COMPARATIVE PHYLOGEOGRAPHY OF NEOTROPICAL BIRDS

A Dissertation

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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, I examined genetic variation in 40 co-distributed species of lowland Neotropical rainforest birds that have populations isolated on either side of the Andes, Amazon River, and Madeira River. I found widely varying levels of genetic divergence among these taxa between the same biogeographic barriers. My investigation of the extent to which ecological traits predicted the level of cross-barrier divergence revealed a significant relationship between the forest stratum at which a species forages and the level of within-population and cross-barrier genetic differentiation. Canopy species had statistically lower divergence values across the Andes and two riverine barriers than did understory birds. I hypothesize that the association reflects an effect of dispersal propensity on the geographic structuring of genetic variation, and, consequently, on the ancestral and extant effective population sizes of each species. This is the first large-scale avian comparative study to document a significant association between ecological traits of a species and its level of genetic differentiation. I examined further the contrasting genetic patterns revealed previously by comparing the range-wide mitochondrial (mtDNA) phylogeography of two canopy and two understory species of lowland Neotropical rainforest birds. All species exhibited divergence between cross-Andean populations. Unlike canopy species, understory birds were structured at smaller spatial scales, particularly across riverine barriers of the Amazon basin. Surprisingly, estimates of isolation-by-distance, a proxy for dispersal propensity, are similar within areas of endemism for all taxa suggesting levels of gene flow are comparable through contiguous habitat in canopy and understory species. Lastly, I examined the multilocus phylogeography of three previously studied species with contrasting mtDNA patterns to investigate the role of historical demography in cross-Andean divergence.

Demographic estimates using an isolation-with-migration model suggest among-taxa variance in cross-Andean divergences reflects a history of staggered isolation versus a simultaneous isolating event. Nuclear sequence data reveal asymmetrical gene flow in two species marked by relatively shallow cross-Andean divergence, further evidence of differential effectiveness of the Andes as a barrier to gene flow among co-distributed taxa.

CHAPTER 1: INTRODUCTION

The rich landscape of the equatorial Neotropics has a dynamic history that offers unparalleled opportunities to explore the changing earth's role in shaping the evolution of birds. The Andean Cordillera effectively isolates tracts of lowland tropical rainforest west of the Andes from the expansive complementary forest of the Amazon Basin. This divide is relatively young as the northern Andes were only half their present elevation approximately 4 million years ago (Guerrero 1997; Gregory-Wodzicki 2000). This recent orogeny rerouted major watercourses to form the modern eastern-flowing Amazonian drainage (Hoorn et al. 1995; Campbell et al. 2006). These geographical features, the Andes and the river courses of Amazonia, are critical in the divergence of populations and the speciation process since they often form taxonomic boundaries for a wide range of lowland rainforest biota (Chapman 1917; Chapman 1926; Haffer 1969; Haffer 1974; Cracraft 1985; Cracraft and Prum 1988). In addition, the uplift of the Panamanian Isthmus approximately 3 million years ago united tracts of lowland tropical rainforest providing an intercontinental corridor for overland dispersal (Duque-Caro 1990; Coates and Obando 1996; Coates et al. 2004). The complex physiography of the Neotropics is thought to have promoted the recent burst of faunal differentiation and, consequently, generated the highest alpha and gamma species diversity of any ecogeographic unit (Pearson 1977; Terborgh 1980a; Remsen and Parker 1983; Terborgh et al. 1990).

For my dissertation, I examined this diversity using a comparative phylogeographic approach, which involves examining intraspecific patterns of genetic structure across multiple co-distributed taxa (Avise et al. 1987a; Bermingham and Moritz 1998; Avise 2000; Arbogast and Kenagy 2001). The overarching goal was to examine processes, both recurrent and historical, associated with biogeography, ecology, and demography in shaping spatiotemporal patterns of genetic variation. To do this, I investigated similarities in across-taxon patterns of genetic variation to detect influences at regional levels that may signify shared responses to historical events. In addition, I employed a large number of species and examined across-taxa differences in genetic variation to statistically test for species-specific correlates of the observed variance in genetic parameters. For my study taxa, I concentrated on co-distributed species of lowland tropical rainforest birds with cross-Andean populations. This design allowed me to focus on a community of relatively closely related species that have shared biogeographic history, comparable rates of evolution, and fewer differences in life-history traits, thus allowing for more robust tests of relationship between ecology and evolution (Bohonak 1999).

All three chapters of my dissertation were aimed at addressing the different processes shaping patterns of geographic variation with special emphasis on cross-Andean divergence. The partitioning of chapters is based largely on the scale of the dataset and, thus, the question being addressed. In the first chapter, I examine species-specific correlates of cross-Andean mitochondrial (mtDNA) divergence for a taxonomically- and ecologically-diverse assemblage of 40 lowland rainforest species. In the second chapter, I selected four taxa (two understory and two canopy) with relatively large range-sizes (Mexico to Amazonia) and with differing levels of cross-Andes genetic differentiation to explore continental-scale phylogeographic patterns in mtDNA. In the final chapter, I use multilocus, multi-allelic nuclear data to examine the comparative phylogeography of three species that have widely varying cross-Andes divergences in mtDNA. The multilocus dataset allowed me to better address the error associated with coalescent and demographic uncertainties (Rosenberg and Nordborg 2002).

CHAPTER 2: ECOLOGY PREDICTS LEVELS OF GENETIC DIFFERENTIATION IN NEOTROPICAL BIRDS

INTRODUCTION

The ecology of a species influences the effective size of populations and the pattern of gene flow among them (Caballero 1994; Turner and Trexler 1998; Bohonak 1999), which, in turn, determines both the amount and spatiotemporal distribution of neutral genetic variation found within and between populations (Wright 1951; reviewed in Charlesworth et al. 2003). Despite the theoretical link between the ecology and population genetics of species (Avise et al. 1987b; Palumbi 1992), little empirical evidence corroborates the association (Loveless and Hamrick 1984; Hamrick and Godt 1996). This is partly because the amount of intraspecific genetic variation, both within and between populations, is influenced by past and present demography as well as a multitude of confounding, potentially opposing, evolutionary processes including genetic drift, gene flow, and mutation (Slatkin 1987; Bossart and Prowell 1998). And 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, I directly address the influence of ecology on evolution by employing a comparative approach.

Comparisons across taxa, particularly among closely related species, provide a means of testing the influence of ecological variables on population genetic differentiation (Turner and Trexler 1998). By treating each species as an independent measure of the ecological correlate of interest, it is possible to evaluate statistical associations between ecological factors and levels of genetic differentiation. The comparative method has typically been used to assess patterns of genetic variation across a relatively small number of species (Dawson et al. 2002; Brouat et al. 2003; Whiteley et al. 2004; Goetze 2005; Lourie et al. 2005; Richards et al. 2007). However, the advantages of this approach are more apparent in comparisons across large numbers of taxa (Peterson and Denno 1998; Turner and Trexler 1998; Bohonak 1999; Moller et al. 2008).

I 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 in taxonomy, with most lowland bird populations on either side of the Andes, the Amazon River, and the Amazon's larger tributaries recognized as distinct taxa (Chapman 1917; Chapman 1926; Haffer 1969; Haffer 1974; Traylor 1979; Cracraft 1985; Cracraft and Prum 1988). The Andes extend in a north-south axis along the entire western margin of South America and effectively isolate the lowland tropical rainforests west of the Andes (*trans*-Andean region) from those east of the Andes (*cis*-Andean; Figure 2.1). 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 rainforests 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 rainforest birds revealed that these physical barriers partition genetic variation of co-distributed taxa similarly (Capparella 1988; Capparella 1991; Brumfield and Capparella 1996; Hackett and Lehn 1997; Marks et al. 2002; Pereira and Baker

2004; Cheviron et al. 2005b; Eberhard and Bermingham 2005; Ribas et al. 2005). Despite this spatial congruence, the interspecific variation in levels of genetic differentiation between allopatric lineages diverging in concert due to the same emergent barriers 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 (Leache et al. 2007), but the combined effects of the coalescent process (Donnelly and Tavare 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 vicariant event (Hickerson et al. 2006a). Here, I examined how the variance in levels of genetic differentiation among the 40 species is partitioned with respect to these factors.

METHODS

Study Species and Molecular Data Collection

I examined 40 species of Neotropical birds with cross-Andean distributions (Appendix A). All breed regularly in *terra firma* forest (tropical lowland evergreen forest; using the classification of Stotz et al. 1996). To maximize taxonomic diversity, I selected species representing 20 families and seven orders. Within the major clades of birds (e.g. thamnophilid antbirds), I included species with differing ecologies (e.g. canopy versus understory) 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

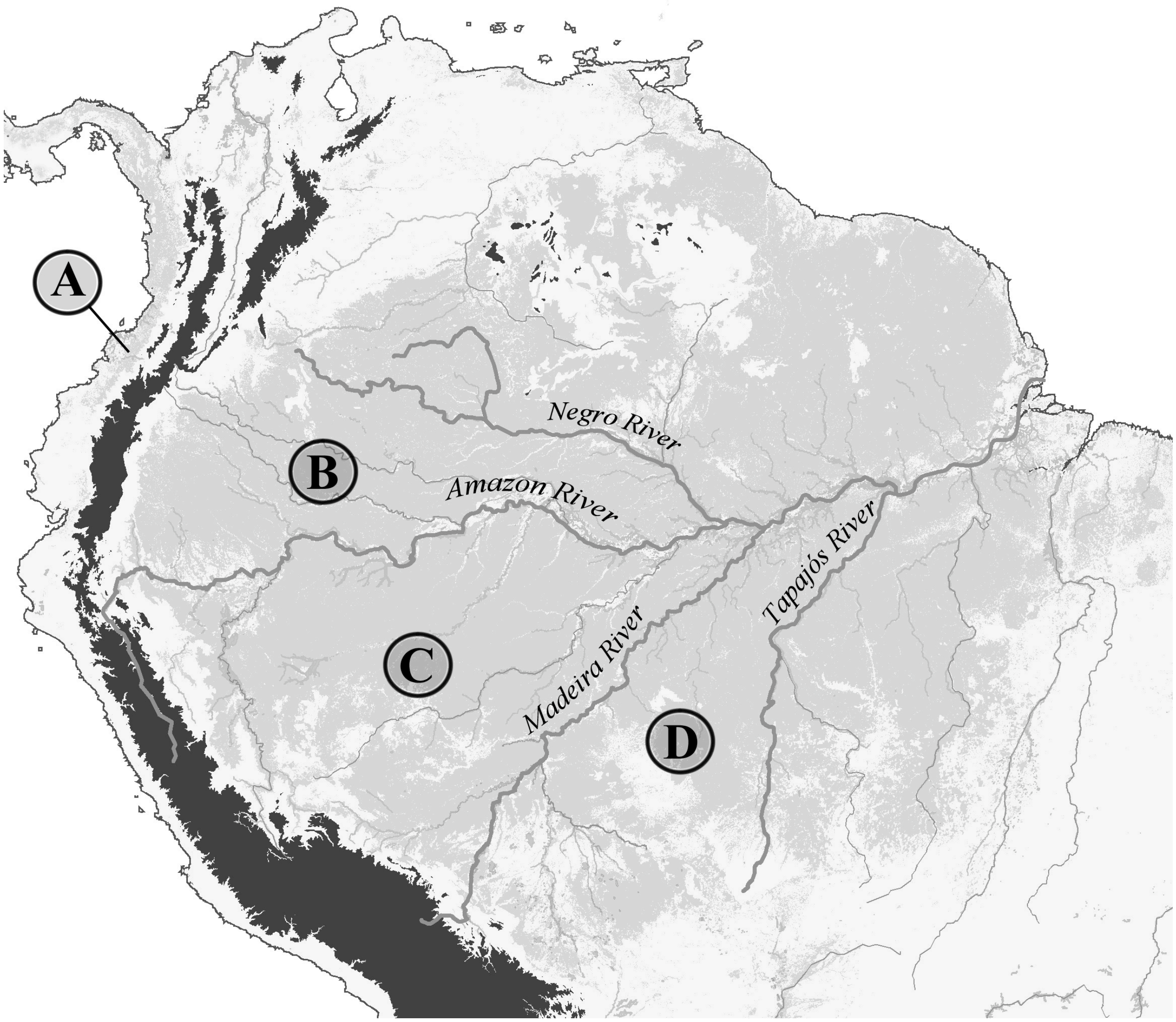


Figure 2.1 Present distribution of lowland moist forest (dark gray) in northern South America (Eva et al. 1999). Mountains above 2000 m elevation are in black. Sampling localities of the 40 study taxa confined to four areas of endemism described by Cracraft (1985): (A) Chocó; (B) Napo; (C) Inambari; and (D) Rondonia.

of the Amazon (Figure 2.1). Where species' ranges and holdings in collections allowed, I sampled individuals from populations on opposite sides of each of the three barriers of interest (Appendix B). 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 multi-locus instead of single-locus measurements of genetic diversity in reducing the variance of population genetic parameter estimates (Brumfield et al. 2003), but I opted to maximize taxonomic diversity at the cost of measurement precision within each species. This was justified in that the statistical effect on my 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.

I extracted DNA from ~25 mg of tissue using the Qiagen DNeasy Tissue Kit (QIAGEN, Inc., Valencia, CA). The polymerase chain reaction (PCR) was used to amplify cytochrome *b* for each individual. PCR amplifications (25 μL) consisted of: 2.5 μL template DNA (~50 ng), 0.3 μL each primer (10 mM, Appendix A), 0.5 μL dNTPs (10 mM: 2.5 mM each dATP, dTTP, dCTP, dGTP), 2.5 μL 10X with $MgCl_2$ reaction buffer (15 mM), 0.1 *Taq* DNA polymerase (5 U/μL AmpliTaq, Applied Biosystems Inc., Foster City, CA), and 18.7 μL sterile dH_2O. PCR temperature profiles consisted of an initial denaturation of 2 min at 94°C followed by 35 cycles of 30 sec at 94°C, 30 sec 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% poly-ethylene glycol (PEG), then cycle-sequenced using 1.75 μL 5X sequencing buffer (ABI), 1 μL sequencing primer (10mM, Appendix A), 2.25 μL template, 0.35 μL Big Dye Terminator Cycle-Sequencing Kit version 3.1 (ABI), and 1.65 μL sterile dH_2O for a total volume of 7 μL. Cycle-sequenced reactions were cleaned using Sephadex (G-50 fine) columns and analyzed on an ABI 3100 Genetic Analzyer. Consensus sequences were compiled from both forward and reverse sequences. Contigs for each individual were assembled and edited using Sequencer version 4.6 (GeneCodes, Ann Arbor, MI) and the entire length of each sequence was examined by eye to confirm base calls. The cyt *b*-coding region was checked in Sequencer 4.6 for the presence of stop codons to confirm open reading frames.

Estimating Levels of Cross-Barrier Genetic Divergence

PAUP* 4.0b10 (Swofford 2001) was used to calculate three pairwise genetic distance measures between individuals composing populations: (1) uncorrected (*p*-distance); (2) the HKY85 finite-sites substitution model (Hasegawa et al. 1985); and the best-fit finite-sites substitution model (Table 2.2) determined using the BIC test implemented in ModelTest 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). Due to sampling and range limits, the number of species incorporated in each of the three comparisons varied (Table 2.4).

Multi-predictor Models of Genetic Divergence

To assess ecological correlates of genetic differentiation I examined species-specific attributes associated with habitat, diet, and relative abundance (Appendix A). Because an organism’s dispersal potential determines the effectiveness of a physical barrier (Mayr 1963) I also included ecological variables that are 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, I included the maximum elevation of a species’ known geographic distribution as a continuous variable. Although untested empirically, one might expect lowland species whose distribution extends to higher elevations (e.g.

the Andean foothills) to more readily traverse mountain barriers relative to species restricted to lower elevations.

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 (non-flooded). This prediction was based on the river-delineated patterns of genetic differentiation revealed in understory species of *terra firma* forest, as well as anecdotal observations concerning the lack of phenotypic variation in populations along opposite banks of the Amazon River in bird species of *várzea* forest. Additional support for this prediction comes from *Xiphorhynchus* woodcreepers, where species inhabiting *várzea* forest were genetically undifferentiated across riverine barriers compared to closely related species restricted to *terra firma* forest (Aleixo 2004; Aleixo 2006). Therefore, I included as a binary variable whether a species uses *várzea* forest as a preferred habitat in addition to *terra firma* forest.

Habitat Breadth. The number of different habitats a species occupies may be positively correlated with dispersal propensity. The idea that habitat generalists are more likely than habitat specialists to cross ecotones or gaps in habitats is supported by several studies (reviewed in Harris and Reed 2002). I counted the total number of preferred habitats (defined as habitat types where a species occurs or breeds in 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. As with habitat breadth, 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). I therefore included the use of edge habitat as a binary variable.

