

# Ecology Predicts Levels of Genetic Differentiation in Neotropical Birds

Curtis W. Burney<sup>1,2</sup> and Robb T. Brumfield<sup>1,2,\*</sup>

1. Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana 70803; 2. Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803

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**ABSTRACT:** Despite the theoretical link between the ecology and the population genetics of species, little empirical evidence is available that corroborates the association. Here, we examined genetic variation in 40 codistributed species of lowland Neotropical rain forest birds that have populations isolated on either side of the Andes, the Amazon River, and the Madeira River. We found widely varying levels of genetic divergence among these taxa across the same biogeographic barriers. Our investigation of the extent to which ecological traits predicted the amount of cross-barrier divergence revealed a strongly significant relationship between the forest stratum at which a species forages and the level of cross-barrier genetic differentiation. Canopy species had statistically lower genetic divergence values across the Andes and the two Amazonian rivers than did understory birds. We hypothesize that the association reflects an effect of dispersal propensity, which is greater in canopy birds, on the movement of alleles among demes (i.e., migration) and, consequently, on the interdemic proportion of the genetic variance. Differences in dispersal propensity may also explain the observation that understory species contain a significantly greater number of subspecies than do canopy species. This result indicates that higher rates of diversification may occur in lineages with lower dispersal propensity.

**Keywords:** comparative phylogeography, Andes, riverine barriers, Neotropical birds, dispersal, speciation.

## Introduction

The ecology of a species influences the effective size of demes and the pattern of gene flow among them (Caballero 1994; Turner and Trexler 1998; Bohonak 1999), which, in turn, determines both the amount and the spatiotemporal distribution of neutral genetic variation found within and between demes (Wright 1951; reviewed in Charlesworth et al. 2003). Despite the theoretical link between the ecology and the population genetics of species (Avice et al. 1987; Palumbi 1992), little empirical evidence cor-

roborates the association (Loveless and Hamrick 1984; Hamrick and Godt 1996). This is partly because the amount of intraspecific genetic variation, both within and between demes, is influenced by past and present demography, as well as by a multitude of confounding, potentially opposing evolutionary processes, including genetic drift, gene flow, and mutation (Slatkin 1987; Bossart and Prowell 1998). Because population genetic studies traditionally focus on a single taxon, any discrimination of mechanistic hypotheses based on species-specific characteristics is not possible. A further difficulty is that ecological data are often insufficient to test hypotheses regarding the influence of ecology on spatial and temporal patterns of population genetic differentiation (Bohonak 1999). Because of these limitations, the population genetic consequences of ecological variables are often restricted in empirical studies to post hoc discussions with multiple interpretations of the data (Croteau et al. 2007; Milot et al. 2008). Here, we directly address the influence of ecology on population differentiation by employing a comparative approach.

We make use of two large biogeographic barriers to lowland birds in northern South America: the Andes Mountains and the Amazon River system. Both barriers are known to influence the genetic structuring of bird populations. Their effect on genetic differentiation is reflected taxonomically, with most lowland bird populations on either side of the Andes, the Amazon River, and the Amazon's larger tributaries recognized as distinct taxa (Peters 1931–1987). The Andes extend in a north-south axis along the entire western margin of South America and effectively isolate the lowland tropical rain forests west of the Andes (trans-Andes) from those east of the Andes (cis-Andes; fig. 1). The youngest range of the Northern Andes, the Eastern Cordillera, serves as the primary Andean barrier between lowland trans-Andean and cis-Andean taxa. The range, which experienced rapid uplift 10 million years ago and was no more than half of its present elevation ~4 million years ago (Guerrero 1997; Gregory-Wodzicki 2000), divided the once continuous lowland rain forests

\* Corresponding author; e-mail: brumfld@lsu.edu.

of northwestern South America (Gentry 1989; Daly and Mitchell 2000; Dick et al. 2004) and rerouted Amazonian watercourses to form the modern eastern-flowing drainage (Hoorn et al. 1995; Campbell et al. 2006).

Previous studies of lowland tropical rain forest birds revealed that these physical barriers partition genetic variation of codistributed taxa similarly (Capparella 1988, 1991; Brumfield and Capparella 1996; Hackett and Lehn 1997; Marks et al. 2002; Pereira and Baker 2004; Cheviron et al. 2005; Eberhard and Bermingham 2005; Ribas et al. 2005). Despite this spatial congruence, interspecific variation in levels of genetic differentiation is substantial. Disparity in the temporal patterns of genetic differentiation among taxa thought to have been simultaneously affected by a single barrier has been observed in multiple studies (Bermingham et al. 1997; Knowlton and Weigt 1998; Avise 2000; Marko 2002; Lessios et al. 2003; Hickerson et al. 2006b). Some studies have interpreted the large variance in genetic divergence values across a common barrier to reflect multiple vicariant events (Brumfield and Edwards 2007) or postvicariance dispersal (Leache et al. 2007), but the combined effects of the coalescent process (Donnelly and Tavaré 1995), molecular rate heterogeneity (Wu and Li 1985), and demography (Edwards and Beerli 2000) can produce a similar pattern (i.e., large variance) with just a single isolating event (Hickerson et al. 2006a). Here, we tested how the variance in levels of genetic differentiation among the 40 species is partitioned with respect to ecological and demographic factors. The experiment does not require an assumption that the isolation of populations on either side of the three barriers occurred simultaneously. The specific event(s) that led to the presence of populations on either side of the barriers (e.g., vicariance, dispersal, or a combination of both processes) introduces noise into the data but should not create a systematic bias with respect to taxa.

