

TESTING THE ROLE OF INTERSPECIFIC COMPETITION IN THE EVOLUTIONARY ORIGIN OF ELEVATIONAL ZONATION: AN EXAMPLE WITH *BUARREMON* BRUSH-FINCHES (AVES, EMBERIZIDAE) IN THE NEOTROPICAL MOUNTAINS

Carlos Daniel Cadena^{1,2,3}

¹Department of Biology and International Center for Tropical Ecology, University of Missouri-St. Louis. One University Boulevard, St. Louis, Missouri 63121

²E-mail: ccadena@uniandes.edu.co

³Departamento de Ciencias Biológicas, Universidad de los Andes, Apartado Aéreo 4976, Bogotá, Colombia

Received July 31, 2006

Accepted January 3, 2007

Interspecific competition might drive the evolution of ecological niches and result in pairs of formerly competing species segregating along ecological gradients following a process of character displacement. This mechanism has been proposed to account for replacement of related species along gradients of elevation in many areas of the world, but the fundamental issue of whether competition is responsible for the origin of elevational replacements has not been tested. To test hypotheses about the role of interspecific competition in the origin of complementary elevational ranges, I combined molecular phylogenetics, phylogeography, and population genetic analyses on *Buarremon torquatus* and *B. brunneinucha* (Aves, Emberizidae), whose patterns of elevational distribution suggest character displacement or ecological release. The hypothesis that elevational distributions in these species changed in opposite directions as a result of competition is untenable because: (1) a historical expansion of the range of *B. brunneinucha* into areas occupied by *B. torquatus* was not accompanied by a shift in the elevational range of the former species; (2) when *B. brunneinucha* colonized the range of *B. torquatus*, lineages of the latter distributions had already diverged; and (3) historical trends in effective population size do not suggest populations with elevational ranges abutting those of putative competitors have declined as would be expected if competition caused range contractions. However, owing to uncertainty in coalescent estimates of historical population sizes, the hypothesis that some populations of *B. torquatus* have declined cannot be confidently rejected, which suggests asymmetric character displacement might have occurred. I suggest that the main role of competition in elevational zonation may be to act as a sorting mechanism that allows the coexistence along mountain slopes only of ecologically similar species that differ in elevational distributions prior to attaining sympatry. The contrasting biogeographic histories of *B. brunneinucha* and *B. torquatus* illustrate how present-day ecological interactions can have recent origins, and highlights important challenges for testing the hypothesis of character displacement in the absence of data on population history and robust reconstructions of the evolution of traits and geographic ranges.

KEY WORDS: Andes, character displacement, ecological release, ecological sorting, elevation gradient, historical ecology, niche conservatism.

Species' ranges result from the interplay of processes that act across many scales of time, so understanding the current distributions of species depends on the integration of various core concepts of ecological and evolutionary theory (Kirkpatrick and Barton 1997; Pulliam 2000; Gaston 2003; Holt 2003; Holt and Keitt 2005). Because ecological processes observable in contemporary time may influence species' ranges over evolutionary time scales (Jackson and Overpeck 2000; Holt 2003), and because current ecology is contingent upon the history of the region and organisms involved (Webb et al. 2002; Ackerly 2003; Ricklefs 2004, 2005, 2006), a critical challenge for ecological (MacArthur 1972; Brown et al. 1996) and historical (Crisci et al. 2003) biogeographers alike is integrating processes that affect geographic ranges across a broad continuum of timescales (Donoghue and Moore 2003; Jackson 2004).

Parapatric distributions, in which pairs of taxa have separate but abutting ranges, have provided a focus for many analyses of geographic ranges (Bull 1991). In particular, since Humboldt's (1807) time, researchers have been interested in the replacement of species along elevational gradients. Ecological hypotheses to explain elevational replacements often invoke local determinism, and focus on individual tolerances to environmental conditions, distribution of resources and habitats, and interactions such as predation, parasitism, or competition that change with elevation (Terborgh 1971; Repasky and Schluter 1994; Carothers et al. 2001; Navas 2003; Buckley and Roughgarden 2005). Observations of pairs of species with restricted and complementary distributions where they coexist, but broader elevational ranges where one or the other is absent, are consistent with the hypothesis that interspecific competition underlies elevational replacements (Lack and Southern 1949; Diamond 1970, 1973; Terborgh and Weske 1975; Mayr and Diamond 1976; Remsen and Cardiff 1990; Remsen and Graves 1995; Hall 2005; but see Prodon et al. 2002).

Purely historical hypotheses have also been advanced to explain vertical zonation of species and geographic variation in the positions of species along elevational gradients. For instance, the uplift of mountains or the subsidence of plates in marine environments might stratify species along vertical gradients of elevation or depth, respectively (Heads 1989, 2005). Similarly, vicariance resulting from mountain uplift, or from fragmentation of habitats driven by climate change, could cause the differentiation of lowland and highland clades (Patton and Smith 1992; Schulte et al. 2000). Other "historical" explanations for elevational zonation include parapatric speciation along elevational gradients (Endler 1982; Hall 2005) and the colonization of newly formed high-elevation areas by taxa from other regions tracking their favored environments (Chapman 1917).

Hypotheses that attribute a protracted role in time for ecological processes affecting geographic ranges lie somewhere in between. Diamond (1970, 1973) described several stages in a

hypothetical process leading to pairs of species with exclusive elevational ranges as a result of interspecific competition. He proposed that when allopatric, ecologically similar species with broadly overlapping elevational distributions expand their ranges and come into contact, competition causes them to segregate with respect to elevation, with each species "giving up" the section of its range in which it is an inferior competitor. This partitioning of the elevational range allows the species to coexist at the landscape scale. Diamond argued that this process of elevational displacement need not entail evolutionary modifications of species' fundamental niches (*sensu* Hutchinson 1957); he believed it often involves only compression of such niches through plastic behavioral responses (Diamond and Marshall 1977). However, Diamond (1973) also entertained the possibility that species' fundamental niches can evolve via adaptation to different elevational zones following competitive segregation, which would lead to fixed elevational distributions. This idea is equivalent to the hypothesis of ecological character displacement (Brown and Wilson 1956; reviewed by Schluter 2000; Dayan and Simberloff 2005).

Whether the concept of character displacement can be applied to elevational distributions depends on whether they reflect traits amenable to evolution by natural selection. Although elevational distributions are population rather than organismal attributes, they do represent evolved functional traits that allow individuals to survive and reproduce within the range of environmental conditions encountered over a range of elevation (Porter et al. 2002; Navas 2003; Altshuler and Dudley 2006). Accordingly, the concept of character displacement applied to elevational ranges is sensible and amenable to testing (see Schluter 2000), and recent theoretical work has demonstrated that interspecific competition can lead to character displacement in the positions of species along environmental gradients, resulting in stable parapatric range margins (Case and Taper 2000; Case et al. 2005). Moreover, specific elements of the character displacement scenario proposed by Diamond (1973) have been identified, including shifts in competitive superiority in pairs of species with elevation (Altshuler 2006) and inability of species that segregate elevationally to expand their elevational ranges as a consequence of evolved niche differences (Angert and Schemske 2005). However, the fundamental issue of whether competition is responsible for the origin of elevational replacements remains untested.

Molecular phylogenies can reveal the evolutionary lability or conservation of elevational ranges, and can show whether inferred changes in elevational distributions occurred at times and places when competition could have been involved with their origin (see Losos 1990). In addition, DNA sequence data can be employed using recently developed methods to estimate population divergence times and to infer the occurrence of historical events, including range expansions and changes in population size (reviewed by Knowles 2004). When these methods are applied to

study the history of species that exist in the same geographical setting and interact ecologically, valuable information can be gained on how these interactions arose through space and time, and on the influence that species may have had on each other (Arbogast and Kenagy 2001; Flanagan et al. 2004). In this study, I develop predictions based on possible effects of interspecific competition resulting in elevationally exclusive ranges, describe how these can be tested using phylogenetic and population genetic methods, and apply this framework to study the origin of elevational replacements in a group of Neotropical birds whose ranges are thought to be strongly influenced by competition. My analyses illustrate how the factors underlying geographic ranges can be better understood if ecological processes that are thought to operate at present are viewed retrospectively in the context of population histories, an approach that has seldom been taken to explain features of species' distributions (e.g., Bernardi 2005).

Study System

In general, Neotropical montane bird species occupy relatively consistent elevation ranges throughout their distributions (Graves 1988), with some remarkable exceptions, such as the brush-finches in the genus *Buarremon* (Emberizidae). Consistent with Diamond's (1973) hypothesis, the stripe-headed (*Buarremon torquatus*) and chestnut-capped (*B. brunneinucha*) brush-finches replace each other along elevational gradients in areas where both exist, but *B. torquatus* occupies most of the montane gradient in areas of allopatry in South America. This suggests that interspecific competition is an important determinant of distributions (Renssen and Graves 1995). Competition-mediated elevational replacements have been argued to be pervasive in Andean birds (Terborgh and Weske 1975; but see Renssen and Graves 1995), yet the case of *Buarremon* is anomalous because the relative elevational positions of the putative competitors vary geographically (Renssen and Graves 1995). In regions where both taxa exist in Peru, Ecuador, and most of Colombia, *B. brunneinucha* occupies the lower part of the gradient, whereas *B. torquatus* exists at high elevations. In some regions of northern South America and Central America the pattern is reversed, and *B. torquatus* is found at lower elevations; in other areas, midmontane populations of *B. brunneinucha* are puzzlingly sandwiched between high- and low-elevation populations of *B. torquatus*.

How did the unusual patterns of elevational distribution of *Buarremon* brush-finches arise? In their test of their competition hypothesis, Renssen and Graves (1995) did not present information on elevational distributions from Central America and Mexico, where *B. brunneinucha* exists mostly in the absence of *B. torquatus*. Therefore, documenting the elevational ranges of *B. brunneinucha* in areas with and without *B. torquatus* remains a crucial missing step toward testing the hypothesis that the ele-

vational ranges of the two species may have evolved in opposite directions as a consequence of competition (Diamond 1973). In addition, previous analyses did not consider distribution patterns in the context of the biogeographic history of species and the ages of different lineages. Therefore, the origin of the differences in elevational distributions of populations of *B. torquatus* and *B. brunneinucha* that replace each other along montane gradients may have predated the coexistence of these species.