Foraging Stratum. The vertical edges of the forest are often equated to the horizontal surfaces of the canopy (Pearson 1971; Levey and Stiles 1992; Cohn-Haft and Sherry 1994; Walther 2002a). Studies suggest canopy species of the open, more exposed treetops show less inhibition crossing gaps in habitat than understory species (reviewed in Harris and Reed 2002). Capparella (1991) observed that canopy birds, similar to *várzea* species, lacked phenotypic differences across the Amazon River and suggested this was due to cross-river dispersal. In contrast, Hayes and Sewlal (2004) used raw taxonomic boundaries to examine the efficacy of the Amazon River as an isolating barrier and found no significant difference between understory and canopy forest birds. However, current taxonomy is based primarily on morphology and may not adequately reflect patterns of genetic differentiation that may be incongruent with bird plumage (Capparella 1991; Seutin et al. 1993; Joseph et al. 2001; Marks et al. 2002). I therefore 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. In birds, frugivores may travel long distances and consequently show marked fluctuation in seasonal abundance in response to changes in fruit availability (Blake and Loiselle 1991; Moegenburg and Levey 2003; Haugaasen and Peres 2007). In contrast, 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). I classified each species as belonging to one of three diet categories (frugivore, insectivore, and omnivore) based on natural history literature.

Relative Abundance. The effective size of populations (N_e), both ancestral and present, affects the timing of gene divergences that precede the actual separation of diverging populations (Edwards and Beerli 2000). I used the relative abundance for a species, described by Stotz et al. (1996), as a proxy for N_e, assuming total population sizes have remained constant through time. Although not a consistent approximation of long-term effective population size, a species' relative abundance can highlight its susceptibility to local extinction and other demographic fluctuations that affect patterns of genetic variation, and hence, estimates of effective population size in both divided and undivided populations (Whitlock and Barton 1997). Here, the timing of cyt *b* divergence (deep versus shallow) is predicted to have a positive association with relative abundance. 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 (GLMs) 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 dataset, an additional transformation (square-root) was required to achieve normality. All variables (Table 2.1) were considered fixed effects. Each variable was first tested for a one-way association with the across-species genetic divergence values. Variables showing $P < 0.15$ were then reanalyzed in multi-predictor models to

Table 2.1 List of variables.

Variable	Type	Values
Maximum elevation	Continuous	(meters)
Várzea	Categorical	Yes, No
Habitat breadth	Categorical	One, Two, Three or more
Forest edge	Categorical	Yes, No
Foraging stratum	Categorical	Understory, Canopy
Diet	Categorical	Frugivore, Insectivore, Omnivore
Relative abundance	Categorical	Common, Fairly common, Uncommon
Geographic distance	Continuous	(kilometers)

Table 2.2 Best-fit model including parameters for all 40 taxa.

Species	Model	Base Frequencies[a]	TI/TV Ratio	Rate Matrix[b]	Shape	Pinv
Crypturellus soui	HKY+I	0.2653, 0.3222, 0.1225	5.2056	equal	-	0.7804
Patagioenas subvinacea	HKY	0.2641, 0.3523, 0.1317	5.2×10^{36}	equal	-	-
Geotrygon saphirina	HKY	0.2734, 0.3553, 0.1211	11.7518	equal	-	-
Pyrrhura melanura	F81	0.2743, 0.3581, 0.1295	-	equal	-	-
Pionus menstruus	HKY	0.2746, 0.3681, 0.1259	5.0×10^{36}	equal	-	-
Amazona farinosa	HKY	0.2692, 0.3491, 0.1386	2.1653	equal	-	-
Piaya cayana	HKY	0.2883, 0.3340, 0.1273	3.8557	equal	-	-
Trogon collaris	HKY	0.2922, 0.3247, 0.1206	4.306	equal	-	-
Trogon rufus	HKY+I	0.2772, 0.3417, 0.1218	18.7553	equal	-	0.8188
Baryphthengus martii	TrN+G	0.2611, 0.3523, 0.1309	-	1.0, 20.4, 1.0, 1.0, 9.6	0.1699	-
Automolus ochrolaemus	HKY+I	0.2835, 0.3127, 0.1243	10.8676	equal	-	0.8168
Automolus rubiginosus	HKY	0.2859, 0.3016, 0.1274	8.7134	equal	-	-
Sclerurus mexicanus	HKY+I	0.2884, 0.3204, 0.1238	12.1958	equal	-	0.7791
Xenops minutus	TrN+G	0.2939, 0.2949, 0.1185	-	1.0, 9.7, 1.0, 1.0, 27.6	0.0904	-
Dendrocincla fuliginosa	K81uf	0.2940, 0.3022, 0.1327	-	1.0, 1.4×10^{12}, 1.4×10^{11}, 1.4×10^{11}, 1.4×10^{11}	-	-
Glyphorynchus spirurus	HKY+G	0.2991, 0.3165, 0.1227	8.6512	gamma	0.1557	-
Cymbilaimus lineatus	HKY	0.2810, 0.3074, 0.1273	36.2921	equal	-	0
Taraba major	HKY+I	0.2793, 0.3211, 0.1260	19.6957	equal	-	0.8097
Myrmotherula ignota	HKY	0.2832, 0.3381, 0.1264	6.5555	equal	-	-
Myrmotherula axillaris	HKY	0.2783, 0.3273, 0.1244	4.8574	equal	-	-
Colonia colonus	HKY	0.2728, 0.3237, 0.1230	11.7141	equal	-	-
Attila spadiceus	HKY	0.2769, 0.3166, 0.1208	3.2351	equal	-	-
Querula purpurata	HKY	0.2703, 0.3283, 0.1257	5.2×10^{36}	equal	-	-
Lepidothrix coronata	HKY+I	0.2703, 0.2998, 0.1255	11.5216	equal	-	0.7886
Tityra inquisitor	HKY	0.2848, 0.3080, 0.1220	13.826	equal	-	-
Tityra semifasciata	HKY	0.2859, 0.2977, 0.1177	5.1×10^{36}	equal	-	-
Schiffornis turdina	HKY	0.2589, 0.3180, 0.1329	14.2881	equal	-	0
Hylophilus ochraceiceps	HKY+I	0.3269, 0.3374, 0.1225	6.8565	equal	-	0.8232
Microcerculus marginatus	HKY+I	0.2833, 0.3487, 0.1368	8.2575	equal	-	0.8325
Henicorhina leucosticta	HKY+I	0.2736, 0.3575, 0.1306	25.48	equal	-	0.8642
Microbates cinereiventris	HKY+I	0.2829, 0.3427, 0.1380	3.2938	equal	-	0.808
Tangara gyrola	HKY+I	0.2726, 0.3538, 0.1385	11.5431	equal	-	0.8918
Tangara cyanicollis	HKY	0.2638, 0.3467, 0.1414	6.0816	equal	-	0
Tersina viridis	HKY	0.2670, 0.3593, 0.1344	5.1×10^{36}	equal	-	0
Cyanerpes caeruleus	TrN	0.2591, 0.3693, 0.1355	-	1.0, 105.5, 1.0, 1.0, 36.3	-	0
Chlorophanes spiza	HKY	0.2649, 0.3611, 0.1334	7.5192	equal	-	0
Arremon aurantiirostris	HKY+I	0.2608, 0.3699, 0.1272	8.0129	equal	-	0.818
Saltator grossus	HKY+I	0.2727, 0.3362, 0.1375	5.0947	equal	-	0.821
Phaethlypis fulvicauda	HKY+I	0.2769, 0.3456, 0.1308	9.3691	equal	-	0.8381
Psarocolius angustifrons	HKY	0.2630, 0.3372, 0.1406	9.3881	equal	-	0

Note: For each taxa, a neighbor-joining tree was estimated using PAUP*v4.0b10 (Swofford 1998) and likelihood scores calculated for a series of nested substitution models. The best-fit model was determined by the Bayesian Information Criterion (BIC) implemented in ModelTest 3.8 (Posada and Crandall 1998).

[a] Order of base frequencies is A, C, G, T.

[b] Order of rate matrix is A to C, A to G, A to T, C to G, C to T, and G to T.

test for second-order interactions. All analyses were computed with JMP statistical package, version 5.0.1.2 (SAS Institute Inc., 2003).

Analyses of Genetic Variation between and within *cis*-Andean Populations

For 16 species (Table 2.5) with adequate sampling across *cis*-Andean regions (Figure 2.1), I 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 analysis of molecular variance (AMOVA; Excoffier et al. 1992) in ARLEQUIN v. 3.1. This program was used to calculate the percentage of variation within and among the three *cis*-Andean populations.

I 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, see Cracraft 1985). Phylogeographic breaks are known to occur within this region (Marks et al. 2002; Cheviron et al. 2005b) and, if present, could confound analyses of within-population genetic variation. Therefore, I first assessed population genetic structure through maximum likelihood (ML) phylogenetic analyses (heuristic search using HKY85 model, TBR branching-swapping, and support for nodes assessed with 100 bootstrap iterations) using PAUP* 4.0b10 (Swofford 2001) to identify major haplotype clades within Inambari. For species exhibiting structure within the region, I included in subsequent analyses only the phylogroup with the largest sample size. Levels of nucleotide diversity (π ; Nei 1987) were calculated within Inambari using DNASP v. 4.50.2 (Rozas et al. 2003). Historical demographic expansion was inferred by the raggedness index (Harpending 1994), Fu's F_S (Fu 1997), and R_2 (Ramos-Onsins and Rozas 2002) using DNASP.

Tests of Rate Heterogeneity

Rates of molecular evolution can differ among phylogenetic groups (Wu and Li 1985; Britten 1986; Li and Wu 1987; Gillooly et al. 2005; Pereira and Baker 2006b; Pereira and Baker 2006a). Although rate heterogeneity across taxa is believed to be more prevalent with increasing phylogenetic scale, there remains considerable debate surrounding the consistency of molecular clocks, even within closely related taxonomic groups (Martin 1995; Bromham et al. 1996; Nunn and Stanley 1998; Witt 2004). Concerning cross-barrier divergences, species with more rapid rates of molecular evolution would have deeper divergences relative to species with coincidental patterns of geographic isolation but slower rates.

I first examined the degree to which variation in cross-Andean divergences are related to phylogenetic history. In the case of rate heterogeneity across lineages, I would expect across-species patterns of genetic divergence to exhibit a phylogenetic signal. My phylogenetic tree of the 40 study species was based primarily on the DNA-DNA hybridization-based tree of Sibley and Ahlquist (1990) and the recently published phylogeny by Hackett et al. (2008). Combined, these studies accommodated the taxonomic breadth of my sampling design by providing higher order relationships among families as well as branch lengths. Given concerns over methodology, particularly with DNA-DNA hybridization (Houde 1987; Harshman 1994; Barker et al. 2004), published family-level phylogenies were used to improve inferences among lower phylogroups whenever possible (Figure 2.2).

To assess phylogenetic signal regarding rate heterogeneity, I used a generalized least squares (GLS) analysis to test whether estimates of genetic divergence across the comparative data set exhibited phylogenetic dependence (Pagel 1999; Freckleton et al. 2002). A single multiplier, λ, is adjusted to measure the degree by which traits (levels of genetic divergence) vary/co-vary across

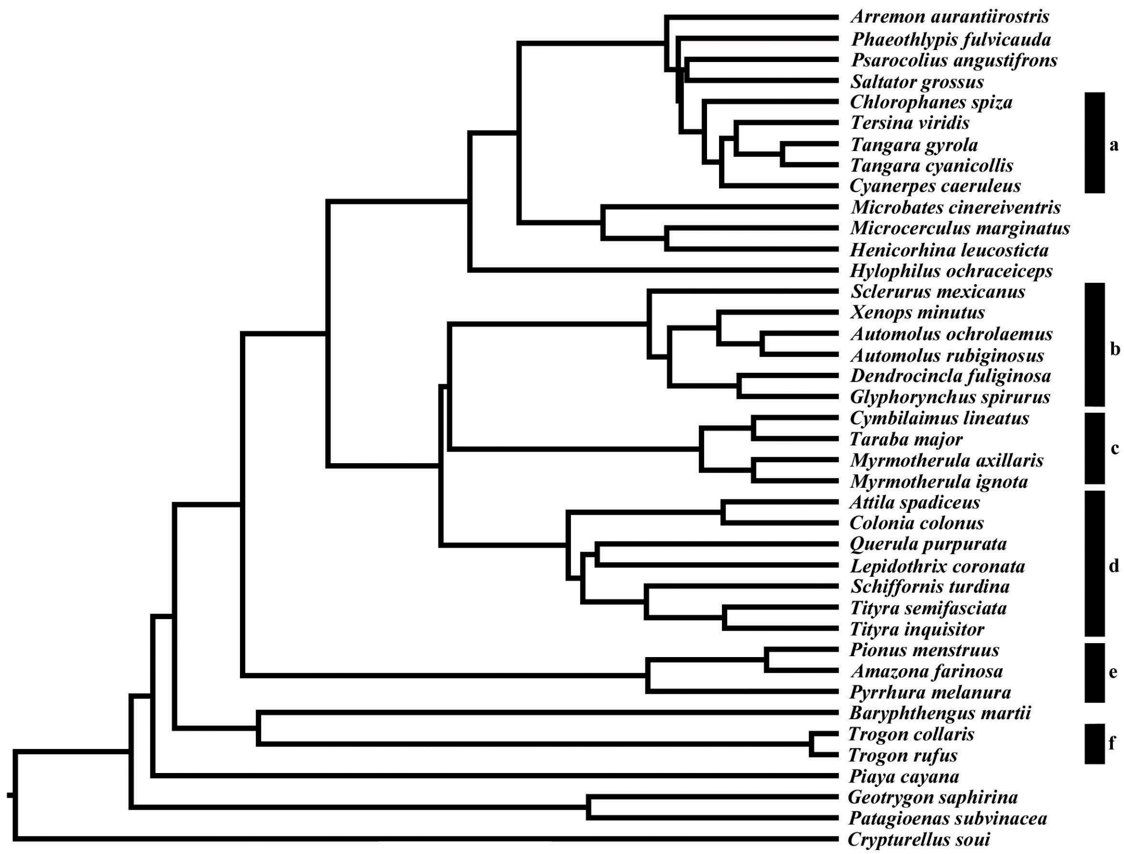


Figure 2.2 Phylogeny of 40 study species based primarily on phylogenetic inferences using DNA-DNA hybridization by Sibley and Ahlquist (1990) and DNA sequence data from Hackett et al. (2008). Where possible, additional phylogenies were incorporated to improve the inferred historical relationships within lower-level phylogenetic groupings.

[a] Burns, K. J. 1997. Molecular systematics of tanagers (Thraupinae): Evolution and biogeography of a diverse radiation of neotropical birds. Molecular Phylogenetics and Evolution 8:334-348; Burns, K. J., and K. Naoki. 2004. Molecular phylogenetics and biogeography of Neotropical tanagers in the genus Tangara. Molecular Phylogenetics and Evolution 32:838-854.

[b] Chesser, R. T. 2004. Molecular systematics of New World suboscine birds. Molecular Phylogenetics and Evolution 32:11-24; Brumfield unpublished.

[c] Brumfield unpublished.

[d] Ericson, P. G. P., D. Zuccon, J. I. Ohlson, U. S. Johansson, H. Alvarenga, and R. O. Prum. 2006. Higher-level phylogeny and morphological evolution of tyrant flycatchers, cotingas, manakins, and their allies (Aves: Tyrannida). Molecular Phylogenetics and Evolution 40:471-483; Tello, J. G., and J. M. Bates. 2007. Molecular phylogenetics of the tody-tyrant and flatbill assemblage of tyrant flycatchers (Tyrannidae). Auk 124:134-154..

[e] Tavares, E. S., A. J. Baker, S. L. Pereira, and C. Y. Miyaki. 2006. Phylogenetic relationships and historical biogeography of Neotropical parrots (Psittaciformes: Psittacidae: Arini) inferred from mitochondrial and nuclear DNA sequences. Systematic Biology 55:454-470.

[f] de los Monteros, A. E. 1998. Phylogenetic relationships among the trogons. Auk 115:937-954.

the phylogenetic tree assuming a "Brownian motion" model of evolution. A value of $\lambda = 1$ indicates traits are evolving across the tree in line with a Brownian process and that phylogeny must be accounted for in further comparative analyses. Conversely, $\lambda = 0$ suggests the given traits exhibit no phylogenetic dependence. A likelihood ratio test was performed to test for significant departure of the likelihood score obtained using an estimated λ and scores given a restricted model where λ was set to 0 (phylogenetic independence) and 1 (phylogenetic dependence).

Rate heterogeneity across lineages, particularly for mitochondrial markers, has also been associated with metabolic rate (Martin and Palumbi 1993). In birds, Nunn and Stanley (1998) revealed a negative relationship between body size, used as a proxy for metabolism, and rates of substitution in cyt *b*. However, Witt (2004) found no evidence linking metabolism and rates of molecular evolution in a large-scale comparative analysis of Neotropical birds. Recently, Weir and Schluter (2008) also examined cyt *b* and found the variance in rates across lineages was not explained by differences in body size. Because results remain equivocal, I tested for potential associations in my data by regressing cross-Andean genetic divergence (square-root transformed) with body mass (log-transformed). For each species, bird mass was calculated using specimens from the Louisiana State University Museum of Natural Science (Appendix A).

RESULTS

I present results using the HKY85 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 2.4). Cross-barrier genetic distances across species varied from 0.0 to 0.104 (Andes: $n = 40$, $\bar{x} = .035$, SD = .024, min = .001, max = .084; Amazon: $n = 29$, $\bar{x} = .018$, SD = .020; Madeira: $n = 26$, $\bar{x} = .021$, SD = .025). Phylogenetic analyses revealed no evidence of phylogenetic dependence

Table 2.3 Analysis of phylogenetic dependence of variation in across-species levels of genetic differentiation (untransformed) between populations separated by the Andes.