## Methods

### *Study Species and Molecular Data Collection*

We examined 40 species of Neotropical birds with cross-Andean distributions (table A1, available as an Excel data file in the online edition of the *American Naturalist*). All breed regularly in terra firma forest (tropical lowland evergreen forest, using the classification of Stotz et al. [1996]). To maximize taxonomic diversity, we selected species representing 20 families and seven orders. Within larger clades, we included species with differing ecologies where possible to balance study design. A practical consideration in selecting the 40 species was that each be well represented in museum genetic resource collections. Levels of genetic divergence were measured across three physical

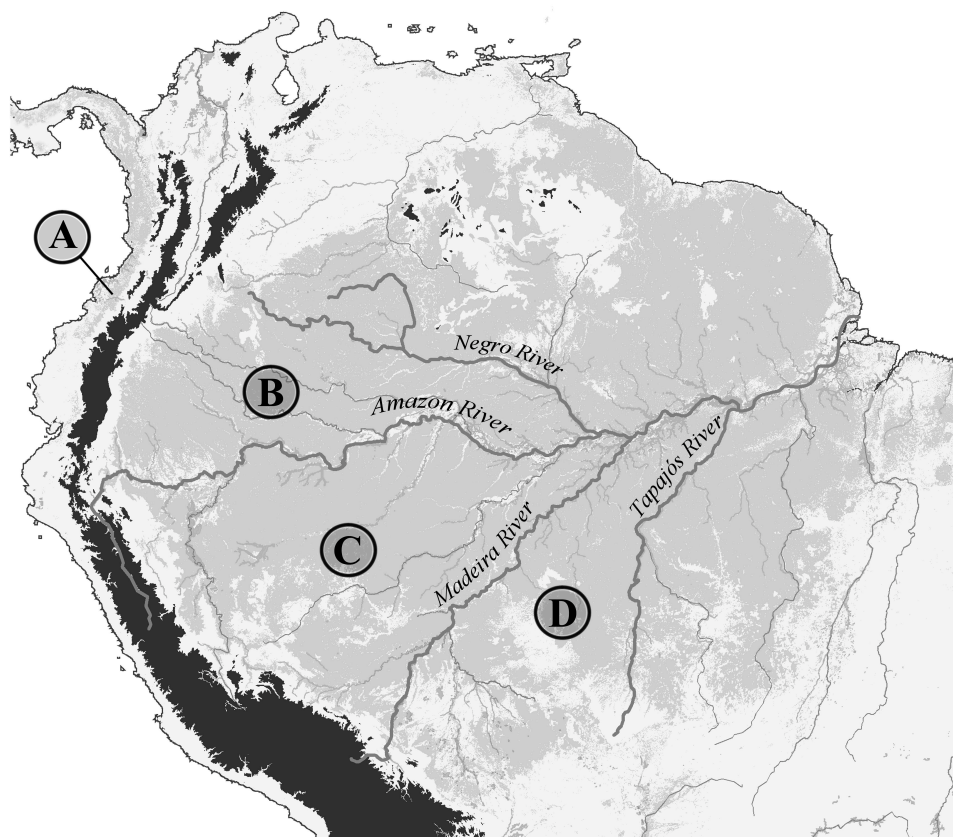
barriers: (1) the Andes, (2) the Amazon River, and (3) the Madeira River, a major tributary of the Amazon (fig. 1). Where species' ranges and holdings in collections allowed, we sampled individuals from populations on opposite sides of each of the three barriers of interest (table A2, available as an Excel data file in the online edition of the *American Naturalist*). All tissues used in this study have accompanying voucher specimens.

Sequences from the mitochondrial protein-coding cytochrome *b* (cyt *b*) gene were used to estimate within- and between-population genetic differentiation for each species. There are good statistical reasons for using multilocus instead of single-locus measurements of genetic diversity in reducing the variance of population genetic parameter estimates (Brumfield et al. 2003), but we opted to maximize taxonomic diversity at the cost of measurement precision within each species. This was justified in that the statistical effect on our tests was to make them more conservative. Any statistical associations between ecological and genetic parameters would have to overwhelm the error associated with the single-locus estimates of genetic diversity.