Predictions

The hypothesis that interspecific competition caused the elevational ranges of *B. torquatus* and *B. brunneinucha* to change in opposite directions (cf. Diamond 1973) predicts that (1) elevational distributions of both species differ between areas of allopatry and areas of sympatry, and (2) that historical changes in elevational ranges occurred within geographical areas and periods of time during which these species could have interacted. Likewise, if the varying elevational distributions of different populations of *B. torquatus*, specifically the existence of members of the group only at the two extremes of the elevational gradient in the Northern Andes, were caused by competition with *B. brunneinucha*, (1) splits among these populations must have occurred at times and places when interacting with this species was possible, and (2) populations replacing *B. brunneinucha* at low and high elevations along the same mountain slope should be sister to each other. Alternatively, even if competition was not involved with the divergence of these populations, competition might have been responsible for the origin of distributions if it caused their elevational ranges to contract after they diverged. Accordingly, populations of *B. torquatus* with limited elevational distributions should show evidence of historical population declines, assuming that all the individuals existing over a broad elevational range cannot be accommodated in a narrow range. Specific tests of these predictions are described in detail below. Although none of the above predictions is sufficient to demonstrate an evolutionary effect of interspecific competition on elevational ranges (see Schluter and McPhail 1992 and Schluter 2000 for reviews of the criteria that need to be met to demonstrate character displacement), they can be considered necessary conditions for the hypothesis of ecological character displacement to be plausible. If these predictions are rejected, then it would not be necessary to perform more detailed tests of character displacement to rule out this hypothesis.

Methods

DATA ON ELEVATIONAL DISTRIBUTIONS

I characterized the elevational distributions of *B. brunneinucha* and *B. torquatus* throughout their geographic ranges based on about 350 georeferenced locality records for each species. Elevations were obtained from the primary data (specimen labels,

field notes) whenever possible, or by overlaying the geographic coordinates of localities onto a 1 km × 1 km digital elevation model (Shuttle Radar Topography Mission; <http://www.jpl.nasa.gov/srtm>) using a geographic information system (GIS; ArcGIS 9.1, ESRI, Inc., Redlands, CA). Details on this procedure, data sources, and protocols followed to verify the accuracy of georeferenced data are presented elsewhere (Cadena 2006).

PHYLOGENETIC AND POPULATION GENETIC DATA

Cadena et al. (in press) reconstructed phylogenetic relationships among species of *Buarremon* and among *Buarremon* and related genera based on sequences from several mitochondrial and nuclear genes. In addition, based on thorough sampling of variation in mitochondrial DNA, they presented a general picture of the biogeographic history of *B. torquatus* and *B. brunneinucha*. Here, I use the inferences about phylogenetic relationships and population history as a framework to guide the development and testing of predictions related to the role of interspecific competition in the origin of elevational distributions in *Buarremon*. I also capitalize on the available sequence data to conduct new analyses on the timing of lineage differentiation and on the demographic history of populations.

THE EFFECT OF *B. TORQUATUS* ON THE ELEVATIONAL RANGE OF *B. BRUNNEINUCHA*

The hypothesis of character displacement predicts that coexistence along mountain slopes with elevational replacement follows secondary sympatry, and that elevational distributions of derived lineages occurring in sympatry with competitors should be shifted in comparison to those of early branching lineages that exist in allopatry. I was able to test this prediction for *B. brunneinucha* because populations from the southern sector of its range, where it coexists with *B. torquatus*, are of recent origin with respect to those of the northern sector, from where *B. torquatus* is absent (Cadena et al. in press). Testing for character displacement requires that environments are similar enough in sympatry and allopatry that differences in species' ecology cannot be accounted for by tracking of varying environmental factors (Grant 1972, 1975; Schluter and McPhail 1992). Therefore, I compared the slopes and intercepts of the relationship between elevation and mean annual temperature measured in areas of allopatry and sympatry. In contrast to elevation, which only limits distributions indirectly through its correlation with other factors, temperature affects organisms directly. This comparison allowed me to assess whether the documented differences in the elevation–temperature relationship between lower and higher latitudes (Janzen 1967) are observable within the study region. If they were, then elevational ranges in different areas would not be readily comparable because, on average, *B. brunneinucha* exists at higher latitudes in allopatry than in sympatry. To set up this analysis, I used GIS to randomly

place 1500 points in the area of allopatry and 1500 in sympatry, with the constraint that they should fall within the elevation range encompassed by all *B. brunneinucha* localities. At each point, I recorded elevation based on the digital elevation model and temperature from an interpolated surface with a 1 km × 1 km resolution (Hijmans et al. 2005).

Because randomly placed points sample different elevations in proportion to their area, I used these data to account for differences in the abundance of sites at different elevations when testing for differences in the mean of the elevational range of *B. brunneinucha* in sympatry and allopatry. That is, the variation in the elevational distribution of the random points in allopatry and sympatry can be taken as a null expectation against which actual differences in elevational distributions can be compared. Deriving such a null expectation was necessary because varying elevational distributions in sympatry and allopatry need not reflect an effect of the putative competitor; differences may arise simply as a result of differences in proportional area at different elevations between regions. I conducted a two-way analysis of variance (ANOVA) with geographic context (i.e., allopatry or sympatry) and elevation data source (i.e., locality records or randomly placed points) as main factors, and elevation as response variable. A significant interaction term would indicate the difference in mean elevational distributions of *B. brunneinucha* between regions deviated from the difference that would be expected as a consequence of varying abundance of sites at different elevations. I also examined elevational distributions in areas where populations of *B. brunneinucha* were either sandwiched, replaced at high elevations, or replaced at low elevations by *B. torquatus*. If displacement in elevational ranges occurred, then populations replaced at low elevations should be shifted toward higher altitudes in comparison to those being replaced at high elevations.

THE EFFECT OF *B. BRUNNEINUCHA* ON THE ELEVATIONAL RANGE OF *B. TORQUATUS*

Timing of differentiation

The hypothesis that competition with *B. brunneinucha* is responsible for the disparate elevational distributions of populations of *B. torquatus* predicts these populations diverged at times when *B. brunneinucha* and *B. torquatus* could have been in sympatry. To test this prediction, I used a relaxed molecular clock approach to compare the ages of South American lineages of *B. torquatus* with the estimated time at which *B. brunneinucha* colonized South America. Based on results of phylogenetic analyses that included multiple individuals of the three species of *Buarremon* and related genera (Cadena et al. in press), I selected a few representatives of major groups and inferred their relationships using sequences of the mitochondrial ND2 gene. Phylogenies inferred from ND2 sequences do not conflict significantly with those inferred with more data from other mitochondrial and nuclear genes, and restricting

analyses to ND2 allowed me to sample lineages for which sequences of other genes are not available.

To root the phylogeny of the clade formed by *Buarremon*, *Arremon*, and *Lysurus*, I used sequences of *Atlapetes* and *Pipilo* as outgroups. I conducted maximum-likelihood phylogenetic analyses in PAUP* (Swofford 2002), as described in Cadena et al. (in press). A likelihood ratio test comparing the scores of the maximum-likelihood tree and of a tree with a molecular clock enforced rejected the null hypothesis of clocklike sequence evolution. Therefore, I used the penalized likelihood method (Sanderson 2002) implemented in r8s version 1.70 (Sanderson 2003) to convert branch lengths to comparable estimates of divergence times. I determined the optimal level of rate smoothing using the cross-validation procedure available in r8s. Because reliable calibrations are not available for *Buarremon* and its near relatives, I did not attempt to infer the absolute timing of historical events, but rely on relative timing. For this purpose, I fixed the node representing the most recent common ancestor of the *Buarremon*–*Arremon*–*Lysurus* clade to have an age of 1.0 and scaled branch lengths relative to this value. Based on the resulting chronogram, I estimated the relative ages of nodes indicating the colonization of South America by *B. brunneinucha* or the divergence of populations of *B. torquatus* with contrasting elevational ranges. To assess the uncertainty of estimates of node ages resulting from data sampling error, I estimated these ages for 100 bootstrap pseudoreplicate datasets (Sanderson and Doyle 2001). To evaluate the influence of error introduced by uncertainty in phylogeny reconstruction, I repeated the analysis for trees in which branches receiving less than 70% bootstrap support were resolved in alternative ways. Because all the poorly supported branches are short, alternative topologies did not influence the conclusions of this analysis. Therefore, I only report results based on the maximum-likelihood phylogeny.

Inferences about the divergence time between populations of a species can be confounded by ancestral polymorphism (Edwards and Beerli 2000). However, I did not employ methods to distinguish between the time of gene divergence and the time of population divergence (e.g., Nielsen and Wakeley 2001) because the data did not meet the assumption of no population structure within the diverging groups. This assumption was particularly unsuited for *B. torquatus*, which comprises several distinct, reciprocally monophyletic, and geographically isolated groups (Cadena et al. in press).

Historical demography

Methods that reconstruct ancestral character states for nodes on phylogenies are not well suited for the study of historical changes in elevational distributions. Consider the hypothetical situation that all extant members of a clade have narrow elevational ranges: ancestral state reconstructions will typically indicate the range of their ancestor was similarly narrow (e.g., Hardy and Linder

2005). This scenario overlooks the possibility that the elevational distributions of all members of the clade may have been compressed in concert since they last shared a common ancestor as a result of competitive displacement. Although one could accommodate this possibility by employing a model of trait evolution that allows high rates of change along branches in the phylogeny, ancestral states estimated under such a model would be imprecise. Therefore, I did not attempt to infer the evolutionary pathways by which current elevational distributions arose. Instead, I use historical patterns of change in population size to determine the plausibility of elevational range contractions because the restriction of a widespread population to a narrow elevational range cannot occur unless there is a reduction in its size, especially if it occurs at or near its carrying capacity. Population genetic theory provides a framework that allows assessing historical demographic trends: alleles sampled from historically stable, shrinking, and expanding populations exhibit different distributions of coalescence times because lineages coalesce back to their common ancestor more rapidly when populations are small and more slowly when they are large (Kingman 1982). Thus, if a population has declined as a consequence of a contraction in its elevational range, this should be detectable in gene genealogies inferred from series of randomly sampled haplotypes (reviewed by Emerson et al. 2001; Knowles 2004). I applied this framework to test the hypothesis that competition with *B. brunneinucha* caused the elevational ranges of populations of *B. torquatus* to contract.