	λ	ln *L*	ln *L* (λ = 0)	ln *L* (λ = 1)
Uncorrected	0.621	97.02	96.01	94.29 *
Hasegawa-Kishino-Yano (HKY) model	0.621	94.00	93.00	91.17 *
Best-fit model determined by ModelTest 3.8	0.000	59.60	59.60	54.87 *

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

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

regarding variation in across-species levels of genetic differentiation (Table 2.3). In addition, there was no significant relationship between genetic divergence and log-transformed mass (F = 2.684; df = 1,38, r^2 = .066, P = .110).

I found that canopy species had significantly lower levels of cross-barrier genetic divergence than did understory species (Table 2.4, Figure 2.3). 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 = 10.837, P = .004), and frugivores were largely composed of canopy species (Pearson X^2 = 6.234, P = .044). When controlling for multiple tests using Bonferroni correction, both habitat breadth and diet showed no significant relationship with levels of genetic divergence. Within insectivores (canopy = 5 species, understory = 14 species), foraging stratum was significantly associated with cross-Andean gene divergences (F = 9.402; df = 1,17, r^2 = .356, P = .007) 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 rainforest (canopy = 4 species, understory = 7 species), foraging stratum showed a strongly significant relationship with cross-Andean genetic distance (F = 29.413; df = 1,9, r^2 = .766, P = .0004), again suggesting 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, I did not include multi-predictor models to test for second-order interactions.

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 2.5). The percentage of overall genetic variation partitioned among populations, relative to within, was significantly higher in understory species compared to those of

Table 2.4 Results of One-way ANOVA (*p*-distance, HKY-corrected, and Best-fit Model)

		Andes	Amazon River	Madeira River
	n =	40	29	26
Maximum elevation, m	*p*-distance	0.0182	1.2208	0.4648
	HKY	0.0224	1.2215	0.4915
	Best-fit Model[a]	0.5172	1.2847	0.2185[b]
Várzae	*p*-distance	3.0764	4.0585	0.4017
	HKY	3.0604	4.0450	0.4348
	Best-fit Model[a]	2.3884	3.7270	0.1646
Habitat breadth	*p*-distance	5.2055 *	4.2889 *	1.9714
	HKY	5.2272 *	4.2545 *	1.9673
	Best-fit Model[a]	5.8995 **	4.1529 *	1.0836[b]
Forest edge	*p*-distance	0.8006	0.1197	0.1962
	HKY	0.8139	0.1165	0.1981
	Best-fit Model[a]	1.1904	0.0556	0.6260[b]
Foraging strata	*p*-distance	37.2539 *** (0.49)	19.2183 *** (0.42)	28.8257 *** (0.55)
	HKY	36.3548 *** (0.49)	19.1894 *** (0.42)	28.4850 *** (0.54)
	Best-fit Model[a]	30.9882 *** (0.45)	18.4715 *** (0.41)	28.6374 *** (0.55)[b]
Feeding guild	*p*-distance	2.8551	3.3758 *	3.8886 *
	HKY	2.8697	3.3785 *	3.8381 *
	Best-fit Model[a]	2.9410	3.5011 *	3.0906[b]
Relative abundance	*p*-distance	2.5248	0.1476	0.0571
	HKY	2.6042	0.1378	0.0567
	Best-fit Model[a]	1.8297	0.0625	0.0834[b]
Geographic distance, km	*p*-distance	1.7237	0.7460	0.1304
	HKY	1.7289	0.7792	0.1479
	Best-fit Model[a]	2.5109	1.0846	0.1340[b]

[a] Best-fit model determined using the AIC test implemented in ModelTest 3.8 (Posada and Crandall 1998). See Table 2.2 for selected model for each taxa.

[b] outlier removed (*Hylophilus ochraceiceps*)

* Values with non-adjusted $P < .05$

** Bonferroni correction within a group (0.05/8, $P < .0062$)

*** Bonferroni correction across all tests (0.05/24, $P < .0021$)

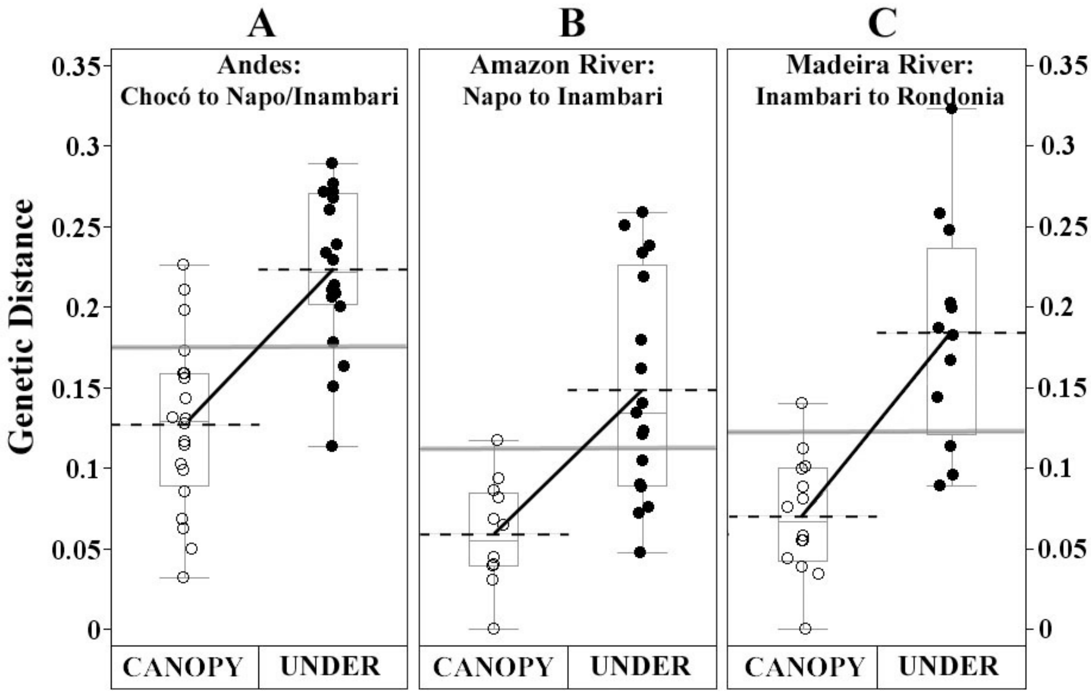


Figure 2.3 Box plot of the relationship of genetic distance (HKY85-corrected, square-root transformed) with foraging stratum across the A) Andes Mountains; B) Amazon River; and C) Madeira River. Dashed lines in each box plot indicate the group mean and the broad gray lines within each panel highlight 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 25th and 75th quartiles. Whiskers denote the outermost data point falling within the upper and lower quartile distances.

Table 2.5 Hierarchical analysis of molecular variance (AMOVA) for *cis*-Andean population centers and results of polymorphism and historical demographic analyses for Inambari.

Species	AMOVA (all areas)				Polymorphism & demographics within Inambari						
	Sample Size[a]			% Variation Among Areas[b]	Nuc. div., π[c] ($\times 10^{-3}$)	Avg. dist. (km)[d]	No. inds. /100 ha[e]	Female Census Size[f] ($\times 10^{6}$)	Tests of pop. expansion[g]		
	N	I	R						r	Fu's F_s	R_2
Understory:											
Baryphthengus martii	2	4 (3)	1	75.5	6.4	700	6	2.12	-	-	-
Automolus ochrolaemus	5	15	10	89.6	2.9	658	5	3.53	-	*	*
Sclerurus mexicanus	2	5 (4)	1	32.3	6.4	733	3	1.06	-	-	-
Xenops minutus	8	10	10	86.2	6.6	635	12	8.48	-	-	-
Dendrocincla fuliginosa	1	8 (6)	2	37.7	4.2	215	8	2.83	-	*	*
Glyphorynchus spirurus	5	5 (3)	1	40.7	7.6	267	5	1.77	-	-	-
Myrmotherula axillaris	5	3	4	67.4	4.5	144	32	22.6	-	-	-
Hylophilus ochraceiceps	7	5	2	85.9	5.4	785	15	10.6	-	-	-
Microcerculus marginatus	7	6	6	95.1	3.1	748	4	2.83	-	-	-
Canopy:											
Attila spadiceus	3	9	5	0.5	1.3	696	8	5.65	*	*	*
Querula purpurata	4	10	-	6.0	0.9	442	10	7.07	-	-	-
Tityra semifasciata	1	6	4	6.4	1.2	663	8	5.65	-	*	*
Tangara gyrola	4	10	4	53.2	3.8	634	6	4.24	-	*	-
Tersina viridis	2	6	5	15.4	2.4	655	6	4.24	-	-	-
Chlorophanes spiza	4	8	3	24.2	1.8	566	6	4.24	-	*	*
Saltator grossus	1	5 (3)	2	6.6	3.1	706	2	0.71	-	-	-

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 to the average distance between sampling localities and estimates of current population size of females.

[a] Number of individuals sampled for the three *cis*-Andean areas of endemism studied: Napo ("N"), Inambari ("I"), and Rondonia ("R"). Since 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 "I", see Supplementary Materials (S#) for details.

[b] Percentage of overall *cis*-Andean variation apportioned to variation among the three areas of endemism (equal to 100 minus % $\text{Variation}_{\text{within}}$).

[c] Nucleotide diversity (π) within Inambari.

[d] Average pairwise geographical distance (km) across sampling localities within Inambari.

[e] Number of individuals per 100 hectares based on Terborgh et al. (1990).

[f] Estimate of census size of females based on total area of Inambari (1.4×10^{8} hectares).

[g] Asterisks (*) represent significant results ($P < 0.05$) 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 1000 coalescent simulations assuming a constant population size and incorporating an estimate of the current population genetic variation (θ).

the canopy (F = 21.658; df = 1,14, r^2 = .607, P = .0004). In addition, nucleotide diversity (π) in understory species was high relative to canopy birds (F = 19.116; df = 1,14, r^2 = .578, P = .0006). There was no significant relationship between π and the mean geographic distance between sampling localities (F = .283; df = 1,14, r^2 = .020, P = .603), nor with species' estimates of census size (F = .164; df = 1,14, r^2 = .012, P = .691). Significance of raggedness values, Fu's F_s, and R_2 varied across species (Table 2.5). Four canopy and two understory species exhibited evidence of historical demographic expansion. There was no predominance of expansion with either stratum (Pearson X^2 = 2.049, P = .152), although this could be due in part to too little statistical power.

DISCUSSION

My results revealed that ecological differences among species explain much of the interspecific variance in population genetic differentiation across three biogeographic barriers in South America. These findings are conservative given the underlying uncertainty inherent in single-locus estimates of population divergence. I suggest that habitat-mediated differences in dispersal propensity between canopy and understory species of lowland rainforest birds have affected historical patterns of gene flow and/or effective population sizes to generate the interspecific variance in across-barrier divergences.

Linking Ecological Pattern to Evolutionary Process

Vertical stratification in Neotropical lowland rainforests has long been studied (Allee 1926a; Allee 1926b). Differences in community structure in birds (Orians 1969; Pearson 1971; Smith 1973; Terborgh 1980b; Greenberg 1981; Stiles 1983; Cohn-Haft and Sherry 1994; Winkler and Preleuthner 2001; Walther 2002a; Walther 2002b) and other organisms (bats: Bernard 2001; small mammals: Vieira and Monteiro 2003; leaf-beetles: Charles and Bassett 2005; bees: Martins and de Souza 2005; termites: Roisin et al. 2006) are driven by marked contrasts in forest structure, lighting, and microclimate observed across strata (Allee 1926b; Longman and Jenik 1974; Richards 1996; Madigosky 2004). The structure of the canopy is complex, with most trees reaching heights of 30 and 45 m, and emergent species towering to 65 m (Munn 1985; Terborgh et al. 1990; Daly and Mitchell 2000; Naka 2004). This produces a two-dimensional surface with large vertical discontinuities and horizontal gaps created by tree fall. Due to direct illumination and the unevenness of its surface, the canopy receives greater amounts of light and experiences more variation in light intensity than the shaded lower strata (Endler 1993; Walther 2002b). Given this energy regime and exposure to weather, the canopy undergoes greater daily, seasonal, and annual variation in temperature and humidity compared to the forest interior (Allee 1926b; Smith 1973; Madigosky 2004). In contrast, the forest understory is fairly uniform in height and degree of openness. Here, tree species are smaller crowned and more closely spaced (Pearson 1971; Terborgh et al. 1990; Richards 1996; Walther 2002a).

How the dichotomy between forest canopy and understory influences ecology in birds has been well studied, but much less so the evolutionary consequences imposed by differing strata. The main result of this study was that foraging stratum is a strong predictor of genetic differentiation across multiple, relatively strong, physical barriers in species of lowland tropical rainforest birds. Given that a species' dispersal propensity is the key determinant of the efficacy of a physical barrier, I conclude that canopy species exhibit lower levels of cross-barrier divergence because these birds have higher dispersal propensity compared to understory species.

Unfortunately, despite being a key dynamic within population biology and determinant of population genetic structure (Slatkin 1987), dispersal remains poorly understood in birds and direct estimates are limited to a handful of taxa (Paradis et al. 1998; Clobert et al. 2001; Winkler et al. 2005). Instead, researchers use indirect assessments to infer patterns of dispersal in birds. For example, a suite of traits, including morphological attributes that govern mobility and behavioral restrictions on movement, are incorporated to define the tendency and ability of a species to disperse across a given landscape. Based on this approach, studies of canopy and understory species of Neotropical birds support the link between dispersal and across-species patterns of genetic differentiation.

First, canopy birds are considered more proficient dispersers because these species tend to forage widely across multiple habitat types compared to understory species. In Costa Rica, Stiles (1980) documented that 70-95 % of canopy birds in tropical wet and dry forest regularly foraged from top-to-bottom along the vertical face of forest edge. The general rule is that canopy species occur in places outside primary forest where two-dimensional surfaces and lighting conditions resemble the canopy exterior. Many canopy species venture downward along treefall gaps and across more open habitat (Orians 1969; Terborgh and Weske 1969; Pearson 1971; Stiles 1980; Terborgh 1980b; Greenberg 1981; Walther 2002a). In contrast, understory birds tend to be confined to particular microhabitats within the shaded forest interior and are rarely observed outside continuous forest (Orians 1969; Remsen and Parker 1984; Terborgh et al. 1990; Cohn-Haft and Sherry 1994; Walther 2002a). In addition, canopy birds are less sensitive to disturbance than understory species (Karr 1982; Bierregaard and Lovejoy 1988; Stouffer and Bierregaard 1995; Harris and Reed 2002; Sekercioglu et al. 2002; Laurance 2004; Laurance et al. 2004; Laurance and Gomez 2005), again suggesting that canopy species are less sedentary.

Second, greater dispersal propensity in canopy birds is linked to spatial and temporal patterns of resource availability, considered more heterogeneous in the forest exterior compared to the understory (Fogden 1972; Frankie et al. 1974; Terborgh 1980b; Greenberg 1981; Terborgh 1986; Loiselle 1988; Levey and Stiles 1994). Large-sized crowns of the canopy, in conjunction with tree fall gaps, separate trees that provide similar resources (i.e. soft fruit, mast, nectar, insects) by distances of tens to hundreds of meters (Terborgh et al. 1990). In contrast, the smaller and more closely spaced crowns of understory trees promote higher densities of a given resource with less traveling distance between similar food types. Studies have found that canopy birds occupy larger-sized territories compared to understory species, potentially a consequence of differing spatial arrangements of trees across strata (Munn 1985; Terborgh et al. 1990). Temporally, fruit in the canopy is more seasonal. Canopy stocks tend to be larger-sized, produced in larger crops, and persist for shorter periods of time than understory fruit which is typically available year round (Karr 1976; Denslow et al. 1986; Fleming et al. 1987; Schaefer and Schmidt 2002). Prey base, particularly that found in the exposed canopy, is likely affected by environmental fluctuations at both seasonal and daily time scales. Unlike the understory, canopy trees tend to suffer substantial leaf loss during seasonal dry periods (Croat 1978; Leigh and Smythe 1979) that can greatly influence prey abundance (Wolda 1978). Even daily fluctuations affect foraging patterns and cause canopy birds to move more relative to understory species. During midday, canopy birds relocate to lower shaded portions of the forest to escape high temperatures (Pearson 1971; Pearson 1977; Walther 2002b). Differences in resource predictability across forest strata is associated with dietary specialization in that canopy birds exhibit less preference than do understory species (Pearson 1975; Sherry 1984; Rosenberg 1990; Cohn-Haft and Sherry 1994). In lowland tropical rainforests of Peru, Terborgh (1980b) found bird species with mixed diets were largely in the canopy, whereas species foraging below 10 m were all dietary specialists.

Additional observations suggest canopy birds have a tendency for long distance movement. Several canopy species respond to resource availability that is more irregular in both space and time by foraging over long distances (parrots and toucans: Karr and James 1975; Moegenburg and Levey

2003). In addition, canopy species tend to fluctuate in local and seasonal abundance (Stiles 1980; Greenberg 1981; Loiselle 1988). This suggests that canopy birds move readily across the landscape, at both small and large spatial scales, in response to temporal changes in habitat, a characteristic that may translate to a predisposition for migration (Levey and Stiles 1992). In contrast, understory species of lowland rainforest birds have experimentally been shown to have dramatic limitations in flight capabilities across gaps in habitat of extremely short distances, less than 100 m in many cases (Moore et al. 2008). Importantly, this study revealed that variance in flight performance across gaps correlated strongly with patterns of extinction and distribution across a Panamanian lacustrine archipelago.