We extracted DNA from ~25 mg of tissue using the DNeasy Tissue Kit (Qiagen, Valencia, CA). Polymerase chain reaction (PCR) amplifications (25  $\mu$ L) of cyt *b* consisted of 2.5  $\mu$ L template DNA (~50 ng), 0.3  $\mu$ L of each primer (10  $\mu$ M; table A1), 0.5  $\mu$ L dNTPs (10 mM), 2.5  $\mu$ L 10X with MgCl<sub>2</sub> reaction buffer, 0.1 Taq DNA polymerase (5 U/ $\mu$ L AmpliTaq; ABI, Foster City, CA), and 18.7  $\mu$ L sterile dH<sub>2</sub>O. PCR temperature profiles consisted of an initial denaturation of 2 min at 94°C, followed by 35 cycles of 30 s at 94°C, 30 s at 45°–48°C, and 2 min at 72°C, with a final extension of 5 min at 72°C. Double-stranded PCR products were purified using 20% polyethylene glycol and then cycle-sequenced using 1.75  $\mu$ L 5X sequencing buffer (ABI), 1  $\mu$ L sequencing primer (10  $\mu$ M), 2.25  $\mu$ L template, 0.35  $\mu$ L Big Dye Terminator Cycle-Sequencing Kit (ver. 3.1; ABI), and 1.65  $\mu$ L sterile dH<sub>2</sub>O, for a total volume of 7  $\mu$ L. Reactions were cleaned using Sephadex (G-50 fine) columns and analyzed on an ABI 3100 Genetic Analyzer. Contigs for each individual were assembled and edited using Sequencher (ver. 4.6; GeneCodes, Ann Arbor, MI), and the entire length of each sequence was examined by eye to confirm base calls. To confirm open reading frames, we checked the cyt *b* coding region for stop codons.

### *Estimating Levels of Cross-Barrier Genetic Divergence*

PAUP\* (ver. 4.0b10; Swofford 2001) was used to calculate three pairwise genetic distance measures between individuals composing demes: (1) uncorrected (*p* distance), (2) the HKY85 finite-sites substitution model (Hasegawa et al. 1985), and the best-fit finite-sites substitution model



**Figure 1:** Present distribution of lowland moist forest (dark gray) in northern South America (Eva et al. 1999). Mountains above 2,000 m elevation are in black. Sampling localities of the 40 study taxa confined to four areas of endemism: (A) Chocó, (B) Napo, (C) Inambari, and (D) Rondonia.

(table A3 in the online edition of the *American Naturalist*), determined using the Bayesian Information Criterion test implemented in MODELTEST (ver. 3.8; Posada and Crandall 1998). For each species, pairwise genetic distances between individuals were averaged to provide a single species-level estimate of genetic distance across the three physical barriers of interest (Andes, Amazon River, and Madeira River). Because of sampling limitations, the number of species incorporated in each of the three comparisons varied.

#### *Multipredictor Models of Genetic Divergence*

To assess ecological correlates of genetic differentiation, we examined species-specific attributes associated with habitat, diet, and relative abundance (table A4 in the online edition of the *American Naturalist*). We also included ecological variables that were indirectly tied to dispersal propensity. All natural history and ecological variables were extracted from Stotz et al. (1996).

*Maximum Elevation.* In considering the Andes as a barrier, we included the maximum elevation of a species' geographic distribution as a continuous variable.

*Várzea.* Capparella (1991) suggested that avian species inhabiting *várzea* forest (flooded tropical evergreen forest) disperse more readily across rivers relative to species of terra firma forest (nonflooded). We included as a binary variable whether a species uses *várzea* forest as a preferred habitat in addition to terra firma forest.

*Habitat Breadth.* We tallied the total number of preferred habitats (defined as habitat types where a species occurs or breeds regularly across a significant portion of its geographic distribution) for each species. These ordinal data were transformed to a three-state categorical variable by grouping species with three or more types of preferred habitat into a single category.

*Forest Edge.* Empirical studies have shown that birds inhabiting forest edge are less sensitive to habitat disturbance

and more prone to crossing habitat gaps and open areas than are species restricted to interior forest (Belisle et al. 2001; Sekercioglu et al. 2002). We included the use of edge habitat as a binary variable.

*Foraging Stratum.* Studies suggest that canopy species of the open, more exposed treetops show less inhibition in crossing gaps in habitat than do understory species (reviewed in Harris and Reed 2002). We included the forest stratum at which species typically forage as a variable. Species were classified as either canopy or understory according to the following guidelines: (i) understory: terrestrial, understory, and understory/midstory and (ii) canopy: canopy and midstory/canopy.

*Diet.* The propensity for dispersal may be linked to mobility requirements associated with spatial and temporal changes in food availability. For example, insectivores exhibit relatively little seasonal variation in abundance (Karr 1976; Greenberg and Gradwohl 1986) and thus are considered more sedentary than frugivores (Levey and Stiles 1992). We classified each species as belonging to one of three diet categories (frugivore, insectivore, and omnivore) on the basis of natural history literature.

*Relative Abundance.* We used the relative abundance for a species as a proxy for effective population size ( $N_e$ ), assuming that total population sizes have remained constant through time. Species were grouped into three categories of relative abundance: common, fairly common, and uncommon/rare.

*Geographic Distance.* Although the sampling across species was largely congruent spatially, geographic distance was included in models to test for isolation-by-distance effects (Wright 1943). For each species, the Euclidean distance between the individual sampling localities was calculated using the program ARCGIS (<http://www.esri.com>). The average intraspecific geographic distance was measured across all three physical barriers of interest.