I used two different coalescent approaches to examine historical trends in population size using ND2 sequence data for *assimilis* and *atricapillus*, two members of the *B. torquatus* complex that could have experienced elevational range contractions as a result of competition with *B. brunneinucha*, and that presently sandwich that species in areas of the Colombian Andes. First, I estimated historical population growth rates using LAMARC version 1.2.2 (Kuhner et al. 2004). LAMARC samples genealogies using a Markov chain Monte Carlo (MCMC) method, and assuming a model of exponential change in population size and no selection, migration, or recombination, it calculates maximum-likelihood estimates of θ , a measure of genetic diversity that reflects female effective population size and mutation rate per site ($\theta = 2N_e\mu$ for mtDNA), and its exponential growth parameter g ($\theta_t = \theta_{\text{now}} \exp[-gt]$, where t is some time in the past). Positive values of g indicate population growth, whereas negative values indicate population decline. I analyzed data for *assimilis* and *atricapillus* independently using 10 short-chain runs of 1000 steps, followed by two long-chain runs of 100,000 steps; chains were sampled every 20 steps, with the first 1000 discarded as burn-in. I also assessed trends in effective population size using the Bayesian skyline plot method (Drummond et al. 2005), a nonparametric approach implemented in BEAST version 1.2 (Drummond and Rambaut 2003) that estimates a posterior distribution of effective population size

through time on the basis of a set of plausible genealogies sampled using MCMC. I used the TrN+I and TrN models of nucleotide substitution (selected based on the AIC using ModelTest 3.7; Posada and Crandall 1998) to analyze data for *assimilis* and *atricapillus*, respectively. Chains were run for 50,000,000 iterations with genealogies and model parameters sampled every 1000 iterations; the first 1% of iterations was discarded as burn-in. I imported the output of each run into Tracer version 1.2 (Rambaut and Drummond 2003) and examined results to verify that parameter estimates were based on acceptable effective sample sizes and that trace plots indicated appropriate mixing. Finally, I generated skyline plots showing the median estimates of population size and their associated credibility intervals (95% highest posterior density) from present time back to the most recent common ancestor of the samples.

These approaches to assessing historical demography assume that sequences are sampled from a single panmictic population. Estimates of migration between Colombian and Ecuadorian–Peruvian highland populations of *B. torquatus* indicate that, on average, one female individual is exchanged between the two regions approximately every five generations (C. D. Cadena, unpubl. data). Although simulations suggest migration would need to be much lower to bias the estimation of g (P. Beerli, pers. comm.), the credible interval for this estimate of gene flow is wide, and cannot distinguish complete isolation from relatively frequent interchange of migrants. Thus, I tested for the sensitivity of the models to population structure by conducting independent analyses with: (1) only sequences of *assimilis* from Colombia; (2) sequences of *assimilis* and *nigrifrons* from Ecuador and Peru; and (3) all sequences of *assimilis* and *nigrifrons* from Colombia, Ecuador, and Peru. Because geographic structure is limited within Colombia and in Ecuador–Peru (Cadena et al. in press), consistent results across analyses would suggest that the models were robust to the possible violation of the assumption of panmixia (Shapiro et al. 2004). Sequences of *nigrifrons* were included in the analyses because this taxon and *assimilis* are not reciprocally monophyletic. Although *nigrifrons* only replaces *B. brunneinucha* at high elevations in part of its range (see below), not considering it would have resulted in gene genealogies with longer coalescent times near the base, which would have biased analyses toward inferring population declines. The sample size for *atricapillus* was too limited to allow for sensitivity analyses, so I considered all available sequences as a single group, except for the fact that I conducted analyses with and without sequences of *tacarcunae*, a closely related taxon. Although the sample size precluded examining the possible effect of violating the assumption of no population subdivision in *atricapillus*, it was probably sufficient to capture the general structure of gene genealogies, and thereby reach the accuracy that can be achieved estimating population genetic parameters from single-locus data (Felsenstein 2006).

Forces other than interspecific competition with *B. brunneinucha* might have influenced population sizes throughout the history of *B. torquatus*, especially because the areas it inhabits have experienced mountain uplifting and displacement of ecological zones as a consequence of climate change (Gregory-Wodzicki 2000; Hooghiemstra and Van der Hammen 2004). Therefore, even if competition caused ranges to contract, these contractions might be difficult to detect from the background of all other events that influenced population sizes over time. This caveat applies particularly to the estimation of g because LAMARC assumes constant exponential growth or decline and, thus, reveals only an overall trend in population size. It is less likely that fluctuations unrelated to competition would obscure a strong pattern of competition-driven decline in skyline plots, which can recover distinct episodes of growth and decline throughout a population's history (Drummond et al. 2005). Nonetheless, I sought to address the possible confounding effect of demographic changes unrelated to competition on the outcome of coalescent analyses by assessing trends in population size in a “control” taxon. An ideal control would be a population of similar age and distribution to the one that may have been displaced by competition; this control population would be expected to have been affected by the same historical processes resulting in population growth and decline, except competition. As a control, I used the lineage formed by *Myioborus ornatus* and *M. melanocephalus* (Parulidae) that extends from the Venezuela–Colombia border through Colombia into northern Peru (Pérez-Emán 2005). The *M. ornatus*–*M. melanocephalus* complex exists in similar environments to *assimilis* and *nigrifrons*, the distribution and elevational ranges of the two groups are remarkably consistent, and sequence data for the same genes indicate similar age and comparable effective population sizes (Cadena et al. in press; Pérez-Emán 2005; J. L. Pérez-Emán and C. D. Cadena, unpubl. data).

Results

HISTORY OF POPULATIONS AND ELEVATIONAL RANGES IN *B. BRUNNEINUCHA*

Although the relationship between elevation and climate varies with latitude, differences are minor within the range of *Buarremon*: the slopes and intercepts of regressions between elevation and temperature do not differ between regions of sympatry and allopatry (data not shown). This suggests that the elevational distributions of *B. brunneinucha* in these regions can be compared to one another.

Elevational distributions of *B. brunneinucha* in sympatry and allopatry differ significantly (Kolmogorov–Smirnov two-sample test, $p = 0.0034$, Fig. 1A), and the mean elevation of records of this species is significantly higher in sympatry than in allopatry (ANOVA, $P < 0.0001$, Fig. 1B). However, the magnitude of

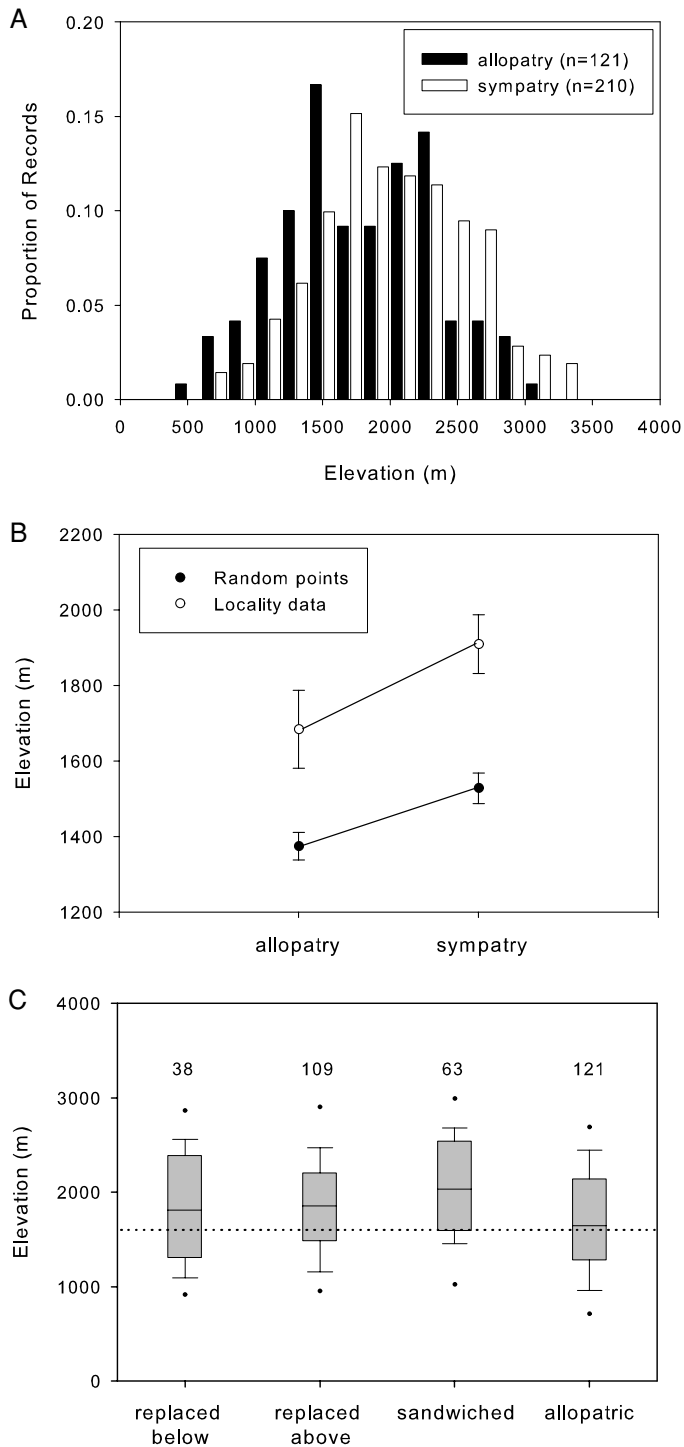


Figure 1. (A). Frequency distribution of elevations obtained from locality records of *Buarremon brunneinucha* from areas where it exists in allopatry from *B. torquatus* (black bars) and areas where it exists with it in sympatry at the landscape scale (white bars) showing a shift in the distribution toward higher elevations in sympatry. (B) Mean elevation (± 2 standard errors) of locality records (open dots) of *B. brunneinucha* and randomly placed points (black dots) in areas of allopatry and sympatry with *B. torquatus*. The magnitude of the differences between allopatry and sympatry is not significantly different for locality data and random data, as

differences in mean elevation of records between areas does not exceed that of differences that would be expected by chance as a result of the varying abundance of sites at different elevations in each area, as indicated by the lack of a significant interaction term in the ANOVA that involved a comparison of the mean elevation of randomly placed points in allopatry and sympatry ($P = 0.42$, Fig. 1B). In addition, distributions in sympatry are shifted toward higher elevations in comparison to allopatry independently of whether *B. brunneinucha* is replaced at low elevations, replaced at high elevations, or sandwiched by *B. torquatus* (Fig. 1C). This is inconsistent with the prediction from competitive displacement that distributions would be shifted toward those elevations not occupied by the putative competitors. Finally, the elevational range of *B. brunneinucha* has similar standard deviations in areas of allopatry ($s = 569 \pm 36$ m SE), and areas where replaced at low elevations ($s = 599 \pm 68.7$ m), replaced at high elevations ($s = 555 \pm 38$ m), and sandwiched ($s = 544 \pm 48$ m) by *B. torquatus*, indicating that ranges are not more compressed in sympatry.