Dispersal Propensity and Genetic Divergence

In a two-population isolation model, patterns of gene divergence are determined by historical patterns of gene flow between diverging populations and the effective population sizes of both ancestral and daughter populations (Arbogast et al. 2002). The dispersal propensity of a species can influence each of these variables with similar effects on the gene genealogies of diverging populations. In terms of historical gene flow, differences in species-specific attributes regarding dispersal may affect the relative efficacy of an arising barrier to gene flow and thus the timing of population separation among co-distributed taxa. In a scenario represented by staggered vicariance, birds with high dispersal propensity may have experienced more recent across-barrier gene flow compared to sedentary species.

The dispersal propensity of a species affects the geographic structuring of genetic variation, and consequently, the effective population size. Subdivision, via restricted migration between demes, increases the effective size of a population (Wright 1943; Wright 1951) and, consequently, the depth of gene genealogies within a metapopulation (Wakeley and Aliacar 2001). Subdivision can lead to overestimates of the inferred timing of divergence between two isolated populations and its effects can be substantial compared to cases of relative panmixia within the ancestral population (Wakeley 2000). Across *cis*-Andean populations, understory species of lowland rainforest birds exhibited greater levels of population subdivision relative to canopy birds, suggesting species found in the lower strata are more sedentary (Templeton 2006). The pronounced structure within understory birds likely translates to greater effective population sizes, which is also suggested by the higher levels of genetic diversity in understory birds compared to canopy species within southwestern Amazonia. Unlike the scenario involving staggered isolation, interspecific variance in across-barrier divergences may reflect simultaneous vicariance among co-distributed taxa with the temporal variation in gene coalescences a reflection of differences in effective sizes of the ancestral population and its dependence on the migration rate among demes.

Hackett and Lehn (1997) described another scenario involving simultaneous vicariance among co-distributed taxa that results in spatial concordance but considerable temporal heterogeneity across phylogeographic records. The "initial genetic conditions" hypothesis posits that ancestral populations with considerable gene flow and little differentiation among demes will have contrastingly shallow divergences post-isolation compared to taxa characterized by low gene flow among demes. This hypothesis suggests that sedentary species have greater genetic differentiation due to effects of isolation by distance and, when strong barriers to gene flow arise, this previously structured genetic variation is responsible for the interspecific variance in genetic divergences among co-distributed taxa with varying dispersal propensities. The "initial genetic conditions" hypothesis seems particularly appropriate for physical barriers to gene flow, such as a mountain range, that form gradually over time.

Low nucleotide diversity is also indicative of younger populations. Several species, both understory and canopy birds, showed evidence of historical demographic expansion. Because levels of nucleotide diversity are not associated with across-species patterns of expansion, it is unclear how lineage age explains low levels of nucleotide diversity within canopy species. It seems implausible that expansion alone is causal in all canopy species. In addition, source populations are not readily identifiable since patterns observed in western Amazonia are repeated in *trans*-Andean populations (C. W. Burney, data unpublished). Undoubtedly, species' demographic histories within western Amazonia are complex, as previous phylogeographic studies have revealed (Marks et al. 2002; Cheviron et al. 2005b). Increased sampling, both at large and small spatial scales, and additional genetic loci are needed to obtain better estimates of divergence parameters and to tease apart the microevolutionary processes and conditions that would cause a reduction in both overall genetic diversity and structure in some species compared to others.

The relationships found in this study add support to previous arguments that low dispersal propensity facilitates geographic isolation and divergence (Slatkin 1987; Bohonak 1999; Belliure et al. 2000). Studies using patterns assessed at the family-level in birds have shown the opposite trend, linking greater dispersal to higher diversification rates (Owens et al. 1999; Phillimore et al. 2006). This conflict is likely the result of differences in the phylogenetic scale at which questions regarding ecological correlates of diversity are being addressed. In my approach, I assessed within-species patterns of diversification. Insights gained at the population-level may better address the factors, including ecology, pertinent to speciation that could be overlooked in studies examining patterns at deeper phylogenetic levels. To my knowledge this is the first large-scale comparative avian study to document a significant association between ecological traits of a species and its level of genetic differentiation.

CHAPTER 3: COMPARATIVE MITOCHONDRIAL DNA PHYLOGEOGRAPHY OF WIDESPREAD SPECIES OF NEOTROPICAL LOWLAND FOREST BIRDS WITH CONTRASTING FORAGING BEHAVIORS

INTRODUCTION

Understanding how diversity arises is of fundamental importance in evolutionary biology, and hinges upon knowledge of the recurrent processes (e.g. gene flow, genetic drift) and historical events (e.g. isolation, expansion) driving the genetic and morphological divergence of populations. Researchers are increasingly relying on the observed spatial and temporal patterns of genetic variation to gain insight into the relative influence of differing microevolutionary forces on diversification and the history of populations (Avise et al. 1987a; Avise 2000). Studies are also concentrating on widespread species in order to assess the evolution of geographic variation at continental-scales. In the neotropics, such studies have found 1) shared genetic breaks across the northern Andes (Brumfield and Capparella 1996; Zamudio and Greene 1997; Cortes-Ortiz et al. 2003) with considerable variance in across-taxona levels of cross-Andean divergence, species represented by multiple cross-Andean distributions (Nyari 2007; Miller et al. 2008), genetic divides across the Amazon River (Armenta et al. 2005) and eastern/western Amazonia (Marks et al. 2002; Symula et al. 2003) contrasted by extensive gene flow across the breadth of the Amazon basin (Dick et al. 2003; Dick et al. 2004; Eberhard and Bermingham 2004), and complex patterns of genetic structure across the Panamanian Isthmus (Brumfield and Braun 2001; Dick et al. 2003; Barker 2007; Dacosta and Klicka 2008; Dick and Heuertz 2008).

While these studies highlight several broad patterns observed in the Neotropics, this region has received comparatively little attention in terms of phylogeographic study and much remains unexplored (Beheregaray 2008). Given that Central and South America support the richest assemblage of birds in the world (Haffer 1990), research in this species-rich region accounts for less than ten percent of bird publications in the last twenty years of phylogeographic study (Beheregaray 2008). Here, I examined the comparative phylogeography of four co-distributed species of tropical lowland rainforest birds found throughout Central and South America. To my knowledge, this study represents the first published comparison of range-wide phylogeographic patterns among multiple species of widely-distributed neotropical birds.

Comparative phylogeographic studies traditionally test for shared biogeographic history across large spatial scales (Avise 1992; Arbogast and Kenagy 2001). Another approach is to concentrate on phylogeographic inconsistencies among co-distributed taxa since these yield information on the relative influence of differing ecological and/or life-history traits on both recurrent processes, such as gene flow (Bohonak 1999) and genetic drift (Matocq et al. 2000), as well as individual species' responses to past changes in the landscape (Zink 1996; Bermingham and Moritz 1998; Nicolas et al. 2008). I used this method to test for ecological correlates of genetic differentiation in 40 widespread species of lowland tropical rainforest birds co-distributed across both sides of the northern Andes mountains (Chapter 2). I found that genetic variation was consistently partitioned into phylogroups east and west of the Andes, yet there was striking discordance in levels of cross-Andean divergence among the study taxa. While much of this variance represents stochastic influences associated with coalescing gene lineages, I found a significant relationship between habitat use and genetic differentiation in that understory birds have deeper cross-Andes divergences and greater population genetic structure than canopy dwellers. This corroborates previous ecological assessments that understory birds are generally more sedentary than canopy birds (Bierregaard et al. 1992).

Here, I investigate how this dichotomy in canopy versus understory patterns of genetic variation relates to continent-wide genetic structuring in four species of lowland Neotropical birds.

Because each species has a congener that is distributed primarily within Amazonia, a *cis*-Andean origin (*cis* refers to lowland tropical rainforest east of the Andes) for each genus-level clade is suggested (however, see Santos 2007). In Chapter 2, I found that these four species had widely varying levels of genetic divergence across several biogeographic barriers, including the Andes and the Amazon River. Here, I examine in detail the range-wide phylogeographic pattern of two canopy species, *Attila spadiceus* and *Tityra semifasciata*, which in the previous study showed extremely low levels of cross-barrier genetic divergence. I compare these patterns to two understory species, *Automolus ochrolaemus* and *Xenops minutus*, which exhibit high levels of genetic divergence across these same barriers. All study taxa are distributed from Mexico south to southern Amazonia (range of *X. minutus* and *A. spadiceus* extends to Atlantic forest of Brazil) and breed predominately in tropical lowland evergreen forest (Stotz et al. 1996).

The objectives of this study were to (i) assess the phylogeographic structure of four co-distributed species of lowland neotropical rainforest birds, (ii) compare range-wide patterns of genetic variation in understory versus canopy birds, and (iii) compare the phylogeographic patterns of the study species with those of other co-distributed neotropical rainforest taxa.

METHODS

Study Species and Taxonomic Sampling

I obtained mitochondrial DNA (mtDNA) sequences for NADH dehydrogenase subunit 2 (ND2; ~1060 base pairs) and cytochrome *b* (cyt *b*; ~1029 base pairs) from a total of 341 individuals.

Automolus ochrolaemus. A relatively large foliage-gleaner that is fairly common to common throughout its extensive distribution (Ridgely 1994). Geographic variation in plumage is most marked in Central America / Chocó (*trans*-Andean region) where the darkest and most colorful subspecies of the Caribbean lowlands of Mexico, *cervinigularis*, occur opposite the distinctively pale-colored race, *pallidigularis*, found in eastern Panama and northwestern South America, (Remsen 2003; see Figure 3.1). Vocal variation is also apparent and seems coincident with subspecies boundaries (Remsen 2003). *A. ochrolaemus* breeds primarily in tropical lowland evergreen forest below 1400 meters (Stotz et al. 1996), but unlike its two most closely related taxa, *A. infuscatus* and *Hyloctistes subulatus* (Brumfield unpublished), is found in more wet and transitional habitat within lowland rainforests. *Trans*-Andean populations reside in secondary growth and disturbed habitat including coffee plantations whereas Amazonian populations are found primarily in várzae, swamp-forest, areas around streams, and tree-fall gaps within *terra firme* (Ridgely and Greenfield 2001; Remsen 2003). *A. ochrolaemus* forages on arthopods within the understory (Ridgely 1994; Stotz et al. 1996; Remsen 2003).

I sampled 103 individuals of *A. ochrolaemus.* All seven subspecies of *A. ochrolaemus* were represented in this study (Appendix C and Figure 3.7). I included 40 individuals of *Automolus infuscatus* and 25 individuals of *Hyloctistes subulatus* for outgroup comparison (not listed).

Xenops minutus. An uncommon to fairly common xenops exhibiting relatively subtle changes in both morphology (Figure 3.2) and vocal variation across its wide range, it is comprised of ten recognized subspecies (Ridgely 1994; Remsen 2003). One exception is nominate *minutus*, which is found in southeastern Brazil (Pernambuco to Santa Catarina), eastern Paraguay, and northeastern Argentina. This subspecies is smaller and has more white on its throat and chest compared to other subspecies, though vocally it sounds similar to other subspecies (Ridgely 1994; Remsen 2003). *X. minutus* breeds regularly in both tropical lowland and flooded evergreen forest largely below 1000 meters but occasionally to 1500 meters (Ridgely 1994; Stotz et al. 1996). Behaviors associated with habitat preference vary across the species' range. Populations west of the Andes are found in several habitat types (primary forest, mature secondary woodland, and their borders) and are more conspicuous than Amazonian populations which remain primarily within *terra firma* and *várzea* fores,t venturing infrequently to edge situations (Ridgely and Greenfield 2001). *X. minutus* forages on arthropods usually singly but sometimes in mixed-species flocks, and, unlike its congeners, remains predominately in the understory (Ridgely 1994; Remsen 2003).

In this study, *Xenops* was represented by 129 individuals; of these, 121 are *X. minutus* distributed across most of this species' range and representing nine of the 11 recognized subspecies (Appendix D and Figure 3.8). The subspecies of the Perijá Mountains of Colombia/Venezuela, *olivaceus*, and of northeastern Colombia/northwestern Venezuela, *neglectus*, were not sampled since tissues were unavailable. *X. milleri* (2 samples), *X. rutilans* (4 samples), and *X. tenuirostris* (1 sample) were included as outgroup taxa and represent all of the remaining congeners of *X. minutus*.

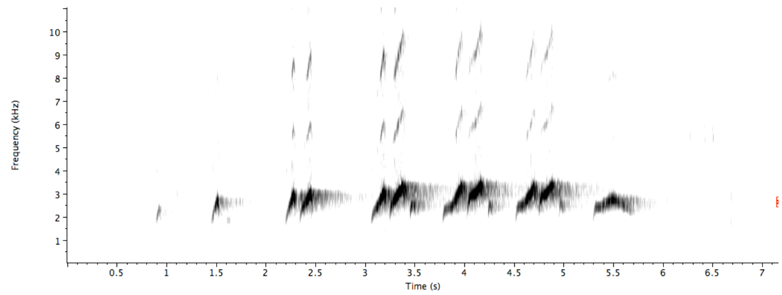
Attila spadiceus. A polymorphic flycatcher represented by gray, rufous, and intermediate forms (Figure 3.3), the frequencies of which do not appear to be strongly tied to geography, subspecies boundaries, or song dialect (Ridgely 1994). Twelve subspecies are currently recognized within *A. spadiceus* (Traylor 1979; Fitzpatrick 2004) although strong vocal differences in the dawn song between Middle and South American populations suggest *A. spadiceus* may be two species (Leger and Mountjoy 2003). Uncommon to locally fairly common, *A. spadiceus* breeds primarily in primary forest of lowland tropical rainforest, but in parts of its wide range can be found in lower montane forest up to 1800 meters as well as tropical deciduous forest (Ridgely 1994; Stotz et al. 1996; Fitzpatrick 2004). It forages on large arthropods and small vertebrates predominately within the forest and its borders but will occasionally explore nearby clearings where large trees persist (Ridgely 1994). *A. spadiceus* forages through all vegetation levels but is mainly found searching for prey from forest mid-story up to the canopy (Skutch 1971; Sherry and McDade 1982; Ridgely 1994; Fitzpatrick 2004).

Figure 3.1 *Automolus ochrolaemus.* LSUMZ specimens, all males: 1) MEXICO: Chiapas, *cervinigularis* voucher number 85777; 2) PANAMA: Bocas del Toro, *hypophaeus* vn 177721; 3) PERU: Pasco, *ochrolaemus* vn 105969; 4) BOLIVIA: Pando, *ochrolaemus* vn 132527; 5) GUYANA: Kopinang River, *turdinus* vn 175385.

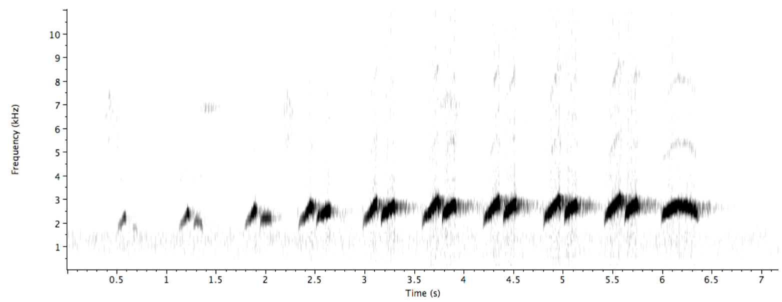
Figure 3.2 *Xenops minutus.* LSUMZ specimens, all males: 1) MEXICO: Chiapas, *mexicanus* voucher number 167154; 2) PANAMA: Panama, *ridgwayi* vn 163566; 3) PANAMA: Darien, *littoralis* vn 108301; 4) GUYANA, *ruficaudus* vn 175388; 5) PERU: Loreto, *obsoletus* vn 92317; 6) BOLIVIA: Beni, *obsoletus* vn 124094; 7) BRAZIL: Sao Paulo, *minutus* vn 52760.

Figure 3.3 *Attila spadiceus.* LSUMZ specimens, all males: 1) MEXICO: Oaxaca, *pacificus* voucher number (vn) 33183; 2) MEXICO: Tabasco, *flammulatus* vn 27202; 3) PANAMA: Panama, *citreopyga* vn 163663; 4) PANAMA: Colon, *sclateri* vn 164225; 5) PERU: San Marten, *spadiceus* vn 117176; 6) PERU: San Marten, *spadiceus* vn 117177; 7) PERU: Loreto, *spadiceus* vn 110648; 8) SURINAME, *spadiceus* vn 178366; and 9) BOLIVIA: Santa Cruz, *spadiceus* vn 137517.

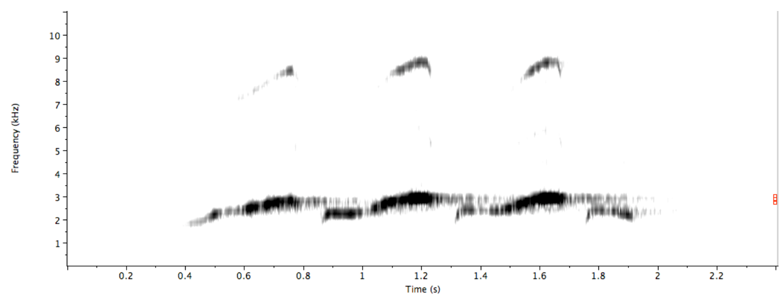
A) MEXICO (Colima), song.
Recorded by Dan Lane.