General linear models were used to assess whether species-specific attributes had statistical associations with across-species levels of genetic differentiation. The average genetic distances for species, across all three barriers, were positively skewed and therefore square root transformed before analysis. For the across-Amazon River data set, an additional transformation (square root) was required to achieve normality. All variables (table A4) were considered fixed effects. Each variable was first tested for a one-way association with the across-species genetic divergence values. Variables showing  $P < .15$  were then reanalyzed in multipredictor models to test for second-order interac-

tions. All analyses were computed with the JMP statistical package (ver. 5.0.1.2; SAS Institute, Cary, NC).

#### *Analyses of Genetic Variation between and within Cis-Andean Populations*

For 16 species (table 3) with adequate sampling across cis-Andean regions (fig. 1), we assessed the spatial clustering of variation at *cyt b* for populations separated by the Amazon and Madeira rivers by partitioning genetic variation within and among populations, using AMOVA (Excoffier et al. 1992) in ARLEQUIN (ver. 3.1).

We also examined levels of within-population variation and tested for historical demographic expansion in the cis-Andean population located south of the Amazon River and west of the Madeira River (Inambari area of endemism). Phylogeographic breaks are known to occur within this region (Marks et al. 2002; Cheviron et al. 2005) and, if present, could confound analyses of within-population genetic variation. Therefore, we first assessed population genetic structure through maximum likelihood phylogenetic analyses (heuristic search using the HKY85 model, tree-bisection-reconnection branch swapping, and support for nodes assessed with 100 bootstrap iterations), using PAUP\* (ver. 4.0b10; Swofford 2001), to identify haplotype clades within Inambari. For species exhibiting structure within the region, we included in subsequent analyses only the clade with the largest sample size. Levels of nucleotide diversity ( $\pi$ ; Nei 1987) were calculated within Inambari, using DnaSP (ver. 4.50.2; Rozas et al. 2003). Historical demographic expansion was inferred by the raggedness index (Harpending 1994), Fu's (1997)  $F_s$ , and  $R_2$  (Ramos-Onsins and Rozas 2002), using DnaSP.

#### *Tests of Rate Heterogeneity*

We used a generalized least squares analysis with a single multiplier ( $\lambda$ ) to test whether estimates of genetic divergence across the comparative data set exhibited phylogenetic dependence (Pagel 1999; Freckleton et al. 2002). Incorporating all 40 study species, we used a phylogenetic tree based on the DNA-DNA hybridization-based tree of Sibley and Ahlquist (1990) and a recently published phylogeny (Hackett et al. 2008). Where possible, published family-level phylogenies were used to improve the tree (fig. A1 in the online edition of the *American Naturalist*). A likelihood ratio test was performed to test whether the data were explained significantly better by restricted models in which  $\lambda$  was constrained to be either 0 (phylogenetic independence) or 1 (phylogenetic dependence) or by an unrestricted model in which  $\lambda$  was estimated from the data.

Rate heterogeneity across lineages, particularly for mi-

tochondrial markers, has also been associated with metabolic rate (Martin and Palumbi 1993). We tested for potential associations in our data by regressing cross-Andean genetic divergence (square root transformed) with body mass (log transformed). For each species, bird mass was calculated by using specimens from the Louisiana State University Museum of Natural Science (table A1).

### Results

We present results using the HKY85 finite-sites genetic distance. This model was selected most frequently (20 of 40 species) as the best-fit model, and the results showed the same patterns of statistical significance regardless of distance measure ( $p$  distance, HKY85 model, or best-fit model; table A5 in the online edition of the *American Naturalist*). Cross-barrier genetic distances varied across species from 0.0 to 0.104 (Andes:  $n = 40$ ,  $\bar{X} = 0.035$ ,  $SD = 0.024$ ; Amazon River:  $n = 29$ ,  $\bar{X} = 0.018$ ,  $SD = 0.020$ ; Madeira River:  $n = 26$ ,  $\bar{X} = 0.021$ ,  $SD = 0.025$ ). Likelihood ratio tests found no evidence for phylogenetic dependence of the across-species levels of genetic differentiation (table 1). In addition, there was no significant relationship between genetic divergence and log-transformed mass ( $F = 2.68$ ,  $df = 1, 38$ ,  $P = .110$ ,  $r^2 = 0.066$ ).

We found that canopy species had significantly lower levels of cross-barrier genetic divergence than did understory species (table 2; fig. 2). Habitat breadth and diet, both correlated with foraging stratum, were also marginally significant. Species having a greater number of preferred habitats (habitat generalists) were associated with the canopy (Pearson  $X^2 = 10.84$ ,  $P = .004$ ), and frugivores were largely composed of canopy species (Pearson  $X^2 = 6.23$ ,  $P = .044$ ). When multiple tests were controlled using Bonferroni correction, both habitat breadth and diet showed no significant relationship with levels of genetic divergence. Within insectivores (canopy, five species; understory, 14 species), foraging stratum was significantly associated with cross-Andean genetic divergence ( $F = 9.40$ ,  $df = 1, 17$ ,  $P = .007$ ,  $r^2 = 0.36$ ), suggesting that the disproportionate number of canopy frugivores did not drive the significant association between foraging stratum and genetic differentiation. Similarly, for species restricted to terra firma lowland tropical rain forest (canopy, four species; understory, seven species), foraging stratum showed a strongly significant relationship with cross-Andean genetic distance ( $F = 29.41$ ,  $df = 1, 9$ ,  $P < .001$ ,  $r^2 = 0.77$ ), again suggesting that foraging stratum alone is a strong predictor of cross-barrier levels of genetic differentiation. Because habitat breadth and diet were both correlated with foraging stratum, we did not include multipredictor models to test for second-order interactions.