HISTORY OF POPULATIONS AND ELEVATIONAL RANGES IN *B. TORQUATUS*

The populations of *B. torquatus* that replace *B. brunneinucha* at high elevations form a well-supported monophyletic group that in turn comprises two distinct lineages, one including forms from Colombia, Ecuador, and northern Peru (*assimilis* and *nigrifrons*), the other a form ranging from central to southern Peru (*poliophrys*) (Fig. 2). Low-elevation taxa do not form a single monophyletic group, but *atricapillus* and *tacarcunae*, which replace *B. brunneinucha* at low elevations, appear to constitute a clade with the low-elevation and allopatric *phygas*, although support is weak. The other low-elevation taxa are sister to all other members of the complex (*costaricensis*), to the high-elevation clade (*laren-sis*), or to the elevationally widespread *basilicus* (*perijanus*), but the latter relationship is not strongly supported. Finally, the three taxa that exist in allopatry from *B. brunneinucha* in Bolivia and Argentina (nominate *torquatus*, *fimbriatus*, and *borelli*) formed a well-supported group (*fimbriatus* is not shown in the figure; this taxon and *borelli* are not reciprocally monophyletic with respect to each other; Cadena et al. in press).

indicated by the slopes of the lines connecting mean values. (C) Elevational distributions of *B. brunneinucha* in areas where it coexists with *B. torquatus* and areas of allopatry. Box plots show the 5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles. The horizontal dotted line indicates the mean of the elevational range in allopatry, which shows that ranges are displaced toward higher elevations in sympatry, regardless of the relative position along mountain slopes of putative competitors. Sample sizes are shown above each box plot.



Figure 2. Maximum-likelihood tree showing relationships of major lineages of *Buarremon brunneinucha*, *B. torquatus*, and related taxa inferred based on mitochondrial DNA sequences. Branches have been scaled to reflect time using penalized likelihood, setting the age of the deepest node to 1 (see scale). The ages of numbered nodes are discussed in the text and the confidence intervals of some are shown in Figure 3. Box plots to the right of taxon names in *B. torquatus* indicate the elevational distribution of each lineage, and whether they replace *B. brunneinucha* at low elevations (gray) or high elevations (black), or if they exist in allopatry (white). Taxon *nigrifrons* is shown in black because where it coexists with *B. brunneinucha* it replaces it at high elevation, but through much of this range this taxon exists in allopatry (see text). The number of locality points on which elevational distributions are based and the geographic distribution of each lineage are shown to the right of box plots. The 5th and 95th percentiles (black dots) are shown only when more than 20 records are available. Data on elevational distributions of the closely allied *atricapillus* and *tacarcunae* are shown in a single plot. Note that the diversification of most South American lineages of *B. torquatus* with disparate elevational ranges predates the divergence between Central and South American populations of *B. brunneinucha* (an indication of its colonization time).

Analyses of timing of diversification suggest the colonization of South America by *B. brunneinucha* occurred substantially more recently than the origin of most South American lineages of *B. torquatus* that presently have disparate elevational distributions (Fig. 2). This result is robust to error introduced by substitutional noise in the mtDNA data, as indicated by the nonoverlapping bootstrap estimates of ages of relevant nodes (Fig. 3). Specifically, estimates of the crown ages of groups of *B. torquatus* that replace *B. brunneinucha* at high- or low-elevation areas (nodes 4 and 6 in Fig. 2) have confidence intervals that do not overlap with the confidence interval around the crown age

of South American *B. brunneinucha* (node 1; Fig. 3A). Differences are more striking when the ages of stem groups (nodes 2 and 3) are compared (Fig. 3B). Likewise, the divergence between the low-elevation taxon *perijanus* and the wide-ranging *basilicus* (node 7) clearly predates the colonization of South America by *B. brunneinucha* (Fig. 3C). In sum, interspecific competition with *B. brunneinucha* in South America is not a parsimonious explanation of the differentiation of *B. torquatus* into distinct lineages that currently replace *B. brunneinucha* at particular elevational zones: these lineages last shared common ancestors well before the onset of sympatry with *B. brunneinucha* in South America. However, it

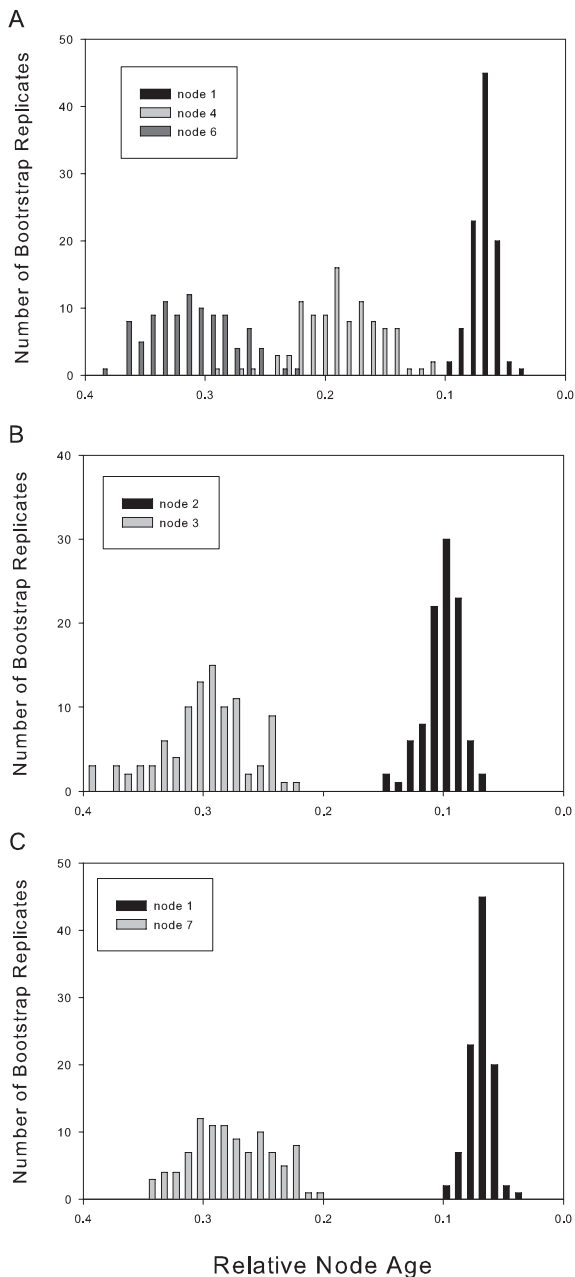


Figure 3. Frequency distributions of the ages of nodes (numbers as in Fig. 2) estimated using penalized likelihood based on 100 bootstrap replicate data sets. Ages of nodes relevant to the colonization of South America by *Buarremon brunneinucha* are shown in black bars and those indicating the divergence of *B. torquatus* lineages in gray. Note that none of the distributions is overlapping. However, confidence intervals are not shown for node 5 in Figure 2 (i.e., divergence between *assimilis* and *nigrifrons*), the age of which is very consistent with the timing of colonization of South America by *B. brunneinucha* (see text).

is important to note that the taxon *nigrifrons* only replaces *B. brunneinucha* at high elevations in the northern extreme of its range; through much of southern Ecuador and northern Peru, it exists in allopatry and extends to low elevation areas. The divergence of

assimilis and *nigrifrons* is recent (they are not reciprocally monophyletic, Cadena et al. in press) and penalized likelihood cannot reject the hypothesis that they diverged after the colonization of South America by *B. brunneinucha* (Fig. 2). This raises the possibility that the elevational range of *assimilis* and *poliophrys*, but not of *nigrifrons*, may have been compressed as a consequence of competition (see below).

HISTORICAL DEMOGRAPHY

Maximum-likelihood estimates of the exponential growth parameter (g) were greater than zero for all populations (Table 1), suggesting histories of demographic growth. However, LAMARC tends to produce upwardly biased estimates of g (Kuhner et al. 1998; Felsenstein et al. 1999). The fact that the 95% confidence intervals of g did not include zero or negative values in some analyses (Table 1) argues more strongly against population decline. The confidence intervals around g estimated for *atricapillus-tacarcunae* are too large to reach definitive conclusions, other than that there is no compelling evidence that these populations have declined. Likewise, Bayesian credibility intervals in skyline plots were wide, particularly for *atricapillus-tacarcunae* (Fig. 4), yet the median estimates of population size in these analyses showed trends that indicate either growth or stable population sizes. For comparison, patterns in the control (*Myioborus ornatus*–*M. melanocephalus*) appear indistinguishable from those of the populations of *B. torquatus* that might have been affected by competition with *B. brunneinucha* (Table 1). Results of analyses did not vary qualitatively with different sampling schemes, indicating that inferences are unlikely to be affected by possible violations of the assumption of panmixia.

Discussion

Biogeographers have long been interested in determining what factors underlie the replacement of species along elevational gradients, a question that is arguably central to explaining patterns such as the turnover of species composition and the changes in species diversity with elevation (reviewed by Rahbek 2005). This issue is especially relevant in the tropical Andes, where elevational turnover is a major component of high regional species richness (e.g., Kattan et al. 2006). In this study I set out to evaluate the hypothesis that abutting elevational distributions result from interspecific competition by testing predictions involving historical scenarios with phylogenetic and population genetic analyses in a group of Neotropical birds. Some conclusions may need to be tempered because they depend on the assumption that the history of mitochondrial lineages reflects the history of populations, but my results can firmly reject some potential historical roles for interspecific competition in elevational zonation in *Buarremon*. Although the results of this study might not be generalizable across

Table 1. Estimates of the exponential growth parameter (g) and population size (θ) for different sets of populations belonging to the *Buarremon torquatus* complex and the control population obtained using LAMARC. Values are the maximum-likelihood estimates and 95% confidence intervals (in parentheses). All estimates of g are greater than zero and confidence intervals do not include zero or negative values in some analyses, indicating that population growth or stasis cannot be rejected in favor of population declines, as predicted by the hypothesis that competition caused the ranges of populations to contract.

Taxa and region	n	g	θ
<i>assimilis</i> Colombia	11	348.5 (−34.4–879.5)	0.035 (0.011–0.160)
<i>assimilis</i> and <i>nigrifrons</i> Ecuador and Peru	19	437.5 (60.9–984.8)	0.041 (0.016–0.130)
<i>assimilis</i> and <i>nigrifrons</i> Colombia, Ecuador, and Peru	30	411.7 (167.3–757.5)	0.077 (0.038–0.174)
<i>atricapillus</i> Colombia	8	96.5 (−292.5–507.4)	0.014 (0.004–0.065)
<i>atricapillus</i> and <i>tacarcunae</i> Colombia and Panama	10	157.1 (−124.6–467.1)	0.027 (0.009–0.102)
Control			
<i>Myioborus ornatus</i> – <i>M. melanocephalus</i>	16	483.5 (−109.4–1530.0)	0.017 (0.006–0.067)

other taxa and regions, of all Neotropical birds, *Buarremon* is the group in which elevational distributions seemed most consistent with the hypothesis that competition may have been involved with their origin (Renssen and Graves 1995).

