.00)	−15.43
Trogons	29	7.335	3.0	0.45 (0.29–0.71)	1.00 (0.88–1.00)	−66.42
Turdus and allies	60	4.224	2.0	0.98 (0.73–1.35)	1.00 (0.94–1.00)	−142.19
Woodpeckers	21	2.773	3.0	1.62 (0.97–2.82)	1.00 (0.92–1.00)	−54.39
Wrens	50	5.382	4.5	0.62 (0.50–0.77)	0.79 (0.66–0.93)	−134.03

[a] The maximum value allowed for ε was 0.99999.