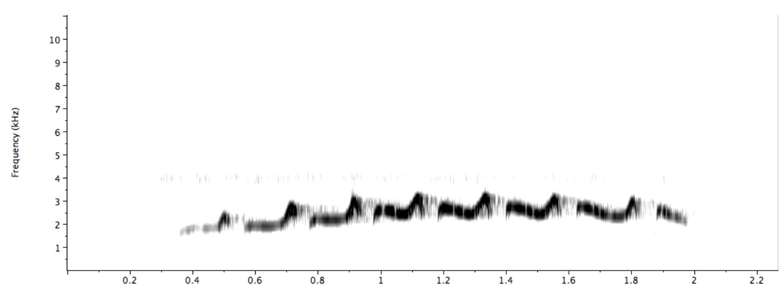
B) COSTA RICA, song.
Recorded by Cesar Sanchez.



C) MEXICO (Colima), call.
Recorded by Dan Lane.



D) COSTA RICA, call.
Recorded by Cesar Sanchez.



E) PERU, song.
Recorded by Dan Lane.

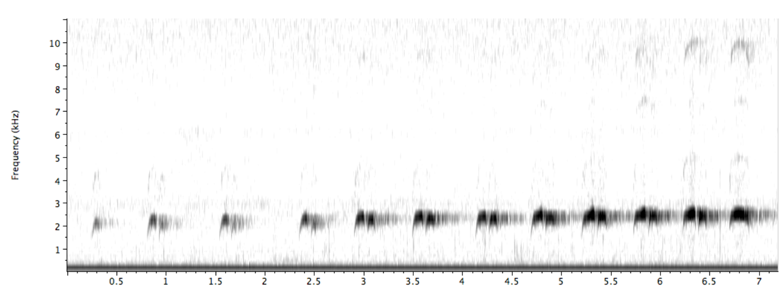


Figure 3.4 Vocalizations of *Attila spadiceus.*

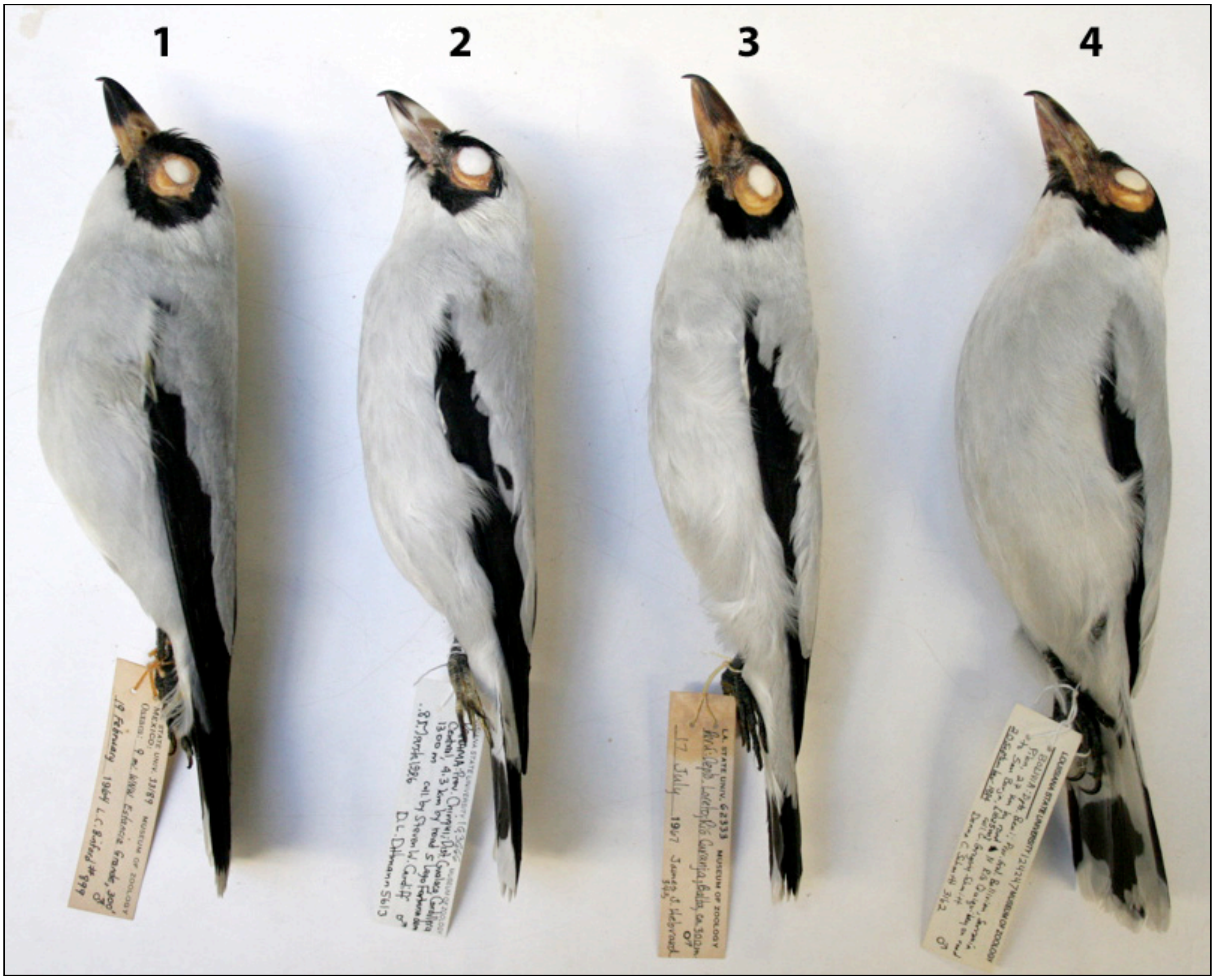


Figure 3.5 *Tityra semifasciata*. LSUMZ specimens, all males: 1) MEXICO: Oaxaca, *griseiceps* voucher number 33189; 2) PANAMA: Chiriqui, *costaricensis* vn 163666; 3) PERU: Loreto, *fortis* vn 62333; 4) BOLIVIA: Beni, *fortis* vn 124247.

I sampled 77 individuals of *A. spadiceus* (Appendix E, Figure 3.9) representing seven of the 12 recognized subspecies (Traylor 1979; Fitzpatrick 2004). Subspecies not represented are taxa with restricted ranges (*cozumelae* of Cozumel Island; *salvadorensis* of El Salvador and northwestern Nicaragua; *uropygiatus* of coastal eastern Brazil) and/or distributions found primarily in Colombia (*parvirostris* of Santa Marta and Maracaibo Basin; *caniceps* of Magdalena and Sinú Valley). *A. cinnamomeus* (1 sample), *A. torridus* (1 sample), *A. citriniventris* (3 samples), and *A. bolivianus* (1 sample) were included as outgroup taxa and represent four of the six congeners of *A. spadiceus*. Previous work has shown the remaining congeners, *A. phoenicurus* and *A. rufus*, are distantly related to *A. s. uropygiatus* despite forming a monophyletic *Attila* with respect to approximately 70 tyrant-flycatcher species of southeastern Brazil (Chaves et al. 2008).

Tityra semifasciata. A mainly frugivorous tityrid (Remsen et al. 2008) with nine recognized subspecies (Fitzpatrick 2004). Across the species' wide range, races vary slightly with no clear breaks related to morphology and voice (Fitzpatrick 2004; see Figure 3.5). Fairly common to common, *T. semifasciata* is more abundant west of the Andes and is largely replaced to the east by *T. cayana*, though both are found together locally (Ridgely 1994). *T. semifasciata* breeds in several types of habitat including montane forests up to 1200 meters, but mainly tropical lowland evergreen forest (Stotz et al. 1996). It forages amid the higher reaches of the canopy in humid forest, secondary woodlands, and their borders, but also ventures into open areas with scattered trees including forest clearings and savanna (Ridgely 1994; Stotz et al. 1996; Ridgely and Greenfield 2001; Fitzpatrick 2004).

I sampled 40 individuals of *T. semifasciata* (Appendix F, Figure 3.10), representing eight of the nine recognized subspecies (Fitzpatrick 2004). Two subspecies (*T. s. hannumi* and *griseiceps*) are found in Sinaloa state in northwestern Mexico and it is uncertain which subspecies (Individual

1, see Figure 3.10.A) was sampled. Both congeners of *T. semifasciata*, *T. cayana* (3 samples) and *T. inquisitor* (10 samples), were included as outgroup taxa.

DNA Extraction and Sequencing

Total genomic DNA was extracted from heart, liver, or muscle tissue preserved by freezing or ethanol using the standard protocol outlined in the Qiagen DNeasy Tissue Kit (QIAGEN, Inc., Valencia, CA). The polymerase chain reaction (PCR) was used to amplify the ND2 and cyt *b* mitochondrial protein-coding genes. PCR amplifications (25 μL) consisted of: 2.5 μL template DNA (~50 ng), 0.3 μL each primer (10 mM, Table 3.1), 0.5 μL dNTPs (10 mM: 2.5 mM each dATP, dTTP, dCTP, dGTP), 2.5 μL 10X with $MgCl_2$ reaction buffer (15 mM), 0.1 *Taq* DNA polymerase (5 U/μL AmpliTaq, Applied Biosystems Inc., Foster City, CA), and 18.7 μL sterile dH_2O. PCR temperature profiles are described in Table 3.1. Double-stranded PCR products were purified using 20% poly-ethylene glycol (PEG), then cycle-sequenced using 1.75 μL 5X sequencing buffer (ABI), 1 μL sequencing primer (10mM, Table 3.1), 2.25 μL template, 0.35 μL Big Dye Terminator Cycle-Sequencing Kit version 3.1 (ABI), and 1.65 μL sterile dH_2O for a total volume of 7 μL. Cycle-sequenced reactions were cleaned using Sephadex (G-50 fine) columns and analyzed on an ABI 3100 Genetic Analzyer. Consensus sequences were compiled from both forward and reverse sequences. Contigs for each individual were assembled and edited using Sequencer version 4.6 (GeneCodes, Ann Arbor, MI) and the entire length of each sequence was examined by eye to confirm base calls. The cyt *b* and ND2 coding regions were checked in Sequencer 4.6 for the presence of stop codons to confirm open reading frames.

Phylogenetic Analyses

Prior to analyzing the combined mitochondrial dataset for each species, I performed a partition-homogeneity test (Farris et al. 1994) using PAUP* 4.0b10 (Swofford 2001) with 100

Table 3.1 Primers and PCR temperature profiles.

ND2:	
L5215	5'-TAT CGG GCC CAT ACC CCG AAA AT-5'
H6313	5'-CTC TTA TTT AAG GCT TTG AAG GC-3'
PCR temperature profiles consisted of an initial denaturation of 2 min at 94°C followed by 35 cycles of 30 sec at 94°C, 30 sec at 50-51°C, and 2 min at 72°C, with a final extension of 5 min at 72°C.	
cyt *b*:	
L14990	5'-CCA TCC AAC ATC TCA GCA TGA TGA AA-3'
H15915	5'-AAC TGC AGT CAT CTC CGG TTT ACA AGA C-3'
PCR temperature profiles consisted of an initial denaturation of 2 min at 94°C followed by 35 cycles of 30 sec at 94°C, 30 sec at 45-48°C, and 2 min at 72°C, with a final extension of 5 min at 72°C.	

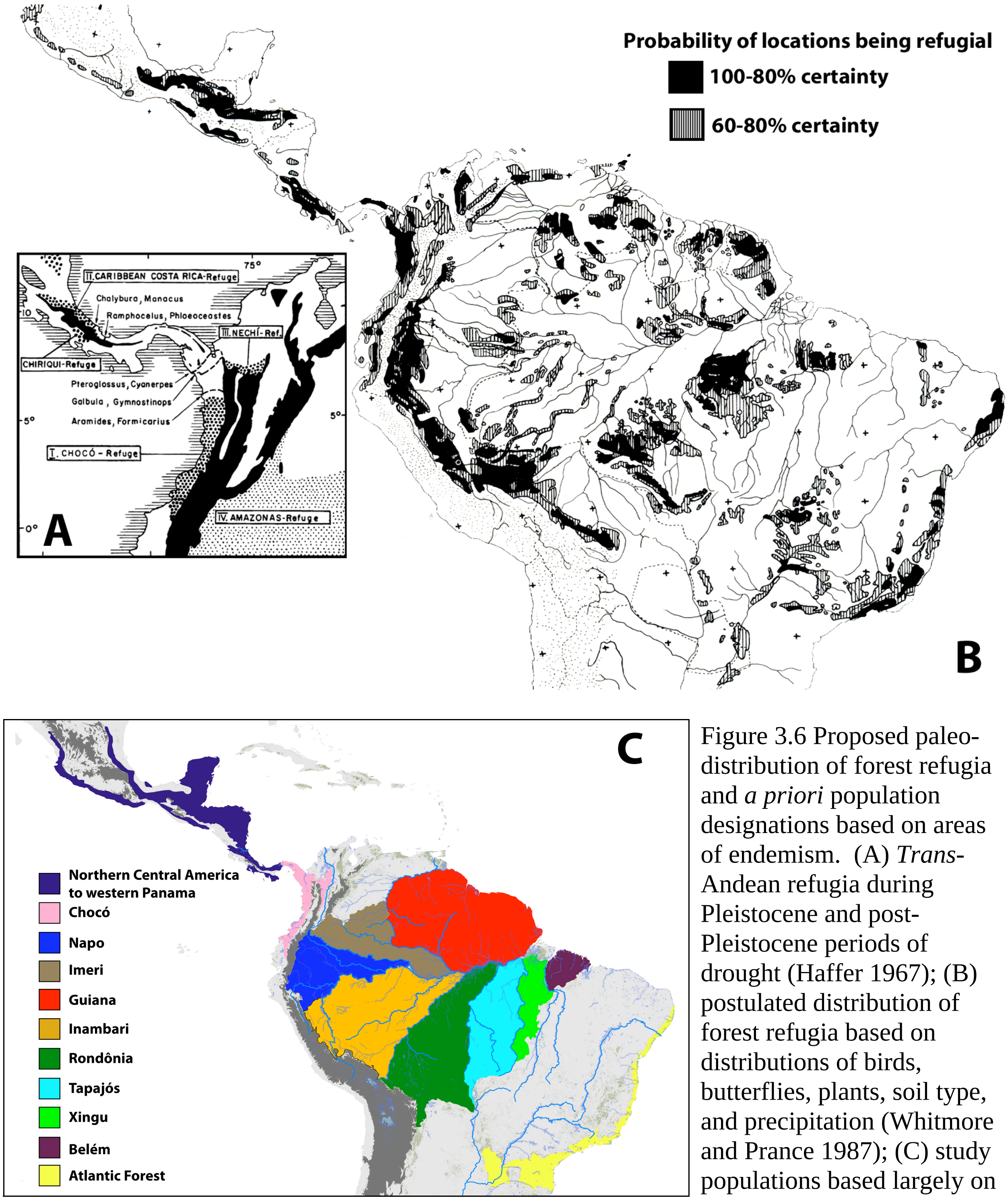


Figure 3.6 Proposed paleo-distribution of forest refugia and *a priori* population designations based on areas of endemism. (A) *Trans*-Andean refugia during Pleistocene and post-Pleistocene periods of drought (Haffer 1967); (B) postulated distribution of forest refugia based on distributions of birds, butterflies, plants, soil type, and precipitation (Whitmore and Prance 1987); (C) study populations based largely on neo-tropical lowland areas of endemism using raw distributions of terrestrial vertebrates (see text).