HISTORICAL EFFECT OF INTERSPECIFIC COMPETITION ON THE ELEVATIONAL RANGE OF *B. BRUNNEINUCHA*

Mitochondrial DNA variation in *B. brunneinucha* suggests that this species colonized the southern portion of its present distribution from northern Central America (Cadena et al. in press). Because members of the *B. torquatus* complex do not exist north of central Costa Rica (and presumably did not extend much further north historically), the biogeographic history of *B. brunneinucha* is well suited to test the hypothesis that its elevational range was modified by interspecific competition once it expanded into the range of *B. torquatus* (Diamond 1973). Although the mean of the elevational distribution of *B. brunneinucha* differs between the region of sympatry and the region of allopatry, the area available at different elevations also differs between regions in parallel, obviating the need to invoke competition. Moreover, a shift toward higher elevations in areas of sympatry is observed regardless of whether *B. brunneinucha* is replaced at high elevations, replaced at low elevations, or sandwiched by its putative competitor, and this shift is not accompanied by a compression in the elevational range. Thus, the hypothesis that the elevational distribution of *B. brunneinucha* has been influenced by competition with *B. torquatus* can be rejected. The more restrictive scenario of ecological character displacement, which requires niche evolution beyond the alternative of ecological plasticity (Schluter 2000; but see Pfennig et al. 2006), must also be rejected.

Although character displacement is typically tested only on the basis of mean differences in traits, the mean and the variation around it are not the only descriptors of elevational ranges that merit consideration. The distributions of *B. brunneinucha* in allopatry and sympatry are not only significantly different in their

means, but also according to a Kolmogorov–Smirnov test, which is sensitive to differences in location, dispersion, and skewness. Also, elevational distributions in allopatry and sympatry differ in terms of their relationship to the relative abundance of sites at different elevations in their respective areas (data not shown). However, it is unlikely that this may reflect an effect of *B. torquatus* because the relationships between proportional use and abundance of sites at different elevations are similar in areas where *B. brunneinucha* is replaced by *B. torquatus* at low elevations, and those where it is replaced at high elevations. Although at a coarse level the relationship between elevation and some environmental variables that may limit species' distributions directly (e.g., temperature) is similar in sympatry and allopatry, it is possible that a finer examination of environmental variation between regions could explain these regional differences in elevational distributions in more detail. I present such an examination based on multivariate analyses and modeling of species ecological niches based on a broad suite of environmental variables elsewhere (Cadena 2006).

EFFECT OF INTERSPECIFIC COMPETITION ON THE DIVERSIFICATION OF LINEAGES IN *B. TORQUATUS*

Distinct lineages of *B. torquatus* currently associated with different elevational zones in South America last shared common ancestors before the colonization of the continent by *B. brunneinucha*. Thus, although compression of elevational ranges might have occurred more recently in response to competition with *B. brunneinucha*, the origin of these lineages predated sympatry. Furthermore, the populations of *B. torquatus* that sandwich *B. brunneinucha* in the Colombian Andes (*assimilis* and *atricapillus*) are not each other's closest relatives, which implies there is no support for a scenario in which competition displaced members of a single lineage to the extremes of the elevational gradient, a pattern that has been described in systems involving competition along other kinds of gradients and by theoretical models of character

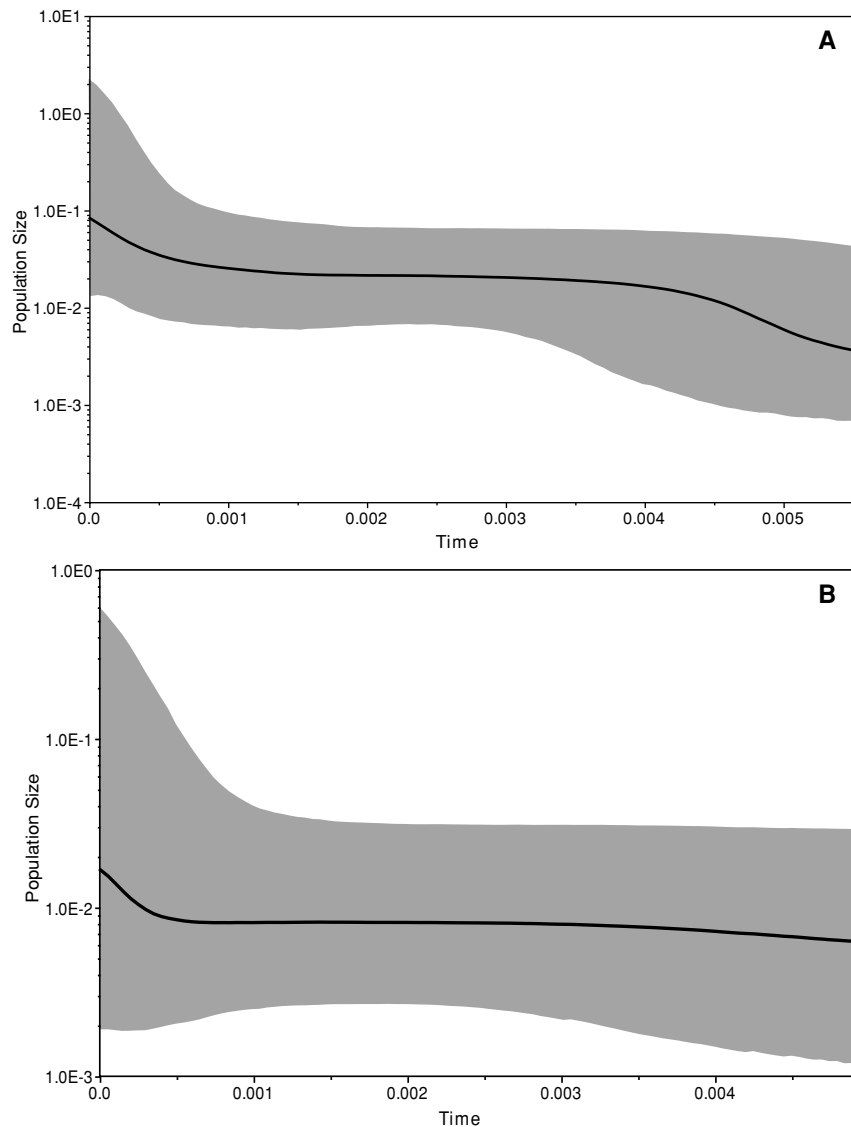


Figure 4. Two examples of Bayesian skyline plots showing population size as a function of time for members of the *Buarremon torquatus* complex inferred using the program BEAST: (A) *assimilis* + *nigrifrons* (Colombia, Ecuador, and Peru); (B) *atricapillus* (Colombia). The solid lines indicate the median estimates of population size and the shaded areas its Bayesian credibility intervals (i.e., 95% highest posterior densities). Time zero is the present, with increasing values representing time into the past. Both axes are scaled by the mutation rate. Although credible intervals are large, these plots do not suggest the population declines that would be expected if competition with *B. brunneinucha* had caused the elevational ranges of these populations to contract.

displacement (Austin et al. 1990; Austin 1999; Doebeli and Dieckmann 2000).

HISTORICAL EFFECT OF INTERSPECIFIC COMPETITION ON THE ELEVATIONAL RANGE OF *B. TORQUATUS*

The plausibility of the hypothesis that competition with *B. brunneinucha* led to contractions in the elevational distributions of lineages of *B. torquatus* (cf. Diamond 1973) remains somewhat uncertain. If ecological niches are conserved, that lineages of *B. torquatus* replacing *B. brunneinucha* at high or low elevations originated prior to sympatry would imply lack of support for

this hypothesis. To some extent, the assumption of elevational niche conservatism is tenable because clades are often associated with particular elevational zones (Patton and Smith 1992; Arcander and Fjelds  1994; Garc a-Moreno et al. 1999; Renner and Won 2001; Moyle et al. 2005; P rez-Em n 2005). More generally, theory argues for niche conservatism (Holt and Gaines 1992; Holt 2003), and empirical studies support this idea (Ricklefs and Latham 1992; Peterson et al. 1999; Hugall et al. 2002; Ackerly 2003; Mart nez-Meyer et al. 2004; Qian and Ricklefs 2004). Also, one could argue that if all members of a clade have similar elevational distributions, it is most parsimonious to assume they

inherited those distributions unchanged from their ancestor. This line of reasoning would imply rejecting the hypothesis that competition with *B. brunneinucha* caused changes in the elevational distributions of *B. torquatus*.

The arguments in favor of niche conservatism and the principle of parsimony notwithstanding, elevational distributions evidently differ between lineages of *B. torquatus*, implying they do change over time. I addressed the possibility of changes in elevational ranges using coalescent models to examine historical trends in population size for *B. torquatus* taxa that replace *B. brunneinucha* along elevational gradients. The analyses did not indicate these populations have experienced declines as would have been expected if competition-driven range displacement occurred, and demographic trends are similar to those observed in a codistributed lineage that presumably was not affected by competition. Thus, the null hypothesis that populations have been stable or even growing cannot be rejected in favor of the hypothesis that they have declined. However, support for scenarios of constant size or growth is not compelling; both coalescent methods rendered reconstructions of demographic history with substantial uncertainty. Part of this uncertainty likely reflects the limitations inherent to employing information from a single locus to infer population history. Because results appear more suggestive of growing or stable than of declining populations, incorporating sequence data from additional loci in the analyses may increase the accuracy and precision of estimates of population size (Felsenstein 2006), and thus may allow rejecting the prediction of population declines with some confidence.

WHAT IS THE HISTORICAL ROLE OF COMPETITION IN ELEVATIONAL REPLACEMENTS?

Although I have shown that it is unlikely that elevational distributions in *Buarremon* arose through a process of reciprocal range contractions as envisioned by Diamond (1973), interspecific competition might still have been of historical importance in this system and in others involving parapatric elevational distributions in alternative ways, some of which are not mutually exclusive. First, my analyses suggest that interspecific competition with *B. torquatus* does not seem to have modified the elevational distribution of *B. brunneinucha*, but it is not entirely clear that the reverse did not occur owing to the wide confidence intervals in coalescent inferences of historical demography. If the latter were to be confirmed, it could imply the occurrence of asymmetric character displacement. Asymmetric displacement is expected when species exhibit varying competitive abilities, with inferior competitors being the ones that become displaced and experience reduced fitness as a consequence of trade-offs resulting from selection to reduce competition (Pfennig and Pfennig 2005). Hence, one could speculate that *B. brunneinucha* may be competitively superior to *B. torquatus*, a hypothesis that can be tested using distributional data and

information on spatial variation in species' abundances (Anderson et al. 2002), or by measuring the effects of release from competition in the field (Martin and Martin 2001). This novel hypothesis regarding the contemporary ecology of these species can only be formulated based on the historical information offered by their phylogeographies, which highlights the value of developing ecological studies in light of an understanding of species' histories.