**Table 1:** Analysis of phylogenetic dependence of variation in across-species levels of genetic differentiation (percentage genetic divergence) between populations separated by the Andes

|   | $\lambda$ | $\ln L$ | $\ln L$<br>( $\lambda = 0$ ) | $\ln L$<br>( $\lambda = 1$ ) |
|---|-----------|---------|------------------------------|------------------------------|
| Uncorrected   | .621      | -87.19  | -88.20                       | -89.92*                      |
| HKY model   | .621      | -90.20  | -91.20                       | -93.03*                      |
| Best-fit model<br>determined by<br>MODELTEST <sup>a</sup> | .000      | -124.61 | -124.61                      | -129.33*                     |

Note: The parameter  $\lambda$  is defined as a maximum likelihood estimate of the degree of correlation between a given phylogenetic inference and associated trait information mapped onto the tree. The maximum likelihood estimate of  $\lambda$  is provided, along with its log likelihood score ( $\ln L$ ). Log likelihood scores for  $\lambda$  set to both 0 (phylogenetic independence) and 1 (phylogenetic dependence) are shown.

<sup>a</sup> The best-fit models determined by MODELTEST are presented in table A3 in the online edition of the *American Naturalist*.

\* Estimated value of  $\lambda$  differs significantly ( $P < .05$ ) from constrained model ( $\lambda$  set to 0 or 1) using a log likelihood ratio test.

An AMOVA of cis-Andean populations, as defined by samples collected from opposite banks of the Amazon and Madeira rivers, showed marked variation in levels of genetic structure across species (table 3). The percentage of overall genetic variation partitioned among demes, relative to within, was significantly higher in understory species compared with those of the canopy ( $F = 21.66$ ,  $df = 1, 14$ ,  $P < .001$ ,  $r^2 = 0.61$ ). Within the Inambari region, nucleotide diversity ( $\pi$ ) in understory species was also higher in comparison with that in canopy birds ( $F = 19.12$ ,  $df = 1, 14$ ,  $P < .001$ ,  $r^2 = 0.58$ ). Because the limited sampling within the Inambari was distributed across multiple subdemes, the higher nucleotide diversity we observed in understory birds was likely due to greater substructuring relative to canopy birds. There was no significant relationship between  $\pi$  and the mean geographic distance between sampling localities ( $F = 0.28$ ,  $df = 1, 14$ ,  $P = .603$ ,  $r^2 = 0.02$ ) or with species' estimates of census size ( $F = 0.16$ ,  $df = 1, 14$ ,  $P = .691$ ,  $r^2 = 0.01$ ). The statistical significance of raggedness values, Fu's  $F_s$ , and  $R_2$  varied across species (table 3). Four canopy and two understory species exhibited evidence of historical demographic expansion. There was no predominance of expansion with either stratum (Pearson  $X^2 = 2.05$ ,  $P = .152$ ).

### Discussion

Ecological differences among species explained much of the interspecific variance in levels of genetic differentiation across three biogeographic barriers in South America. This result suggests that habitat-mediated differences in dispersal propensity between canopy and understory species

**Table 2:** Summary of univariate analyses ( $F$  statistic) of across-species *cyt b* divergences (HKY85 corrected) testing relationships with species-specific attributes and geographic distance

| Variable            | Andes<br>( $n = 40$ ) | Amazon River<br>( $n = 29$ ) | Madeira River<br>( $n = 26$ ) |
|---------------------|-----------------------|------------------------------|-------------------------------|
| Maximum elevation   | .02                   | 1.22                         | .49                           |
| <i>Várzea</i>       | 3.06                  | 4.05                         | .44                           |
| Habitat breadth     | 5.23*                 | 4.26*                        | 1.97                          |
| Forest edge         | .81                   | .12                          | .20                           |
| Foraging strata     | 36.36** (.49)         | 19.19** (.42)                | 28.49** (.54)                 |
| Diet                | 2.87                  | 3.38*                        | 3.84*                         |
| Relative abundance  | 2.60                  | .14                          | .06                           |
| Geographic distance | 1.73                  | .78                          | .15                           |

Note: Values in parentheses are  $r^2$  for terms found significant.

\* Values with nonadjusted  $P < .05$ .