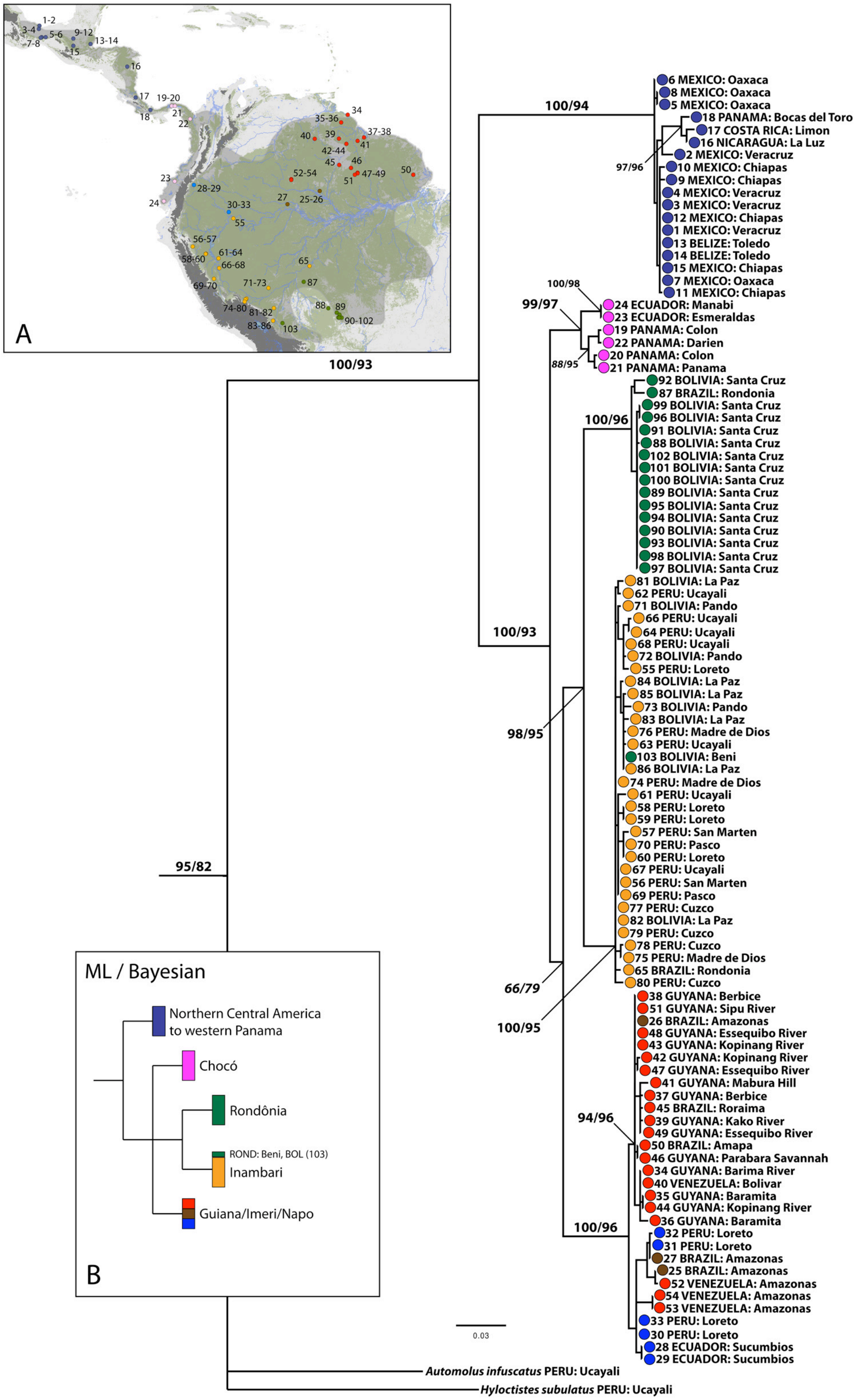


Figure 3.7 Maximum-likelihood gene tree for *Automolus ochrolaemus*. Node support given by ML bootstrap values and, second, Bayesian posterior probabilities. (A) Map of sampling localities and species range provided by InfoNatura (2007). (B) Tree summary.

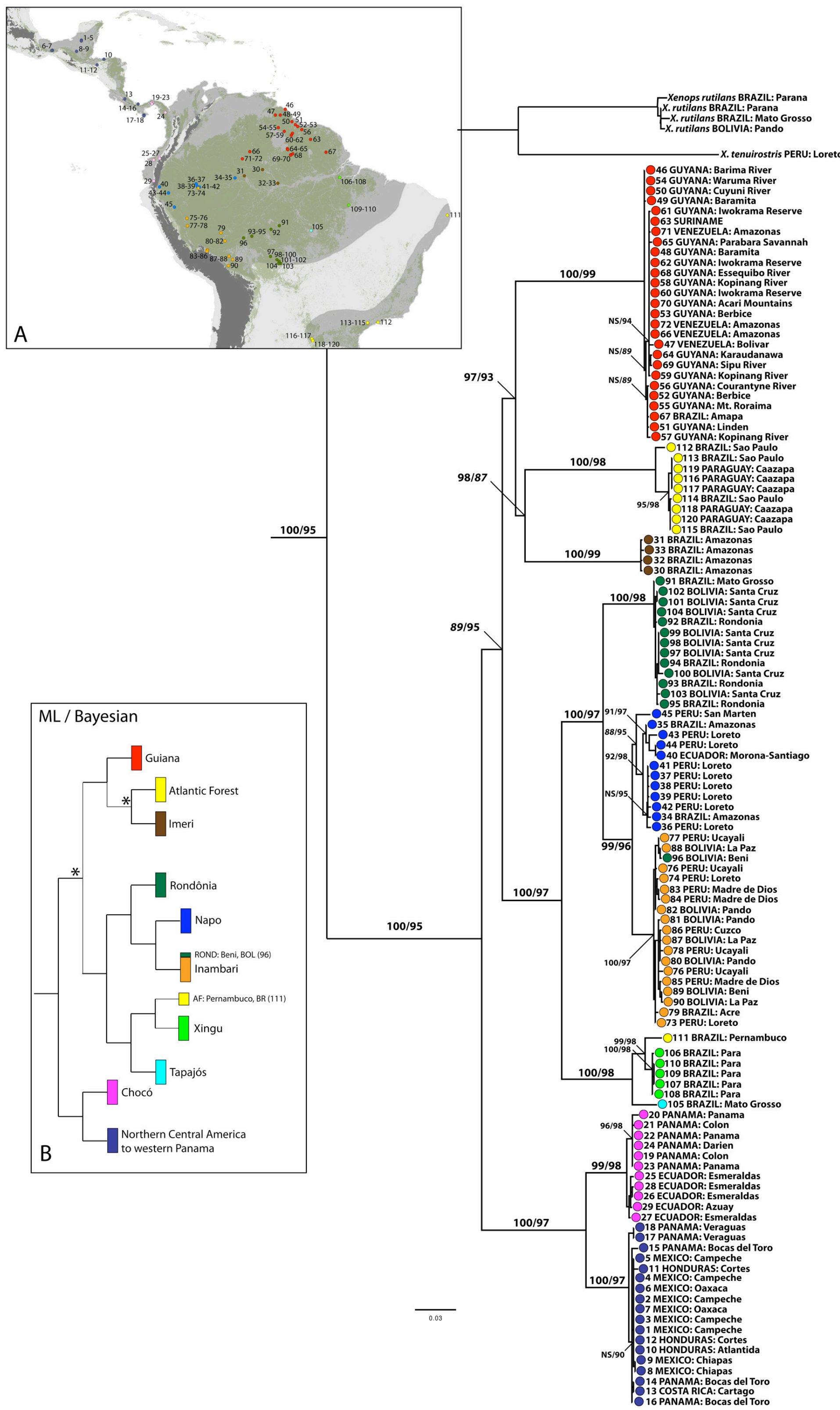


Figure 3.8 Maximum-likelihood gene tree for *Xenops minutus*. Node support given by ML bootstrap values and, second, Bayesian posterior probabilities. (A) Map of sampling localities and species range provided by InfoNatura (2007). (B) Tree summary.

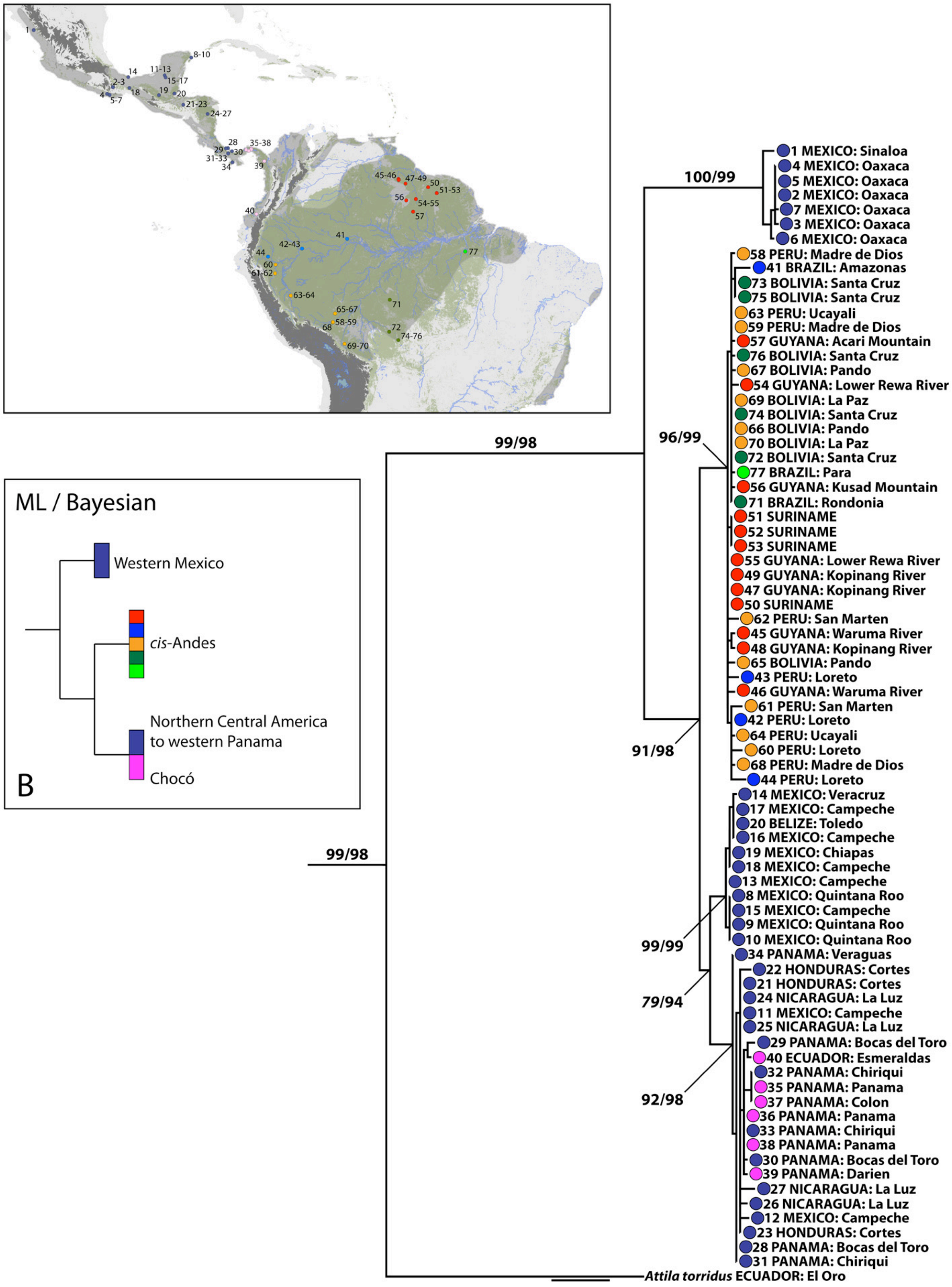


Figure 3.9 Maximum-likelihood gene tree for *Attila spadiceus*. Node support given by ML bootstrap values and, second, Bayesian posterior probabilities. (A) Map of sampling localities and species range provided by InfoNatura (2007). (B) Tree summary.

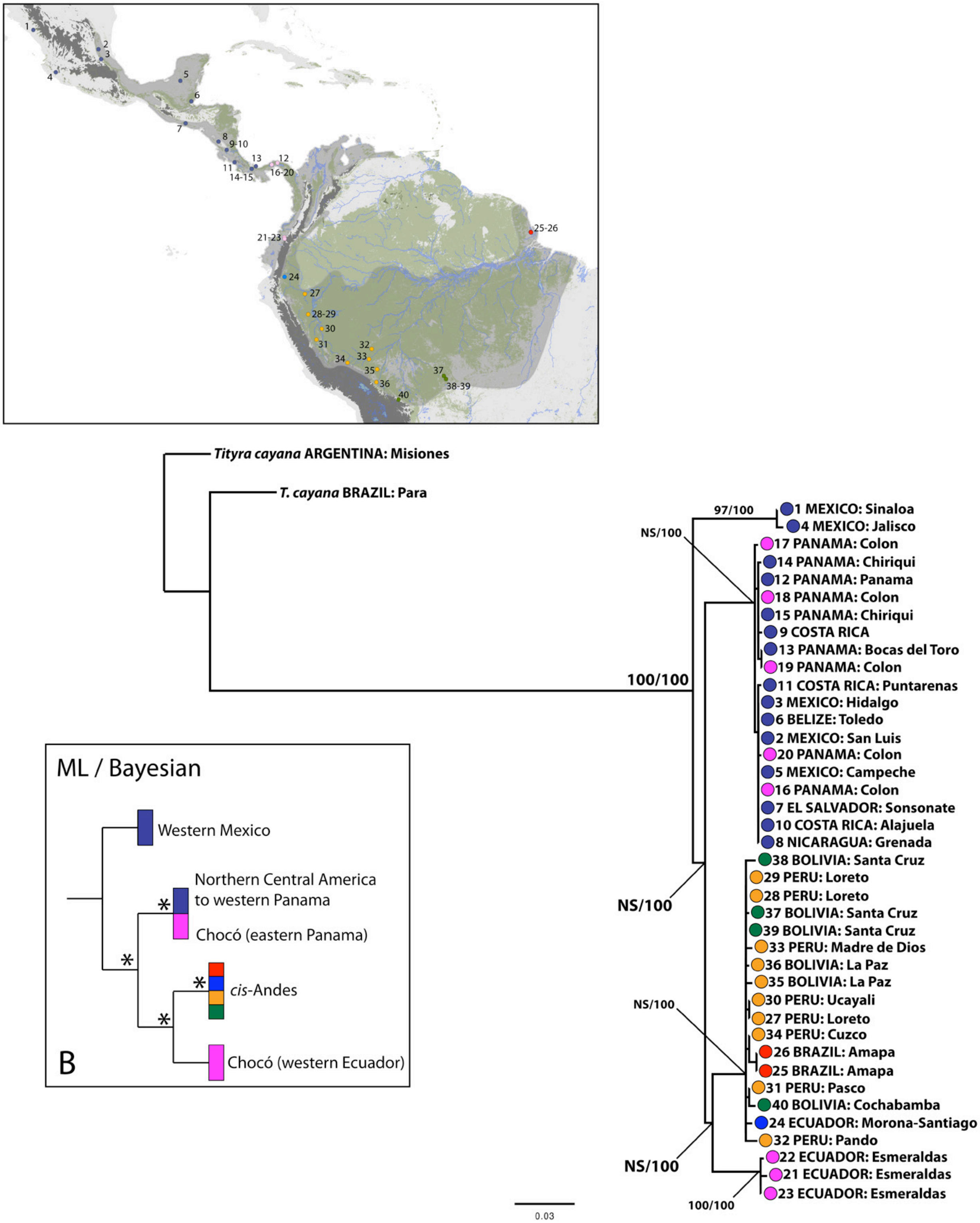


Figure 3.10 Maximum-likelihood gene tree for *Tityra semifasciata*. Node support given by ML bootstrap values and, second, Bayesian posterior probabilities. (A) Map of sampling localities and species range provided by InfoNatura (2007). (B) Tree summary

heuristic replicates to detect any incongruence between the phylogenetic signals of cyt *b* versus ND2. Phylogenetic analyses were performed using maximum-likelihood (ML) methods with RAxML v. 7.0.4 (Stamatakis 2006) and Bayesian methods with MRBAYES v. 3.1 (Hulsenbeck and Ronquist 2001). ML analysis was conducted using the rapid bootstrap (with 1000 replicates) assuming a General Time Reversible (GTR) model of nucleotide substitution (-m GTRCAT). A final ("best tree") ML search was performed using a GTR model with gamma distribution approximated by 4 discrete categories and included an estimate of the proportion of invariable sites (-m GTRGAMMAI). To assess nodal support in the ML analysis I constructed a consensus tree using the 1000 bootstrap replicates and 50% majority-rules in PAUP* 4.0b10. Bayesian analysis was conducted using the GTR model with gamma-distributed rate variation across sites (nst = 6, rates = gamma). Four Markov chains were run simultaneously for 2,000,000 generations with trees sampled every 1000 generations. For each chain, stable likelihood values were obtained at approximately 20,000 generations, thus trees sampled prior to this point were discarded as burn-in. The remaining 1,980 trees were used to construct a 50% majority rules consensus tree in PAUP* 4.0b10. For the Bayesian analyses, support for nodes was assessed using posterior probabilities.

Population Structure

Analysis of Molecular Variance. I assessed the spatial clustering of genetic variation using analysis of molecular variance (AMOVA; Excoffier et al. 1992) in ARLEQUIN v. 3.1. For this analysis, I first made *a priori* delineations of population boundaries (Figure 3.6.C) based on postulated distributions of refugia (Figure 3.6.A and 3.6.B) and identified areas of endemism (Haffer 1974; Haffer 1978; Cracraft 1985; Haffer 1985; da Silva and Oren 1996; Ron 2000; lowland Amazonian areas of endemism used in this study largely adopted from da Silva et al. 2005). The AMOVA was performed at three hierarchical levels: between east and west of the Andes (*cis*/*trans* populations), among areas of endemism within *cis*- and *trans*-Andes, and within designated areas of endemism. Additional *post-hoc* analyses were conducted to account for cryptic population genetic breaks revealed during phylogenetic analyses.

Isolation by Distance. For each species, the geographic distance between individual sampling localities was compared to genetic distance to test for isolation by distance (IBD) effects (Wright 1943). The Euclidean distance between individual sampling localities was calculated with an equidistant conic projection (South America Equidistant Conic; central meridian: -60.00; standard parallel 1: -5.00; standard parallel 2: -42.00; latitude of origin: -32.00) using the program ARCGIS (http://www.esri.com). PAUP* 4.010 (Swofford 2001) was used to calculate pairwise genetic distance between individuals under an HKY85 finite-sites substitution model (Hasegawa et al. 1985). I tested for the influence of IBD on patterns of genetic variation at two spatial scales: (1) within *cis*- and *trans*-Andes; and (2) within areas of endemism previously described. The first assignment included both longer transects and those that traversed known physical barriers, rivers in particular, permitting assessment of IBD in the context of a heterogeneous landscape. The second treatment was sampled at a smaller spatial scale and across relatively contiguous habitat.