Second, bidirectional interspecific competition may have not been involved with the origin of patterns of elevational replacement, but may play a pivotal role in their maintenance (Remsen and Cardiff 1990). Testing this hypothesis experimentally by manipulating the presence or absence of species and examining changes in fitness components or in the boundaries of elevational ranges would be challenging for *Buarremon*, but assessing the potential for interference competition through interspecific territoriality in areas of parapatry could shed some light on its plausibility (Robinson and Terborgh 1995). I have conducted a limited number of playback experiments that indicate that *B. torquatus* and *B. brunneinucha* respond to each other's vocalizations, which suggests that interspecific territoriality between them is possible.

Third, because I tested only for the historical signals of one-to-one competition between *B. brunneinucha* and *B. torquatus*, I cannot rule out the possibility that their elevational ranges could have been shaped by competition with other species individually, or through diffuse competition at the community level (Terborgh and Weske 1975; Mayr and Diamond 1976). Addressing these hypotheses in detail is beyond the scope of this study, but I note that the absence of *Buarremon* species from particular geographical areas in some cases correlates with the absence of other taxa, suggesting it is possible that compressed elevational ranges in sympatry may partly reflect competition with a suite of species, not only with each other. For instance, Remsen and Graves (1995) demonstrated a marked expansion of the elevational range of *B. torquatus* south of northern Bolivia; because *B. brunneinucha* does not exist in this region, a sensible explanation for the expanded range of *B. torquatus* was release from competition with *B. brunneinucha*. However, the absence of *B. brunneinucha* from this region also correlates with a conspicuous decline in overall avian species richness (Rahbek and Graves 2001).

Finally, there might be a role for interspecific competition in the origin of elevational zonation that would imply turning Diamond's (1973) original argument on its head: coexistence with elevational segregation may be possible only if the elevational distributions of species that colonize any given mountain slope are different enough at the outset that they do not compete (cf. Losos 1990; Pfennig and Murphy 2003). In other words, the role of interspecific competition may be to act as a sorting mechanism that allows coexistence along mountain slopes only of ecologically similar species with pre-existing differences in elevational distributions that minimize the potential for competition (Rice and

Pfennig 2007). The idea that ecological sorting enables the coexistence of species with contrasting niches evolved prior to community assembly has gained ample support from studies combining data on community structure with phylogenetic analyses of the evolution of ecological traits (reviewed by Webb et al. 2002; see also Kozak et al. 2005; Vitt and Pianka 2005). The patterns of elevational replacement in *Buarremon* may thus be the result of a process in which upon colonizing the range of *B. torquatus*, *B. brunneinucha* established populations at elevations that matched its ecological requirements, without any modifications of elevational ranges in either species.

BIOGEOGRAPHIC HISTORY AND THE ORIGIN OF ELEVATIONAL DISTRIBUTIONS

Although the hypothesis that competition with *B. brunneinucha* was involved with the origin of the contrasting elevational distributions of different lineages of *B. torquatus* (a phenomenon ornithologists have long been interested in explaining; Paynter 1978; Fjeldså and Krabbe 1990; Remsen and Graves 1995) could not be rejected firmly in this study, it appears to be unlikely. More generally, the origin of elevational replacements may not be related to interspecific competition, which leaves open for discussion the question of how patterns of abrupt turnover of congeners along elevational transects arise.

The hypothesis that populations may be displaced vertically as mountains uplift (Heads 1989) would predict that lineages associated with elevational zones diverged during periods of tectonic activity. The Cordillera Oriental of Colombia increased rapidly in elevation between five and two million years ago (Mya), achieving its modern altitudes by around 2.7 Mya (Gregory-Wodzicki 2000). If branch lengths are transformed to approximate divergence times based on existing calibrations of nucleotide substitution rates in avian protein-coding mtDNA (reviewed by Lovette 2004; Weir 2006), then the divergence among Northern Andean lineages of *B. torquatus* would appear to have taken place concurrently with events of mountain uplifting in this region. Thus, orogenic processes might have been involved with the differentiation of lineages with distinct elevational distributions. An additional prediction of this hypothesis that would allow for a much more robust test is that consistent patterns in phylogenetic relationships and timing of differentiation of lineages with similar elevational distributions should be observed in other organisms. Owing to the lack of comprehensive phylogenetic and phylogeographic studies on other North Andean taxa, this prediction is not yet testable.

In contrast to the idea that species may be stratified along elevational gradients as a result of limited dispersal abilities that “trap” populations in vertical geological movements, elevational zonation can also be explained on the basis of dispersal scenarios: species replacing others in high-elevation areas may have colonized these environments from temperate latitudes tracking

their favored environmental conditions (Chapman 1917; reviewed by Vuilleumier 1986). This hypothesis is supported by phylogenetic evidence that taxa existing at high elevations in the Northern Andes had their origin in alpine temperate areas (Chesser 2000; von Hagen and Kadereit 2003; Chesser 2004; Bell and Donoghue 2005; Hughes and Eastwood 2006). Although basal relationships among major South American lineages of *B. torquatus* are not well supported, it is intriguing that populations existing in distant geographical areas appear to be closely allied (Cadena et al. in press). Because they may reflect extinction of intervening populations of formerly widespread lineages, these disjunct patterns need not involve scenarios of long-distance dispersal, but do illustrate the potential for complex historical changes in the geographic distributions of montane lineages (see also Dingle et al. 2006). If species’ niches remain conserved despite range expansions and shifts, colonization processes coupled with “niche tracking” (Stephens and Wiens 2004) may be an important determinant of patterns of elevational zonation.

Finally, speciation along elevational gradients can result in closely related species with abutting elevational ranges, although this hypothesis does not apply to *Buarremon* brush-finches. Speciation may occur as a consequence of varying selective pressures along the elevational gradient that lead to differentiation of continuously distributed populations into pairs of daughter species (reviewed by Smith et al. 2005), or as a result of allopatric differentiation following dispersal across elevations, with parapatry resulting from subsequent range expansions. Although they cannot distinguish between these two scenarios, phylogenetic studies on Andean taxa provide evidence of speciation into the highlands, with successively sister taxa distributed parapatrically and the most recently diverged species existing at the highest elevations (Bates and Zink 1994; Hall 2005).

Conclusion

This study demonstrates that two taxa that were thought to have influenced the limits of their geographic ranges mutually have had quite contrasting biogeographic histories. *Buarremon brunneinucha* appears to have colonized the range of *B. torquatus* only recently, and this colonization does not seem to have involved a modification of its elevational range in response to the possible onset of interspecific competition. Although the possibility that the elevational distributions of lineages of *B. torquatus* were shaped by competition with *B. brunneinucha* cannot be entirely ruled out, this appears unlikely, and if it happened it must have occurred relatively recently in the history of these taxa. This insight adds to mounting evidence that, regardless of their pervasiveness in present time, ecological interactions may have played out over only short snapshots of the evolutionary history of lineages with contrasting histories (Sorenson et al. 2003; Flanagan et al. 2004;

DeChaine and Martin 2006). This underscores the importance of framing hypotheses related to the effect of current species interactions on geographic ranges and on the evolution of ecological niches in an explicitly historical context.

The results of this study also highlight a challenge for researchers testing hypotheses of character displacement using phylogenetic comparative methods. Phylogenetic tests of character displacement (Losos 1990; Butler and Losos 1997; Radtkey et al. 1997; Giannasi et al. 2000) attempt to distinguish whether exaggerated differences between species in sympatry reflect evolution of derived character states taken place in situ, or the retention of plesiomorphic states acquired elsewhere prior to the potential onset of interspecific competition (see also Rice and Pfennig 2007). Although this approach has provided much valuable insights, under some circumstances it may be misleading as a consequence of the dynamic nature of geographic ranges. As illustrated by *Buarremon* brush-finches, although two species may now coexist with ecological segregation in a particular geographical setting, it is possible that these species have had different residence times in such setting, implying that ecological differences that allow them to coexist may have evolved in situ but effectively in allopatry in areas where they are currently sympatric. This scenario cannot be distinguished from evolution in real sympatry only on the basis of phylogenetic relationships, species distributions, and geographic variation in ecological traits. It follows that an additional prediction of character displacement is that differences between species evolved within a time period in which they could have been sympatric. In other words, ideally, one would like to determine not only where but also precisely *when* did ecological differences arise, especially in studies with little or no replication of areas of sympatry and allopatry. However, the difficulty of obtaining precise and accurate reconstructions of trait evolution (Webster and Purvis 2002) represents a major obstacle to implementing robust tests of predictions about the timing of ecological differentiation. As probabilistic approaches for inferring the evolution of organismal traits (Huelsenbeck et al. 2003) and geographic ranges (Ree et al. 2005) continue to be developed, the current hurdles may be overcome in the not too distant future.

ACKNOWLEDGMENTS

I am very grateful to curators and collection managers at the institutions that allowed me to obtain locality data from specimens under their care: Instituto de Ciencias Naturales (Universidad Nacional de Colombia), Instituto Alexander von Humboldt, Louisiana State University Museum of Natural Science, Museum of Comparative Zoology (Harvard University), Museo de la Universidad de San Marcos, Museo de La Salle, American Museum of Natural History, The Field Museum, Colección Nacional de Aves (Universidad Nacional Autónoma de México), Universidad del Valle, Zoological Museum of the University of Copenhagen, Academy of Natural Sciences of Philadelphia, Western Foundation of Vertebrate Zoology, Marjorie Barrick Museum (University of Nevada-Las Vegas), University of Kansas Natural History Museum, Peabody Museum (Yale

University), and Museum of Vertebrate Zoology (University of California-Berkeley). For help with the implementation and interpretation of coalescent analyses, I thank P. Beerli, M. Kuhner, and A. Rambaut. P. Sweeney helped install programs in a computer cluster, which greatly facilitated my analyses. This manuscript benefited from insightful comments by B. A. Loiselle, J. V. Remsen, S. J. Hackett, E. A. Kellogg, Associate Editor D. Pfennig, two anonymous reviewers, and especially by R. E. Ricklefs. Support for field and laboratory work on which this study builds on was provided by the International Center for Tropical Ecology (Development Board Scholarship and Parker-Gentry Fellowship), the American Museum of Natural History (Chapman Memorial Fund), the American Ornithologists' Union (Wetmore Award), the Organization for Tropical Studies (Donald and Beverly Stone Fund), The Explorers' Club (Exploration Fund Grant), SigmaXi (Grants in Aid of Research), and Idea Wild. I thank B. A. Loiselle and R. E. Ricklefs for their support and advice during the development of this study.