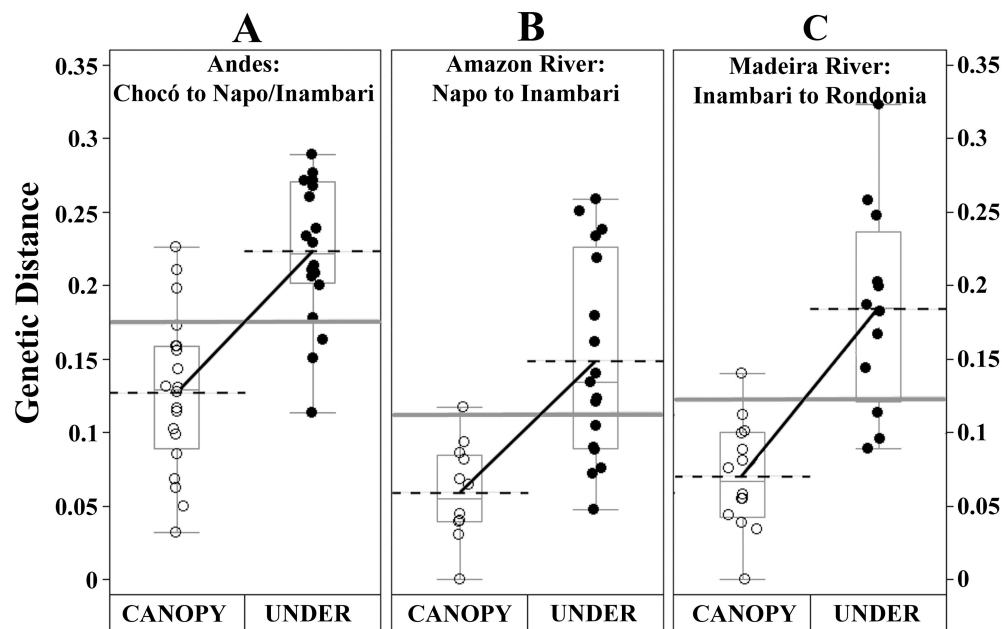
\*\* Values significant after Bonferroni correction for multiple tests both within a group ( $0.05/8$ ,  $P < .006$ ) and across all tests ( $0.05/24$ ,  $P < .002$ ).

of lowland rain forest birds have affected historical patterns of gene flow and, consequently, the amount of genetic variation between demes. The population genetic effects of geographic structuring and migration (the population genetic term for dispersal) on within- and between-deme neutral genetic variation depend on many variables, including the effective population sizes of both the metapopulation and the individual demes, the amount of migration among demes, and the length of time the population has been substructured. Restricted migration has been demonstrated theoretically to increase the amount of variation between demes within a metapopulation (Wright 1943, 1951; Whitlock and Barton 1997; Notohara 2001; Wakeley and Aliacar 2001). However, Charlesworth et al. (2003) noted that the coalescent in a structured metapopulation can be indistinguishable from that of a panmictic population if there has been sufficient time for migration to distribute ancestral lineages uniformly across demes. Matsen and Wakeley (2006) also found that structured populations with restricted migration converge to the island-model coalescent if migration tends to occur over long distances. If either of these theoretical scenarios is more applicable to canopy than to understory birds, this could explain some of the variance in among-deme genetic differentiation that we observed between species of the two foraging strata.

Because the speciation histories of the 40 species examined herein remain poorly understood, our primary population genetic inference is that the dispersal propensity in these species has had a pronounced effect on the level of genetic variation observed between demes. That genetic diversity within the Inambari area of endemism (fig. 1) was higher in understory than in canopy birds is probably indicative of greater substructuring in understory birds, even in the absence of pronounced biogeographic

barriers. Unfortunately, the number of samples from any one locality within the Inambari was limited (table 3), so we were unable to compare levels of intrademe genetic diversity between understory and canopy species. We expect that better geographic sampling within demes would illustrate isolation-by-distance effects that are suggestive of stepping-stone migration (Wakeley and Aliacar 2001) and that the isolation effects will be more pronounced in understory than in canopy birds.

Why canopy birds would have higher dispersal propensity, on average, than understory birds is explained partially by the physiognomy of lowland Neotropical terra firma forests. Differences in the community structure of many rain forest organisms (Orians 1969; Pearson 1971; Smith 1973; Terborgh 1980; Bernard 2001; Vieira and Monteiro 2003; Charles and Bassett 2005; Roisin et al. 2006) are driven by the marked contrasts in forest structure, lighting, and microclimate observed across strata (Allee 1926; Longman and Jenik 1974; Richards 1996; Madigosky 2004). Because the canopy has a two-dimensional surface with large vertical discontinuities and horizontal gaps created by treefalls (Terborgh et al. 1990; Daly and Mitchell 2000), it receives greater amounts of light and experiences more variation in light intensity than do the shaded lower strata (Endler 1993; Walther 2002b). In contrast, the forest understory is fairly uniform in height and degree of openness, with smaller-crowned and more closely spaced tree species (Terborgh et al. 1990; Richards 1996; Walther 2002a). As a consequence of these differences, canopy species tend to occur across more habitat types than do understory species, including outside the primary forest (e.g., forest edge, treefall gaps), where the two-dimensional surfaces and lighting conditions resemble the canopy exterior (Terborgh and Weske 1969; Pearson 1971; Terborgh 1980; Walther 2002a).



**Figure 2:** Box plots of the relationship of genetic distance (HKY85 corrected, square root transformed) with foraging stratum across the (A) Andes Mountains, (B) Amazon River, and (C) Madeira River. Dashed lines in each box plot indicate the group mean, and the thick gray lines within each panel highlight the grand mean. Diagonal lines connect means between canopy and understory. Solid horizontal lines within boxes identify the median sample value, and box ends are the twenty-fifth and seventy-fifth quartiles. Whiskers denote the outermost data point falling within the upper and lower quartile distances.