Genetic Diversity

For each species, I also examined levels of genetic diversity and tested for historical demographic expansion. These analyses were performed at hierarchical spatial scales (entire dataset, within *cis*- and *trans*-Andes, and within areas of endemism) to compare, across species, the relative role of distance and barriers on both measures. Levels of nucleotide diversity (π ; Nei 1987) were calculated using DNASP v. 4.50.2 (Rozas et al. 2003). Historical demographic expansion was inferred by the raggedness index (Harpending 1994), Fu's F_S (Fu 1997), and R_2 (Ramos-Onsins and Rozas 2002) using DNASP.

RESULTS

For all four species, partition-homogeneity tests failed to reject the null hypothesis of a shared phylogenetic signal between ND2 and cyt *b* (*Automolus ochrolaemus*, P = 0.99; *Xenops minutus*, P = 0.97; *Attila spadiceus*, P = 0.59; *Tityra semifasciata*, P = 1.00). All results presented here were obtained using a concatenated ND2/cyt *b* dataset for all individuals.

Phylogenetic Analyses

Phylogeographical mtDNA differentiation was relatively weak in the canopy species, *Attila spadiceus and Tityra semifasciata* (mean uncorrected pair-wise divergence: AS, 0.9 ± 0.8%; TS, 1.0 ± 0.7%), moderate in *Automolus ochrolaemus* (AO, 2.4 ± 1.6%), and strongest in *Xenops minutus* (XM, 5.6 ± 2.8%). Despite varying levels of genetic divergence across major barriers, there were no shared haplotypes in cross-Andean populations and, with the exception of *Automolus ochrolaemus*, species exhibited reciprocal monophyly across this barrier. Generally speaking, the Andean cordillera marked a deep divergence for all species examined (Figures 3.7, 3.8, 3.9, and 3.10). However, in three of the four species, the deepest genetic break was found within *trans*-Andean populations. The lone exception, *Xenops*, exhibited a strong break in Panama dividing the Chocó from the clade composed of all individuals west of the Panamanian isthmus.

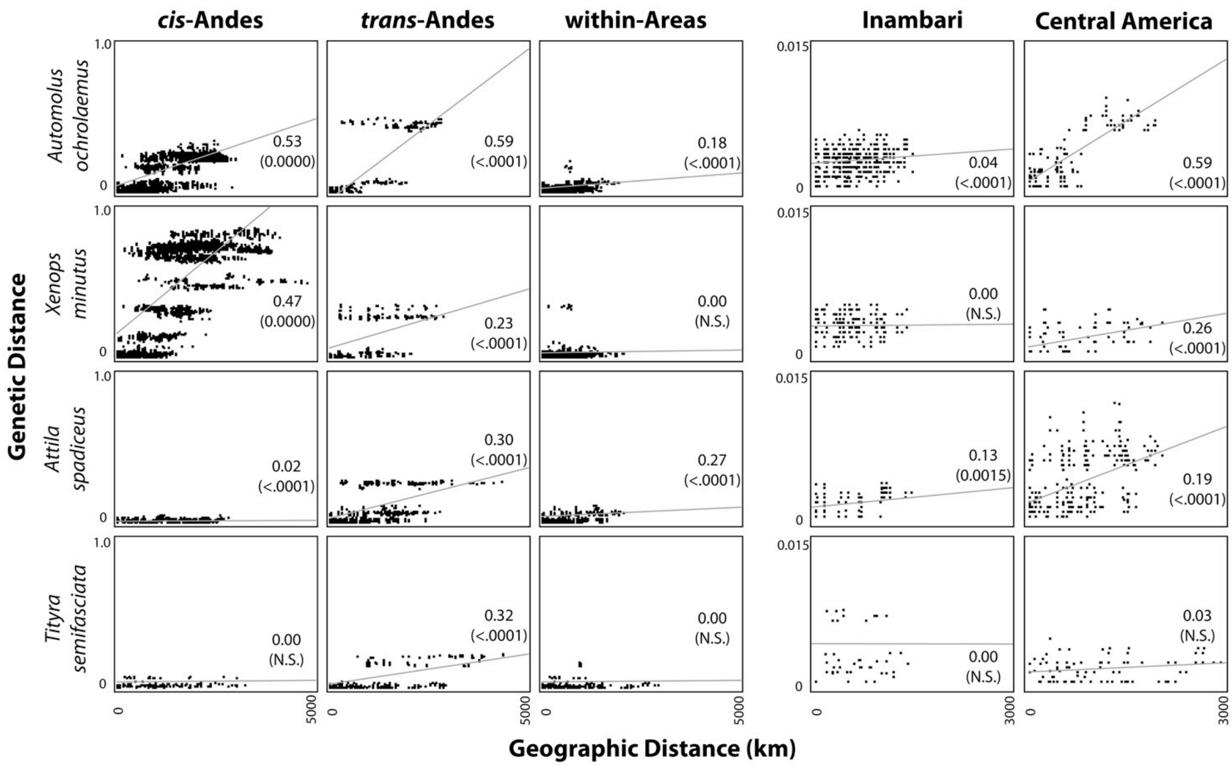
Population Structure

For all four species, an AMOVA revealed a large portion of overall genetic variation was partitioned across the Andes (range 41-71%, Table 3.2). However, these values differed according to foraging stratum. The percentage of overall genetic variation partitioned across the Andes, relative to within, was significantly higher (F = 50.1; df = 1,2, r^2 = .96, P = .02) in the two canopy species compared to those of the understory while partitioning among areas of endemism was significantly higher (F = 85.6; df = 1,2, r^2 = .98, P = .01) in understory versus canopy. In the

Table 3.2 Hierarchical analysis of molecular variance (AMOVA).

Source of variation	Percentage of variation (significance)[a]			
	Automolus ochrolaemus	*Xenops minutus*	*Attila spadiceus*	*Tityra semifasciata*
Among *cis*- and *trans*-Andes	40.9 (P = 0.11)	31.8 (P = 0.02)	70.7 (P = 0.05)	68.4 (P = 0.07)
Among areas of endemism within *cis*- and *trans*-Andes	51.6 (P < 0.0001)	63.2 (P < 0.0001)	3.8 (P < 0.01)	1.4 (P = 0.04)
Within areas of endemism	7.5 (P < 0.0001)	5.0 (P < 0.0001)	25.48 (P < 0.0001)	30.2 (P < 0.0001)

[a] Percentage of overall genetic variation apportioned to variation at three hierarchical spatial scales.



Regression of genetic distance versus geographic distance, r^2 and level of significance (in parentheses) provided.

Figure 3.11 Genetic distance (HKY-corrected) versus geographic distance at two spatial scales: within *cis*-/*trans*-Andes and within areas.

isolation-by-distance (IBD) analyses (Figure 3.11), *trans*-Andes populations had moderate effects across all four taxa. Within the *cis*-Andes, canopy birds showed no relationship between genetic distance and geographic distance across the entire Amazon basin in sharp constrast to patterns observed in understory taxa. Interestingly, IBD within areas of endemism, putatively contiguous lowland rainforest, was absent to low for all four species.

Genetic Diversity

At larger spatial scales, where genetic structure is apparent in both understory taxa, nucleotide diversity (π) was higher relative to canopy birds, but not significantly different (F = 3.74; df = 1,2, r^2 = .65, P = .19). For three of the four taxa, after accounting for within-area structure, average within-area nucleotide diversity was lower in Amazonian than in *trans*-Andean populations. Across all taxa, there were no signatures of historical demographic expansion in *trans*-Andean populations, which contrasted to that observed within the Amazonian areas of endemism (Figure 3.12).

DISCUSSION

I found that patterns of within-species genetic variation reflect contrasting regional biogeographic histories between *trans*-Andean and Amazonian populations. Levels of genetic diversity and partitioning of genetic variation were comparable among species of the same foraging stratum. While both canopy and understory birds exhibited marked divergence between cross-Andean populations, understory species were structured at smaller spatial scales, particularly across riverine barriers of the Amazon basin. Surprisingly, estimates of isolation by distance, a proxy for dispersal propensity, are similar through contiguous habitat for all study taxa. Lastly, unique patterns of population structuring were observed for all four taxa.

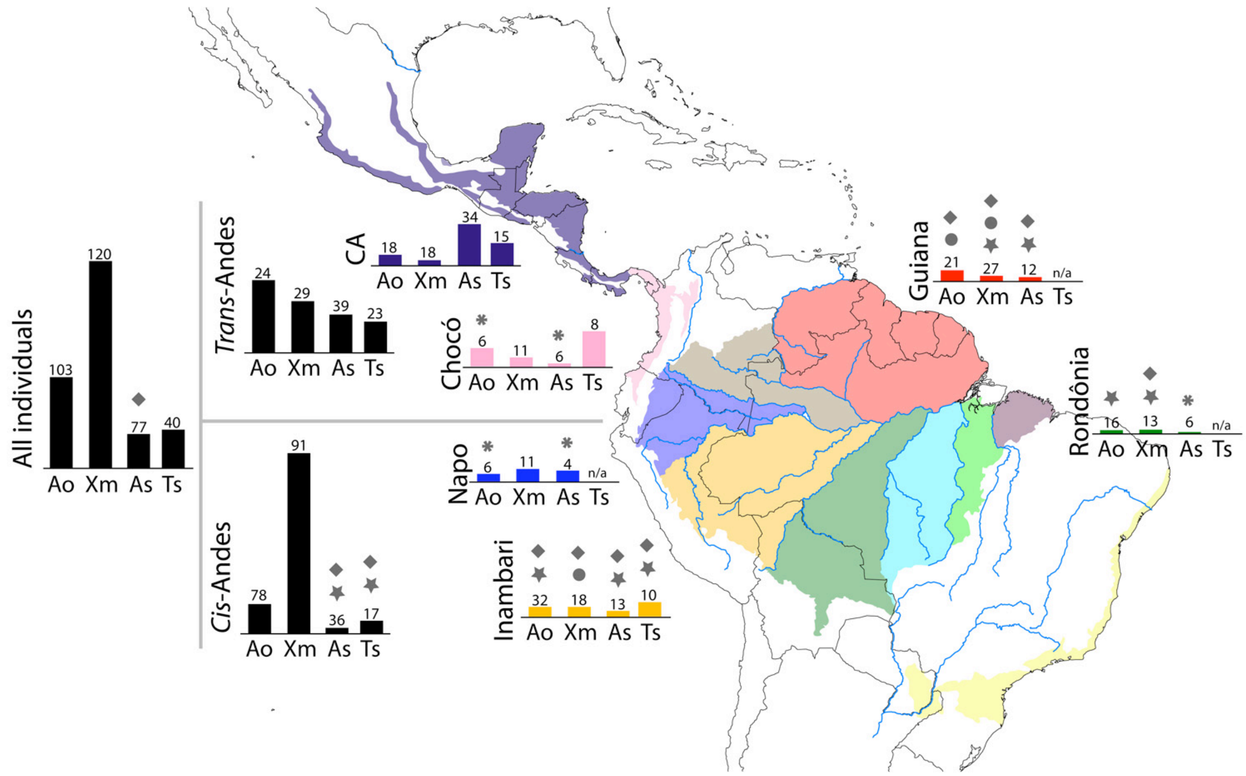


Figure 3.12 Relative levels of nucleotide diversity and tests of historical demographic expansion across multiple spatial scales. Ao = *Automolus ochrolaemus*, Xm = *Xenops minutus,* As = *Attila spadiceus,* and Ts = *Tityra semifasciata.*

Numbers above bar represent sample sizes. Symbols above bars (◆, ●, ★) represent significant results ($P < 0.05$) for tests of historical demographic expansion. Low R_2 values (★) and large negative F_s values (◆) are associated with demographic expansion. Raggedness (r) is a measure of the smoothness of the mismatch distribution with low values of r (●) characteristic of rapid 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 1000 coalescent simulations assuming a constant population size and incorporating an estimate of the current population genetic variation (θ). Astericks (✱) denote instances where low sample size precluded tests of expansion. Sample sizes for *Tityra semifasciata* were small for several areas of endemism and precluded measures of genetic diversity.

Cis- Versus *Trans*-Andean Histories

Across all study taxa, there was evidence of historical demographic expansion within the Guiana, Inambari, and Rondonia areas of endemism and relatively stable demographic histories within the Napo and *trans*-Andean populations. Cheviron et al. (2005a) found identical patterns of historical demography in *Lepidothrix coronata*, a widespread, understory piprid with cross-Andean distribution. A similar pattern of population size stasis in the Napo versus expansion in southwestern Amazonia was demonstrated in a widespread lowland Amazonian forest frog, *Physalaemus petersi* (Funk et al. 2007). In a species complex of *Amazona* parrot, Eberhard and Bermingham (2004) revealed complex levels of cryptic diversity within Mesoamerica contrasted by complete lack of geographic structure across more than 2,000 km of Amazon basin. This same relationship was found in two widespread species of lowland rainforest trees, *Swietenia macrophylla* (Novick et al. 2003) and *Symphonia globulifera* (Dick et al. 2003; Dick and Heuertz 2008). Lessa et al. (2003) compared the demographic histories of North American versus southwestern Amazonian mammals and found relatively moderate signatures of expansion in Inambari populations. The authors commented that Inambari populations were highly structured geographically and this may have biased inferences, but interestingly, ten of the 11 Amazonian species exhibited evidence of population growth using coalescent-based methods. Additional species comparisons are needed to assess whether regional differences observed here indeed represent community-wide processes.

Understory Versus Canopy

Range-wide levels of genetic structure and diversity were strikingly similar among species of the same foraging stratum. In contrast, levels and partitioning of genetic variation were different between understory and canopy species at various spatial scales. Within *cis*-Andean distributions, phylogeographic structure of understory species was clearly delineated by riverine barriers while both canopy species showed widespread connectivity across 3000km of the Amazon basin. Interestingly, isolation by distance effects were comparable across foraging strata when assessed within the areas of endemism. This finding suggests levels of gene flow within contiguous habitat are similar between canopy and understory birds and that differences in population genetic structuring across bird groups arise due to differences in gene flow across major barriers, largely rivers.

Automolus ochrolaemus

The basal split between Central America and Chocó/*cis*-Andes aligns with the contrasting plumages and vocalizations observed across the Panamanian Isthmus in the subspecies *cervinigularis* of Central America and *pallidigularis* of the Chocó (Remsen 2003; see Figure 3.1 in supplemental for examples of plumage variation within species). Overall, the level of genetic structuring and differentiation within *A. ochrolaemus* is intermediate of the canopy species and *Xenops*. This pattern was observed in a previous study involving 20 canopy and 20 understory species. *Automolus ochrolaemus* was among two other understory species (*Myrmotherula axillaris* and *Dendrocincla fulliginosa*) exhibiting relatively low genetic differentiation compared to other understory species. All three species are able to persist in fragmented habitats and use secondary growth, forest edge, and gaps (Willis 1972; Loiselle and Blake 1994; Stouffer and Bierregaard 1995; Cohn-Haft et al. 1997; Laurance 2004; Ferraz et al. 2007; Van Houtan et al. 2007). The ability of these species to move more readily outside primary forest and across heterogeneous landscapes likely translates to greater dispersal potential compared to other understory species.

Xenops minutus

This species exhibited the highest degree of population structuring and showed striking congruence with boundaries, largely riverine barriers, delineating proposed areas of endemism. One notable exception was an individual from the Rondônia area of endemism, collected south of the Beni River, with a haplotype nested within the Inambari haplogroup. This finding is possibly due to error in processing of the sample or contamination, and warrants additional investigation since it suggests barriers are perhaps permeable and that other forces (e.g. sexual selection) could be operating to structure populations. The individual from Pernambuco, Brazil (sample 111, Figure 3.8) grouped with Para (Tapajós and Xingu) birds of eastern Amazonia and not with southern Atlantic Forest *Xenops*, suggesting the nominate race is paraphyletic (Remsen 2003). This finding corroborates previous studies regarding the rich history of this region (da Silva et al. 2004; Carnaval and Bates 2007; Santos et al. 2007; Carnaval and Moritz 2008), and, importantly, mirrors relationships recently observed in another furnariid complex, *Automolus leucophthalmus* and *A. paraensis* (Zimmer 2008).

The phylogenetic relationship among *X. minutus* haplogroups is complex and represents a previously undescribed topology regarding area-relationships within *cis*-Andean populations (Bates et al. 1998). The close relationship of the Guiana area of endemism with the Atlantic Forest is similar to inferences made in the *Phaeothlypis* complex (Lovette 2004b). Surprisingly, this clade, distributed north-south from eastern Amazonia to the southern Atlantic Forest is completely bisected by a clade extending from Napo/Inambari areas of endemism east to Pernambuco in northern Atlantic Forest.

Attila spadiceus

The basal split within *Attila* occurs between the disjunct distribution located along the southwestern coast of Mexico and the remaining individuals sampled. The phylogenetic pattern, both temporally and spatially, is identical to that observed in *Tityra semifasciata* and suggests shared biogeographic history. This region in Mexico was postulated as a forest refugia during the last glacial maximum (Whitmore and Prance 1987; see Figure 3.6.B) and isolation may have occurred during periods of glacial cooling. However, assuming an avian molecular clock of 2% mtDNA divergence per million years (Lovette 2004a), gene divergence (average pairwise ~2.5%) occurred within the Pleistocene but well before the LGM.