LITERATURE CITED

- Ackerly, D. D. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *Int. J. Plant Sci.* 164:S165-S184.
- Altshuler, D. L. 2006. Flight performance and competitive displacement of hummingbirds across elevational gradients. *Am. Nat.* 167:216-229.
- Altshuler, D. L., and R. Dudley. 2006. The physiology and biomechanics of avian flight at high altitude. *Integr. Comp. Biol.* 46:62-71.
- Anderson, R. P., A. T. Peterson, and M. Gómez-Laverde. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos* 98:3-16.
- Angert, A. L., and D. W. Schemske. 2005. The evolution of species' distributions: reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. *Evolution* 59:1671-1684.
- Arbogast, B. S., and G. J. Kenagy. 2001. Comparative phylogeography as an integrative approach to historical biogeography. *J. Biogeogr.* 28:819-825.
- Arctander, P., and J. Fjeldså. 1994. Andean tapaculos of the genus *Scytalopus* (Aves, Rhinocryptidae): a study of speciation using DNA sequence data. Pp. 205-225 in V. Loeschke, J. Tomiuk, and S. K. Jain, eds. *Conservation Genetics*. Birkhauser Verlag, Basel, Switzerland.
- Austin, M. P. 1999. A silent clash of paradigms: some inconsistencies in community ecology. *Oikos* 86:170-178.
- Austin, M. P., A. O. Nicholls, and C. R. Margules. 1990. Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecol. Monogr.* 60:161-177.
- Bates, J. M., and R. M. Zink. 1994. Evolution into the Andes: molecular evidence for species relationships in the genus *Leptopogon*. *Auk* 111:507-515.
- Bell, C. D., and M. J. Donoghue. 2005. Phylogeny and biogeography of Valerianaceae (Dipsacales) with special reference to the South American valerians. *Organ. Divers. Evol.* 5:147-159.
- Bernardi, G. 2005. Phylogeography and demography of sympatric sister surf-perch species, *Embiotoca jacksoni* and *E. lateralis* along the California coast: historical versus ecological factors. *Evolution* 59:386-394.
- Brown, J. H., G. C. Stevens, and D. M. Kaufman. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.* 27:597-623.
- Brown, W. L., and E. O. Wilson. 1956. Character displacement. *Syst. Zool.* 5:49-69.
- Buckley, L. B., and J. Roughgarden. 2005. Effect of species interactions on landscape abundance patterns. *J. Anim. Ecol.* 74:1182-1194.

- Bull, C. M. 1991. Ecology of parapatric distributions. *Annu. Rev. Ecol. Syst.* 22:19–36.
- Butler, M. A., and J. B. Losos. 1997. Testing for unequal amounts of evolution in a continuous character on different branches of a phylogenetic tree using linear and square-changed parsimony: an example using Lesser Antillean *Anolis* lizards. *Evolution* 51:1623–1635.
- Cadena, C. D. 2006. Biogeography of *Buarremon* Brush-Finches (Aves, Emberizidae): Integrating Ecology, Evolution, and Systematics. Ph.D. diss., University of Missouri-St. Louis, St. Louis, MO.
- Cadena, C. D., J. Klicka, and R. E. Ricklefs. Evolutionary differentiation in the Neotropical montane region: molecular phylogenetics and phylogeography of *Buarremon* brush-finches (Aves, Emberizidae). *Mol. Phylogenet. Evol.* *In press*.
- Carothers, J. H., F. M. Jaksic, and P. A. Marquet. 2001. Altitudinal zonation among lizards of the genus *Liolaemus*: questions answered and unanswered questions. *Revista Chilena de Historia Natural* 74:313–316.
- Case, T. J., R. D. Holt, M. A. McPeck, and T. H. Keitt. 2005. The community context of species' borders: ecological and evolutionary perspectives. *Oikos* 108:28–46.
- Case, T. J., and M. L. Taper. 2000. Interspecific competition, environmental gradients, gene flow, and the coevolution of species' borders. *Am. Nat.* 155:583–605.
- Chapman, F. M. 1917. The distribution of bird life in Colombia. *Bull. Am. Museum Nat. Hist.* 36:1–169.
- Chesser, R. T. 2000. Evolution in the high Andes: the phylogenetics of *Muscisaxicola* ground-tyrants. *Mol. Phylogenet. Evol.* 15:369–380.
- . 2004. Systematics, evolution, and biogeography of the South American ovenbird genus *Cinclodes*. *Auk* 121:752–766.
- Crisi, J. V., L. Katinas, and P. Posadas. 2003. Historical biogeography: an introduction. Harvard Univ. Press, Cambridge, MA.
- Dayan, T., and D. Simberloff. 2005. Ecological and community-wide character displacement: the next generation. *Ecol. Lett.* 8:875–894.
- DeChaine, E. G., and A. P. Martin. 2006. Using coalescent simulations to test the impact of Quaternary climate cycles on divergence in an alpine plant-insect association. *Evolution* 60:1004–1013.
- Diamond, J. 1970. Ecological consequences of island colonization by Southwest Pacific birds. I. Types of niche shifts. *Proc. Natl Acad. Sci. USA* 67:529–536.
- Diamond, J. M. 1973. Distributional ecology of New Guinea birds. *Science* 179:759–769.
- Diamond, J., and A. G. Marshall. 1977. Niche shifts in New Hebridean birds. *Emu* 77:61–72.
- Dingle, C., I. J. Lovette, C. Canaday, and T. B. Smith. 2006. Elevational zonation and the phylogenetic relationships of the *Henicorhina* woodwrens. *Auk* 123:119–134.
- Doebeli, M., and U. Dieckmann. 2000. Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Am. Nat.* 156:S77–S101.
- Donoghue, M. J., and B. R. Moore. 2003. Toward an integrative historical biogeography. *Integ. Comp. Biol.* 43:261–270.
- Drummond, A. J., and A. Rambaut. 2003. BEAST. Ver. 1.2. Available at <http://evolve.zoo.ox.ac.uk/beast>
- Drummond, A. J., A. Rambaut, B. Shapiro, and O. G. Pybus. 2005. Bayesian coalescent inference of past population dynamics from molecular sequences. *Mol. Biol. Evol.* 22:1185–1192.
- Edwards, S. V., and P. Beerli. 2000. Gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. *Evolution* 54:1839–1854.
- Emerson, B. C., E. Paradis, and C. Thébaud. 2001. Revealing the demographic histories of species using DNA sequences. *Trends Ecol. Evol.* 16:707–716.
- Endler, J. A. 1982. Pleistocene refuges: fact or fancy? Pp. 641–657 in G. T. Prance, ed. *Biological diversification in the tropics*. Columbia Univ. Press, New York.
- Felsenstein, J. 2006. Accuracy of coalescent likelihood estimates: do we need more sites, more sequences, or more loci? *Mol. Biol. Evol.* 23:691–700.
- Felsenstein, J., M. K. Kuhner, J. Yamato, and P. Beerli. 1999. Likelihoods on coalescents: a Monte Carlo sampling approach to inferring parameters from population samples of molecular data. *IMS Lect. Notes – Monogr. Ser., Inst. Math. Stat.* 33:163–185.
- Fjeldså, J., and N. Krabbe. 1990. *Birds of the high Andes*. Zoological Museum, University of Copenhagen and Apollo Books, Svendborg, Denmark.
- Flanagan, N. S., A. Tobler, A. Davison, O. G. Pybus, D. D. Kapan, S. Planas, M. Linares, D. Heckel, and W. O. McMillan. 2004. Historical demography of Müllerian mimicry in the Neotropical *Heliconius* butterflies. *Proc. Natl Acad. Sci. USA* 101:9704–9709.
- García-Moreno, J., P. Arctander, and J. Fjeldså. 1999. Strong diversification at the treeline among *Metallura* hummingbirds. *Auk* 116:702–711.
- Gaston, K. J. 2003. *The structure and dynamics of geographic ranges*. Oxford Univ. Press, Oxford, U.K.
- Giannasi, N., R. S. Thorpe, and A. Malhotra. 2000. A phylogenetic analysis of body size evolution in the *Anolis roquet* group (Sauria: Iguanidae): character displacement or size assortment? *Mol. Ecol.* 9:193–202.
- Grant, P. R. 1972. Convergent and divergent character displacement. *Biol. J. Linn. Soc.* 4:39–68.
- . 1975. The classical case of character displacement. *Evol. Biol.* 5:237–337.
- Graves, G. R. 1988. Linearity of geographic range and its possible effect on the population structure of Andean birds. *Auk* 105:47–52.
- Gregory-Wodzicki, K. M. 2000. Uplift history of the Central and Northern Andes: a review. *Geol. Soc. Am. Bull.* 112:1091–1105.
- Hall, J. P. W. 2005. Montane speciation patterns in *Ithomiola* butterflies (Lepidoptera: Riodinidae): are they consistently moving up in the world? *Proc. R. Soc. Lond. B* 272:2457–2466.
- Hardy, C. R., and H. P. Linder. 2005. Intraspecific variability and timing in ancestral ecology reconstruction: a test case from the Cape flora. *Syst. Biol.* 54:299–316.
- Heads, M. 1989. Integrating earth and life sciences in New Zealand natural history: the parallel arcs model. *N. Z. J. Zool.* 16:549–585.
- . 2005. Towards a panbiogeography of the seas. *Biol. J. Linnean Soc.* 84:675–723.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25:1965–1978.
- Holt, R. D. 2003. On the evolutionary ecology of species' ranges. *Evol. Ecol. Res.* 5:159–178.
- Holt, R. D., and M. S. Gaines. 1992. Analysis of adaptation in heterogeneous landscapes – implications for the evolution of fundamental niches. *Evol. Ecol.* 6:433–447.
- Holt, R. D., and T. H. Keitt. 2005. Species' borders: a unifying theme in ecology. *Oikos* 108:3–6.
- Hooghiemstra, H., and T. Van der Hammen. 2004. Quaternary ice-age dynamics in the Colombian Andes: developing an understanding of our legacy. *Philos. Trans. R. Soc. Lond. B* 359:173–181.
- Huelsenbeck, J. P., R. Nielsen, and J. P. Bollback. 2003. Stochastic mapping of morphological characters. *Syst. Biol.* 52:131–158.
- Hugall, A., C. Moritz, A. Moussalli, and J. Stanisic. 2002. Reconciling paleodistribution models and comparative phylogeography in the wet tropics rainforest land snail *Gnarosiphia bellendenkerensis* (Brazier 1875). *Proc. Natl Acad. Sci. USA* 99:6112–6117.