Greater dispersal propensity in canopy birds is also linked to spatial and temporal patterns of resource availability, which are considered more heterogeneous in the forest exterior compared with the understory (Fogden 1972; Frankie et al. 1974; Terborgh 1980, 1986; Greenberg 1981; Loiselle 1988; Levey and Stiles 1994). Differences in resource predictability across forest strata are often associated with dietary specialization, with canopy birds often exhibiting less preference than understory species (Pearson 1975; Terborgh 1980; Sherry 1984; Rosenberg 1990; Cohn-Haft and Sherry 1994). In accord with the greater heterogeneity of canopy resource availability, canopy species tend to exhibit greater fluctuations in local and seasonal abundance (Stiles 1980; Greenberg 1981; Loiselle 1988). These patterns all provide indirect evidence that canopy species have greater dispersal propensity than do understory birds.

To provide more direct insights into the relationship between dispersal propensity and canopy occurrence, we examined wing morphology in the 40 study species. Marchetti et al. (1995) found that species of *Phylloscopus* warblers with more pointed wings were more arboreal than those with rounder wings. In general, wings of higher aspect ratio (i.e., pointed wings that are long relative to their width) are expected in bird species that rely on long-distance movements, whereas short, rounded wings, which

allow for increased flight maneuverability, are associated with species found in cluttered habitats (Savile 1957). From measurements collected by C. W. Burney on study skins of the 40 species, we calculated Kipp's index ( $I_k = 100 \times \Delta S1/W$ , where  $\Delta S1$  represents the distance from first secondary to wing tip when the wing is folded and  $W$  is the length of the folded wing; see table A1), which is used commonly as a proxy for aspect ratio (Kipp 1959; Lockwood et al. 1998). In support of the greater dispersal propensity of canopy species, we found that canopy birds had a significantly lower Kipp's index (i.e., a higher aspect ratio) than did understory birds ( $F = 9.97$ ,  $df = 1, 38$ ,  $P = .003$ ,  $r^2 = 0.21$ ). Moreover, a regression of  $I_k$  with cross-Andes levels of genetic divergence revealed a significant relationship ( $F = 4.96$ ,  $df = 1, 38$ ,  $P = .032$ ,  $r^2 = 0.12$ ), further corroborating the association between dispersal propensity and genetic divergence.

Because natural history traits (Mitra et al. 1996; Seddon et al. 2008) have been implicated in explaining some of the variance in rates of cladogenesis observed across the avian tree, we investigated whether dispersal propensity influenced rates of diversification. Using subspecies as the unit of diversification (Peters 1931–1987; see table A1), we found that understory species were significantly more diverse than canopy birds ( $F = 4.60$ ,  $df = 1, 38$ ,  $P =$

**Table 3:** Hierarchical AMOVA for cis-Andean population centers and results of polymorphism and historical demographic analyses for Inambari

| Species                         | AMOVA (all areas)        |       |     |  | Polymorphism and demographics within Inambari     |                                    |                              |   |  |            |       |
|---------------------------------|--------------------------|-------|-----|--|---|------------------------------------|------------------------------|---|--|------------|-------|
|                                 | Sample size <sup>a</sup> |       |     | Variation among areas (%) <sup>b</sup> | Nucleotide diversity ( $\pi$ ; $\times 10^{-3}$ ) | Average distance (km) <sup>c</sup> | No. ind./100 ha <sup>d</sup> | Female census size ( $\times 10^6$ ) <sup>e</sup> | Tests of population expansion <sup>f</sup> |            |       |
|                                 | N                        | I     | R   |  |   |                                    |                              |   | <i>r</i>                                   | Fu's $F_s$ | $R_2$ |
| Understory:                     |                          |       |     |  |   |                                    |                              |   |  |            |       |
| <i>Baryphthengus martii</i>     | 2                        | 4 (3) | 1   | 75.5                                   | 6.4   | 700                                | 6                            | 2.12  | ...  | ...        | ...   |
| <i>Automolus ochrolaemus</i>    | 5                        | 15    | 10  | 89.6                                   | 2.9   | 658                                | 5                            | 3.53  | ...  | *          | *     |
| <i>Sclerurus mexicanus</i>      | 2                        | 5 (4) | 1   | 32.3                                   | 6.4   | 733                                | 3                            | 1.06  | ...  | ...        | ...   |
| <i>Xenops minutus</i>           | 8                        | 10    | 10  | 86.2                                   | 6.6   | 635                                | 12                           | 8.48  | ...  | ...        | ...   |
| <i>Dendrocincla fuliginosa</i>  | 1                        | 8 (6) | 2   | 37.7                                   | 4.2   | 215                                | 8                            | 2.83  | ...  | *          | *     |
| <i>Glyphorynchus spirurus</i>   | 5                        | 5 (3) | 1   | 40.7                                   | 7.6   | 267                                | 5                            | 1.77  | ...  | ...        | ...   |
| <i>Myrmotherula axillaris</i>   | 5                        | 3     | 4   | 67.4                                   | 4.5   | 144                                | 32                           | 22.6  | ...  | ...        | ...   |
| <i>Hylophilus ochraceiceps</i>  | 7                        | 5     | 2   | 85.9                                   | 5.4   | 785                                | 15                           | 10.6  | ...  | ...        | ...   |
| <i>Microcerculus marginatus</i> | 7                        | 6     | 6   | 95.1                                   | 3.1   | 748                                | 4                            | 2.83  | ...  | ...        | ...   |
| Canopy:                         |                          |       |     |  |   |                                    |                              |   |  |            |       |
| <i>Attila spadiceus</i>         | 3                        | 9     | 5   | .5                                     | 1.3   | 696                                | 8                            | 5.65  | *  | *          | *     |
| <i>Querula purpurata</i>        | 4                        | 10    | ... | 6.0                                    | .9  | 442                                | 10                           | 7.07  | ...  | ...        | ...   |
| <i>Tityra semifasciata</i>      | 1                        | 6     | 4   | 6.4                                    | 1.2   | 663                                | 8                            | 5.65  | ...  | *          | *     |
| <i>Tangara gyrola</i>           | 4                        | 10    | 4   | 53.2                                   | 3.8   | 634                                | 6                            | 4.24  | ...  | *          | ...   |
| <i>Tersina viridis</i>          | 2                        | 6     | 5   | 15.4                                   | 2.4   | 655                                | 6                            | 4.24  | ...  | ...        | ...   |
| <i>Chlorophanes spiza</i>       | 4                        | 8     | 3   | 24.2                                   | 1.8   | 566                                | 6                            | 4.24  | ...  | *          | *     |
| <i>Saltator grossus</i>         | 1                        | 5 (3) | 2   | 6.6                                    | 3.1   | 706                                | 2                            | .71   | ...  | ...        | ...   |