- Hughes, C., and R. Eastwood. 2006. Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proc. Natl Acad. Sci. USA* 103:10334–10339.
- Humboldt, A. v. 1807. *Ideen zu einer Geographie der Pflanzen nebst einem Naturgemälde der Tropenländer*. Bey F. G. Cotta, Tübingen, Germany.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22:415–442.
- Jackson, S. T. 2004. Quaternary biogeography: linking biotic responses to environmental variability across timescales. Pp. 47–65 in M. V. Lomolino and L. R. Heaney, eds. *Frontiers in biogeography: new directions in the geography of nature*. Sinauer Associates, Sunderland, MA.
- Jackson, S. T., and J. T. Overpeck. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26:194–220.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101:233–249.
- Kattan, G. H., P. Franco, C. A. Saavedra-Rodríguez, C. Valderrama, V. Rojas, D. Osorio, and J. Martínez. 2006. Spatial components of bird diversity in the Andes of Colombia: implications for designing a regional reserve system. *Conserv. Biol.* 20:1203–1211.
- Kingman, J. F. C. 1982. The coalescent. *Stoch. Proc. Their Appl.* 13:235–248.
- Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. *Am. Nat.* 150:1–23.
- Knowles, L. L. 2004. The burgeoning field of statistical phylogeography. *J. Evol. Biol.* 17:1–10.
- Kozak, K. H., A. Larson, R. M. Bonett, and L. J. Harmon. 2005. Phylogenetic analysis of ecomorphological divergence, community structure, and diversification rates in dusky salamanders (Plethodontidae: *Desmognathus*). *Evolution* 59:2000–2016.
- Kuhner, M. K., P. Beerli, J. Yamato, E. Rynes, L. Smith, and E. Walkup. 2004. LAMARC. Ver. 1.2.2. Available at <http://evolution.genetics.washington.edu/lamarc.html>
- Kuhner, M. K., J. Yamato, and J. Felsenstein. 1998. Maximum likelihood estimation of population growth rates based on the coalescent. *Genetics* 149:429–434.
- Lack, D., and H. N. Southern. 1949. Birds on Tenerife. *Ibis* 91:607–626.
- Losos, J. B. 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. *Evolution* 44:558–569.
- Lovette, I. J. 2004. Mitochondrial dating and mixed support for the “2% rule” in birds. *Auk* 121:1–6.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper and Row, New York.
- Martin, P. R., and T. E. Martin. 2001. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. *Ecology* 82:189–206.
- Martínez-Meyer, E., A. T. Peterson, and W. W. Hargrove. 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecol. Biogeogr.* 13:305–314.
- Mayr, E., and J. M. Diamond. 1976. Birds on islands in the sky: origin of the montane avifauna of Northern Melanesia. *Proc. Natl Acad. Sci. U.S.A.* 73:1765–1769.
- Moyle, R. G., M. Schilthuizen, M. A. Rahman, and F. H. Sheldon. 2005. Molecular phylogenetic analysis of the white-crowned fork-tail *Enicurus leschenaulti* in Borneo. *J. Avian Biol.* 36:96–101.
- Navas, C. A. 2003. Herpetological diversity along Andean elevational gradients: links with physiological ecology and evolutionary physiology. *Comp. Biochem. Physiol. Part A* 133:469–485.
- Nielsen, R., and J. Wakeley. 2001. Distinguishing migration from isolation: a Markov chain Monte Carlo approach. *Genetics* 158:885–896.
- Patton, J. L., and M. F. Smith. 1992. mtDNA phylogeny of Andean mice: a test of diversification across ecological gradients. *Evolution* 46:174–183.
- Paynter, R. A., Jr. 1978. Biology and evolution of the avian genus *Atlapetes* (Emberizinae). *Bull. Mus. Comp. Zool.* 148:323–369.
- Pérez-Emán, J. L. 2005. Molecular phylogenetics and biogeography of the Neotropical redstarts (*Myioborus*; Aves, Parulinae). *Mol. Phylogenet. Evol.* 37:511–528.
- Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285:1265–1267.
- Pfennig, D. W., and P. J. Murphy. 2003. A test of alternative hypothesis for character divergence between coexisting species. *Ecology* 84:1288–1297.
- Pfennig, K. S., and D. W. Pfennig. 2005. Character displacement as the “best of a bad situation”: fitness tradeoffs resulting from selection to minimize resource and mate competition. *Evolution* 59:2200–2208.
- Pfennig, D. W., A. M. Rice, and R. A. Martin. 2006. Ecological opportunity and phenotypic plasticity interact to promote character displacement and species coexistence. *Ecology* 87:769–779.
- Porter, W. P., J. L. Sabo, C. R. Tracy, O. J. Reichman, and N. Ramankutty. 2002. Physiology on a landscape scale: plant-animal interactions. *Integr. Comp. Biol.* 42:431–453.
- Posada, D., and K. A. Crandall. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818.
- Prodon, R., J.-C. Thibault, and P.-A. DeJaifve. 2002. Expansion vs. compression of bird altitudinal ranges on a Mediterranean island. *Ecology* 83:1294–1306.
- Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecol. Lett.* 3:349–361.
- Qian, H., and R. E. Ricklefs. 2004. Geographical distribution and ecological conservatism of disjunct genera of vascular plants in eastern Asia and eastern North America. *J. Ecol.* 92:253–265.
- Radtkey, R. R., S. M. Fallon, and T. J. Case. 1997. Character displacement in some *Cnemidophorus* lizards revisited: a phylogenetic analysis. *Proc. Natl Acad. Sci. USA* 94:9740–9745.
- Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecol. Lett.* 8:224–239.
- Rahbek, C., and G. R. Graves. 2001. Multiscale assessment of patterns of avian species richness. *Proc. Natl Acad. Sci. USA* 98:4534–4539.
- Rambaut, A., and A. J. Drummond. 2003. Tracer. Ver. 1.2. Available at <http://evolve.zoo.ox.ac.uk/beast/>
- Ree, R. H., B. R. Moore, C. O. Webb, and M. J. Donoghue. 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* 59:2299–2311.
- Remsen, J. V., Jr., and S. W. Cardiff. 1990. Patterns of elevational and latitudinal distribution, including a “niche switch” in some guans (Cracidae) of the Andes. *Condor* 92:970–981.
- Remsen, J. V., Jr., and W. S. Graves. 1995. Distribution patterns of *Buarremon* Brush-finches (Emberizinae) and interspecific competition in Andean birds. *Auk* 112:225–236.
- Renner, S. S., and H. Won. 2001. Repeated evolution of dioecy from monoecy in Siparunaceae (Laurales). *Syst. Biol.* 50:700–712.
- Repasky, R. R., and D. Schluter. 1994. Habitat distributions of wintering sparrows along an elevational gradient: tests of the food, predation and microhabitat structure hypotheses. *J. Anim. Ecol.* 63:569–582.
- Rice, A. M., and D. W. Pfennig. 2007. Character displacement: in situ evolution of novel phenotypes or sorting of pre-existing variation? *J. Evol. Biol.* 20:448–459.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.* 7:1–15.

- . 2005. Phylogenetic perspectives on patterns of regional and local species richness. Pp. 16–40 in E. Bermingham, C. W. Dick and C. Moritz, eds. *Tropical rainforests: past, present, and future*. The Univ. Chicago Press, Chicago, IL.
- . 2006. Evolutionary diversification and the origin of the diversity-environment relationship. *Ecology* 87:S3-S13.
- Ricklefs, R. E., and R. E. Latham. 1992. Intercontinental correlation of geographic ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *Am. Nat.* 139:1305–1321.
- Robinson, S. K., and J. Terborgh. 1995. Interspecific aggression and habitat selection in Amazonian birds. *J. Anim. Ecol.* 64:1–11.
- Sanderson, M. J. 2002. Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Mol. Biol. Evol.* 19:101–109.
- . 2003. r8s: inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. *Bioinformatics* 19:301–302.
- Sanderson, M. J., and J. A. Doyle. 2001. Sources of error and confidence intervals in estimating the age of angiosperms from *rbcL* and 18S rDNA data. *Am. J. Bot.* 88:1499–1516.
- Schluter, D. 2000. Ecological character displacement in adaptive radiation. *Am. Nat.* 156:S4–S16.
- Schluter, D., and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. *Am. Nat.* 140:85–108.
- Schulte, J. A., II, J. R. Macey, R. E. Espinoza, and A. Larson. 2000. Phylogenetic relationships in the iguanid lizard genus *Liolaemus*: multiple origins of viviparous reproduction and evidence for recurring Andean vicariance and dispersal. *Biol. J. Linn. Soc.* 69:75–102.
- Shapiro, B., A. J. Drummond, A. Rambaut, M. C. Wilson, P. E. Matheus, A. V. Sher, O. G. Pybus, M. T. P. Gilbert, I. Barnes, J. Binladen, E. Willerslev, A. J. Hansen, G. F. Baryshnikov, J. A. Burns, S. Davydov, J. C. Driver, D. G. Froese, C. R. Harington, G. Keddie, P. Kosintsev, M. L. Kunz, L. D. Martin, R. O. Stephenson, J. Storer, R. Tedford, S. Zimov, and A. Cooper. 2004. Rise and fall of the Beringian steppe bison. *Science* 306:1561–1565.
- Smith, T. B., R. K. Wayne, D. Girman, and M. W. Bruford. 2005. Evaluating the divergence-with-gene-flow model in natural populations: the importance of ecotones in rainforest speciation. Pp. 148–165 in E. Bermingham, C. W. Dick, and C. Moritz, eds. *Tropical rainforests: past, present, and future*. The Univ. Chicago Press, Chicago, IL.
- Sorenson, M. D., K. M. Sefc, and R. B. Payne. 2003. Speciation by host switch in brood parasitic indigobirds. *Nature* 424:928–931.
- Stephens, P. R., and J. J. Wiens. 2004. Convergence, divergence, and homogenization in the ecological structure of emydid turtle communities: the effects of phylogeny and dispersal. *Am. Nat.* 164:244–254.
- Swofford, D. L. 2002. PAUP* Version 4.0b10: Phylogenetic analysis using parsimony (and other methods). Sinauer Associates, Sunderland, MA.
- Terborgh, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52:23–40.
- Terborgh, J., and J. S. Weske. 1975. The role of competition in the distribution of Andean birds. *Ecology* 56:562–576.
- Vitt, L. J., and E. R. Pianka. 2005. Deep history impacts present-day ecology and biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* 102:7877–7881.
- von Hagen, K. B., and J. W. Kadereit. 2003. The diversification of *Halenia* (Gentianaceae): ecological opportunity versus key innovation. *Evolution* 57:2507–2518.
- Vuilleumier, F. 1986. Origins of the tropical avifaunas of the high Andes. Pp. 586–622 in F. Vuilleumier and M. Monasterio, eds. *High altitude tropical biogeography*. Oxford Univ. Press, New York.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33:475–505.
- Webster, A. J., and A. Purvis. 2002. Testing the accuracy of methods for reconstructing ancestral states on continuous characters. *Proc. R. Soc. Lond. B* 269:143–149.
- Weir, J. T. 2006. Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution* 60:842–855.

Associate Editor: D. Pfennig