Note: For species with adequate sampling east of the Andes, overall genetic variation was apportioned into variation both within and among the three cis-Andean areas of endemism studied. For Inambari, the area with the most intensive sampling, levels of within-population polymorphism were estimated after accounting for within-Inambari structure. To assess whether levels of polymorphism are related to sampling effects and/or present-day demography, assessments of within-Inambari polymorphism were compared with the average distance between sampling localities and estimates of current population size of females.

<sup>a</sup> Number of individuals sampled for the three cis-Andean areas of endemism studied: N = Napo, I = Inambari, and R = Rondonia. Because known phylogeographic breaks occur within Inambari, phylogenetic analyses were used to identify major clades. For species exhibiting structure within Inambari, the clade most sampled was used in subsequent within-Inambari analyses. Adjusted sample sizes are shown in parentheses in column for I.

<sup>b</sup> Percentage of overall cis-Andean variation apportioned to variation among the three areas of endemism (equal to  $100 - \text{percent variation}_{\text{within}}$ ).

<sup>c</sup> Average pairwise geographical distance (km) across sampling localities within Inambari.

<sup>d</sup> Number of individuals per 100 ha, based on Terborgh et al. (1990).

<sup>e</sup> Estimate of census size of females, based on total area of Inambari ( $1.4 \times 10^8$  ha).

<sup>f</sup> Asterisks represent significant results ( $P < .05$ ) for tests of historical demographic expansion. Raggedness ( $r$ ) is a measure of the smoothness of the mismatch distribution, with low values of  $r$  characteristic of rapid demographic expansion. Low  $R_2$  values and large negative  $F_s$  values are also associated with demographic expansion;  $P(r)$ ,  $P(R_2)$ , and  $P(F_s)$  describe the one-tailed probability that the observed estimate is lower than expected, given a distribution of scores generated via 1,000 coalescent simulations, assuming a constant population size and incorporating an estimate of the current population genetic variation ( $\theta$ ).

.038,  $r^2 = 0.11$ ). When we excluded one canopy-dwelling outlier species that had a number of island subspecies (*Piaya cayana*), the difference in subspecies between the two foraging strata was even more significant ( $F = 11.27$ ,  $df = 1, 37$ ,  $P = .002$ ,  $r^2 = 0.23$ ). With the caveat that the number of subspecies represents a crude measure of diversity, these results suggest that rates of diversification may be higher in understory birds than in those of the canopy. Previous studies at the family level in birds found the opposite trend, linking greater dispersal to higher diversification rates (Owens et al. 1999; Phillimore et al. 2006). This conflict may result from the differences between our studies in the phylogenetic scale (macro-

evolutionary vs. microevolutionary) used to test the association. If extinction played a lesser role in shaping the diversification patterns observed within species relative to those found among species, then population-level studies may provide a more subtle view of how dispersal influences rates of diversification. However, the relationship between dispersal propensity and diversification rate also depends on the geographic context. For example, high dispersal propensity in *Zosterops* white-eyes has led to their colonization of and subsequent diversification in many islands of the Old World tropics (Moyle et al. 2009). Because the stochastic component of the variance in diversification rates is high at any taxonomic level (Ricklefs 2003), larger-

scale macroevolutionary and microevolutionary studies will be needed to further document significant associations between ecological traits and diversification rates and to understand their underpinnings. Finally, our study highlights the critical and continued need for basic natural history information in generating and testing diversification hypotheses at all taxonomic levels (Futuyma 1998).

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