The three major mtDNA haplogroups (western Mexico, eastern Mexico to the Chocó, and *cis*-Andes) align with geographic variation in vocalizations (Figure 3.4; see also Leger and Mountjoy 2003). The dialect from western Mexico, both song and call, have fewer elements compared to vocalizations heard elsewhere in Central America and the Chocó. Also, the west Mexican song is higher pitched, and call is much flatter in frequency (pers. obs. Dan Lane and Cesar Sanchez). Differences between *cis*- and *trans*-Andean vocalizations were previously described by Leger and Mountjoy (2003).

Tityra semifasciata

Similar to *Attila*, phylogeographic structure in *Tityra semifasciata* is largely constrained to *trans*-Andean populations with the deepest split occurring between western Mexico populations and the remaining individuals, including the *cis*-Andean haplogroup. The weakly differentiated clade of *trans*-Andean birds extending from eastern Mexico south to Panama is distinct from *T. s. nigriceps* of western Ecuador. The phylogeographic break within the Chocó, an area of relatively small-size but with high rates of endemism, clearly shows patterns of isolation in the Neotropics are complex at many spatial scales (Haffer 1967; Gentry 1982).

Here, I used a comparative phylogeographic approach, incorporating widely-distributed species, to examine the influence of species-specific traits on continental-scale patterns of genetic variation as well as to investigate differences in regional history, as was shown between Amazonia and Central America/Chocó. Both findings are key in explaining large-scale patterns of beta-diversity (McKnight et al. 2007) and elucidating evolutionary processes promoting the rich avian diversity in the Neotropics. Future efforts should focus on adding species comparisons and investigating other species-specific traits, such as sociality and mating strategy, that are known to impact spatiotemporal structuring of populations. Also, the influence of such traits on genetic variation is linked to mode of inheritance so emphasis should be placed on multilocus datasets, which will also provide more robust estimates of phylogenetic relationship and measures of historical demography.

CHAPTER 4: STAGGERED ISOLATION ACROSS THE NORTHERN ANDES IN LOWLAND TROPICAL RAINFOREST BIRDS REVEALED BY COMPARATIVE MULTILOCUS PHYLOGEOGRAPHY

INTRODUCTION

Large-scale geologic events are thought to be a common barrier to gene flow for entire communities of organisms (Avise 2000). Empirical studies have found these barriers indeed partition genetic variation of co-distributed taxa into similar geographic regions (Knowlton et al. 1993; Bermingham et al. 1997; Marko 2002; Lessios et al. 2003; Hickerson et al. 2006b). Despite marked spatial congruence, there is often substantial across-taxa variation in pairwise genetic divergence between sister lineages presumed to have formed in concert due to the same emergent barrier (Bermingham and Lessios 1993; Knowlton et al. 1993; Brumfield and Capparella 1996; Bermingham et al. 1997; Knowlton and Weigt 1998; Lessios et al. 2001; Marko 2002; Hoffmann and Baker 2003; Lessios et al. 2003; Hickerson et al. 2006b).

Several explanations may account for this variance. One source occurs when presumed species pairings from either side of a barrier are not in fact sister taxa of one another (Bermingham et al. 1997). Also, differences in rates of molecular evolution across taxa can generate inconsistencies in branch lengths unrelated to biogeographic history, particularly among taxa with disparate life-histories (Bermingham and Lessios 1993; Bermingham et al. 1997). However, given adequate sampling and comparisons made across closely related taxa, both taxonomic uncertainty and rate heterogeneity are not likely to explain the variance in observed genetic divergences. Instead, researchers have suggested the possibility of staggered isolation, via vicariance and/or across-barrier dispersal, in generating phylogeographic discontinuities across common barriers (Knowlton et al. 1993; Knowlton and Weigt 1998; Lessios et al. 2001; Marko 2002).

In these cases, species may have responded differently during formation of a barrier with the timing of population divergences linked to species-specific traits that determine the relative effectiveness of the barrier to gene flow. In Chapter 2, I tested for association between species-specific traits and cross-Andean levels of genetic differentiation in cytochrome *b* across 40 co-distributed species of lowland tropical rainforest birds. I found a relationship between foraging stratum and levels of cross-Andes divergence with canopy species having significantly shallower divergences relative to understory birds. In addition, I compared phylogeographic patterns across the 40 species and found understory species had significantly higher levels of population structure within Amazonia than canopy species. These results suggest canopy birds have higher dispersal propensity compared to understory dwellers, a finding suggested by earlier studies (Capparella 1988; Bierregaard 1990; Sekercioglu et al. 2002).

The timing of gene divergences is determined by historical patterns of gene flow and both the effective size and structuring of ancestral and daughter populations (Arbogast et al. 2002). Given a structured coalescent framework (Notohara and Umeda 2006), the dispersal propensity of a species influences these factors with similar effects on the gene genealogies of diverging populations. The shallower cyt *b* divergences observed in canopy species relative to understory birds may be the result of more recent cross-Andes gene flow or due to a faster coalescence within smaller and/or less structured populations. Thus, it remains unclear if the observed variance in cross-Andean divergences across the 40 taxa is the result of staggered versus simultaneous isolation.

To better address this question, I used a multi-locus approach to reexamine cross-Andean divergence in three co-distributed species of lowland tropical rainforest birds, *Automolus ochrolaemus*, *Xenops minutus*, and *Attila spadiceus*. These species are representative of the wide array of cross-Andean divergence, and its positive association with levels of population structure, observed in both Chapters 2 and 3. Given that a distribution of gene trees underly the true historical relationship of populations comprising a species (Rosenberg and Nordborg 2002), I sampled additional loci and the variability of additional gene divergences in order to reduce the variance in estimates of population divergence and other demographic parameters, including migration (Donnelly and Tavare 1995; Jennings and Edwards 2005).

The objectives of this study were to (i) assess the phylogeographic structure of three widely distributed Neotropical birds species using mitochondrial and nuclear markers, (ii) compare patterns of cross-Andean divergences, and (iii) determine whether across-taxa divergences represent staggered versus simultaneous isolation.

METHODS

Study Species and Taxonomic Sampling

I obtained mitochondrial DNA (mtDNA) sequences for NADH dehydrogenase subunit 2 (ND2; ~1060 base pairs), cytochrome *b* (cyt *b*; ~1029 base pairs) and three noncoding regions of autosomal DNA, intron 7 of the beta-fibrinogen gene (ßf7; 398-454 base pairs), and introns 17483 (491-541 base pairs) and 16214 (404-414 base pairs) described by Backstöm et al. (2008) from a total of 309 individuals: 103 *Automolus ochrolaemus* (Appendix C, Figure 4.1.A), 129 *Xenops minutus* (Appendix D, Figure 4.2.A), 77 *Attila spadiceus* (Appendix E, Figure 4.3.A).

DNA Extraction and Sequencing

Total genomic DNA was extracted from heart, liver, or muscle tissue preserved by freezing or ethanol using the standard protocol outlined in the Qiagen DNeasy Tissue Kit (QIAGEN, Inc., Valencia, CA). The polymerase chain reaction (PCR) was used to amplify all markers. PCR amplifications (25 μL) consisted of: 2.5 μL template DNA (~50 ng), 0.3 μL each primer (10 mM,

Table 4.1), 0.5 μL dNTPs (10 mM: 2.5 mM each dATP, dTTP, dCTP, dGTP), 2.5 μL 10X with $MgCl_2$ reaction buffer (15 mM), 0.1 *Taq* DNA polymerase (5 U/μL AmpliTaq, Applied Biosystems Inc., Foster City, CA), and 18.7 μL sterile dH_2O. PCR temperature profiles are described in Table 4.1. Double-stranded PCR products were purified using 20% poly-ethylene glycol (PEG), then cycle-sequenced using 1.75 μL 5X sequencing buffer (ABI), 1 μL sequencing primer (10mM, Table 4.1), 2.25 μL template, 0.35 μL Big Dye Terminator Cycle-Sequencing Kit version 3.1 (ABI), and 1.65 μL sterile dH_2O for a total volume of 7 μL. Cycle-sequenced reactions were cleaned using Sephadex (G-50 fine) columns and analyzed on an ABI 3100 Genetic Analzyer. Consensus sequences were compiled from both forward and reverse sequences. Contigs for each individual were assembled and edited using Sequencer version 4.6 (GeneCodes, Ann Arbor, MI) and the entire length of each sequence was examined by eye to confirm base calls. The cyt *b* and ND2 coding regions were checked in Sequencer 4.6 for the presence of stop codons to confirm open reading frames.

Phasing of Nuclear Haplotypes

There were sites represented by three nucleotides for ßf7 in *Automolus ochrolaemus* and all three nuclear loci in *Xenops minutus*. I assumed these do not represent nuclear paralogs due to the prevalence of insertions/deletions and that sequences composed of more than two insertion/deletions were extremely rare. Since methods of phasing do not accept sites represented by more than two nucleotides, where triplets occurred, the least common nucleotide was coded to the most common nucleotide. I used two methods to infer the gametic phase of individuals that were polymorphic for more than one segregating site. For individuals that contained one indel, where the forward and reverse sequences each contained an unambiguous 5'-end and an ambiguous 3'-end represented by double peaks, I used the program *CHAMPURU* version 1.0

Table 4.1 Primers and PCR temperature profiles

ND2:

L5215 5'-TAT CGG GCC CAT ACC CCG AAA AT-5'

H6313 5'-CTC TTA TTT AAG GCT TTG AAG GC-3'

PCR temperature profiles consisted of an initial denaturation of 2 min at 94°C followed by 35 cycles of 30 sec at 94°C, 30 sec at 50-51°C, and 2 min at 72°C, with a final extension of 5 min at 72°C.

cyt *b*:

L14990 5'-CCA TCC AAC ATC TCA GCA TGA TGA AA-3'

H15915 5'-AAC TGC AGT CAT CTC CGG TTT ACA AGA C-3'

PCR temperature profiles consisted of an initial denaturation of 2 min at 94°C followed by 35 cycles of 30 sec at 94°C, 30 sec at 45-48°C, and 2 min at 72°C, with a final extension of 5 min at 72°C.

BF7:

Fib7-453L 5'-GTA CTT TAC AAC TGA GCT CCT-3'

Fib7-U 5'-GGA GAA AAC AGG ACA ATG ACA ATT CAC-3'

PCR temperature profiles consisted of an initial denaturation of 5 min at 94°C followed by 35 cycles of 30 sec at 94°C, 30 sec at 55°C, and 1 min at 72°C, with a final extension of 10 min at 72°C.

16214:

16214For 5'-GCA TAC ATC AGA CCA TCT CC-3'

16214Rev 5'-TCA ACC ATA TCA GCC ACA GC-3'

PCR temperature profiles consisted of an initial denaturation of 5 min at 94°C followed by 35 cycles of 30 sec at 94°C, 30 sec at 55°C, and 1 min at 72°C, with a final extension of 10 min at 72°C.

17483:

17483For 5'-GAA ATG TGG TCT GAA CAG TC-3'

17483Rev 5'-TTG CTC TTG GCA CGA TAT GC-3'

PCR temperature profiles consisted of an initial denaturation of 5 min at 94°C followed by 35 cycles of 30 sec at 94°C, 30 sec at 54°C, and 1 min at 72°C, with a final extension of 10 min at 72°C.

(Flot et al. 2006; Flot 2007, available at http://134.157.186.185/champuru/champuru.htm) to resolve haplotypes. Next, I used a Bayesian inference with the program *PHASE* version 2.1 (Stephens et al. 2001; Stephens and Donnelly 2003, available at http://www.stat.washington.edu/stephens/software.html) to determine the most probable phase of alleles given the entire dataset. Inferred alleles for an individual were considered "phased" whenever the posterior probability was 0.9 or greater. Using this criteria, I ran iterations using both unambiguous, including previously "phased" individuals, and ambiguous sequence data until results were unchanging. For the final dataset, I discarded individual allelic data with probabilities less than 0.6.

Genetic Diversity

For each species, I examined levels of genetic diversity. These analyses were performed at two hierarchical spatial scales: using the entire dataset and within *cis*- and *trans*-Andes. Levels of nucleotide diversity per site (π ; Nei 1987) were calculated using DNASP v. 4.50.2 (Rozas et al. 2003).

Population Structure

Analysis of Molecular Variance. For each nuclear locus, I assessed the spatial clustering of genetic variation using analysis of molecular variance (AMOVA; Excoffier et al. 1992) in ARLEQUIN v. 3.1. For this analysis, I first made *a priori* delineations of population boundaries (Figure 3.6.C) based on postulated distributions of refugia (Figure 3.6.A and 3.6.B) and identified areas of endemism (Haffer 1974; Haffer 1978; Cracraft 1985; Haffer 1985; da Silva and Oren 1996; Ron 2000; lowland Amazonian areas of endemism used in this study largely adopted from da Silva et al. 2005). The AMOVA was performed at three hierarchical levels: between east and west of the Andes (*cis*/*trans* populations), among areas of endemism within *cis*- and *trans*-Andes, and within designated areas of endemism. The mitochondrial AMOVA can be referenced in Chapter 3 (Table 3.2).

Networks. Using the median-joining algorithm in NETWORK v. 4.1. (Bandelt et al. 1999; www.fluxus-engineering.com), I constructed haplotype networks for the three nuclear loci.

Geneland. I inferred the number of populations (*K*) and their spatial arrangement using the Bayesian clustering program GENELAND (Guillot et al. 2005a; Guillot et al. 2005b; Guillot 2008; Guillot et al. 2008) via R (2008). This model-based method uses multilocus genotypes from georeferenced individuals to assign population membership and generate spatial patterns of genetic discontinuities. In these analyses, I incorporated only inferred allelic data from the three nuclear markers and assume all loci assort independently. For each final run, I used information from preliminary runs to set priors (minimum/maximum number of populations) and employed both the uncorrelated frequency and spatial models (Guillot et al. 2005b; Guillot, Santos, and Estoup 2008, available at http://folk.uio.no/gillesg/Geneland/Geneland.html). Final runs consisted of 10,000,000 iterations with every hundredth iteration saved (thinning = 100) and post-processing draws using a "burn in" of 1000.

Isolation with Migration Coalescent Analysis

I used the computer program "Isolation with Migration" (IM) to analyze the divergence between *cis*- and *trans*-Andean populations (Hey and Nielsen 2004). Based on coalescent theory, IM uses Bayesian methodology via Markov chain Monte Carlo (MCMC) simulation to generate posterior probability distributions for multiple demographic parameters, including divergence time, all of which are scaled by mutation rate, μ. For each species and marker, I tested for intralocus recombination using a four-gametes test in SITES (Hey and Wakeley 1997) and incorporated the largest non-recombining block in subsequent IM analyses.

RESULTS

Regarding the nuclear dataset (see Chapter 3 for ND2/cyt *b*), levels of population structure varied across taxa while estimates of nucleotide diversity at both scales showed no clear patterns (Table 4.2). In terms of phylogeograhic structure, *Automolus* is intermediate of *Xenops* and *Attila* with considerable partitioning across *cis*- and *trans*-Andes, however, loci vary widely (Figure 4.1.B). GENELAND identified two distinct clusters (K = 2) in the nuclear dataset (Figure 4.1.C) that correspond to the basal node in the mitochondrial gene tree (Figure 4.1.B). *Xenops* exhibited the highest degree of structure between *cis*-/*trans*-Andes accounting for 28-49% of the variation across the three loci (Figure 4.2.B). This species also had the highest values of partitioned variation among the areas of endemism. This is clearly evident in the GENELAND analysis where K = 8 clusters were calculated based on the nuclear dataset (Figure 4.2.C). These clusters map strongly to haplogroups in the mitochondrial gene tree (Figure 4.2.B). Interestingly, the Imeri haplogroup grouped with individuals from the Atlantic Forest in the cluster analysis. Within *Attila*, genetic variation was partitioned largely within the areas of endemism (85-93%) for all loci (Figure 4.3.B), showing only minor partitioning between *cis*- and *trans*-Andes. Despite the low structure detected using AMOVA, GENELAND estimated K = 3 clusters in *Attila* (Figure 4.3.C) across the nuclear loci though support for each individual membership is low as seen by the contour mapping. The north cluster from western Mexico is separated at the basal node in the mitochondrial gene tree. Interestingly, the rest of Central America and Chocó are partitioned with the eastern Panama/western Ecuador individuals grouping with *cis*-Andean individuals as was clearly detected within *Automolus*.

Presumably due to the structure and levels of sequence divergence in *Xenops* (see discussion), I was unable to provide meaningful results for *cis*-/*trans*-Andes divergence. Instead, for comparison, I conducted an analysis examining the break across the Isthmus of Panama between the Chocó and western Panama-Mexico (Figure 4.5). Theta (θ) estimates were comparable across all analyses. In *Automolus*, estimates of θ for *cis*-Andean/North Amazonian populations were slightly larger in size than *trans*-Andean/Chocó population, thought 95% highest posterior distributions (95HPD) overlap considerably (Figure 4.4.A). In the *trans*-Andean *Xenops* comparison, estimated θ for the Chocó population is over twice that found west of the Isthmus (Figure 4.5.A). *Attila* showed no differences in θ, with or without the western Mexico clade found at the base of the mitochondrial gene tree (Figure 4.6.A). In all three taxa, there was evidence of asymmetric gene flow in an east to west direction. Both *Automolus* (Figure 4.4.B) and *Attila* (Figure 4.6.B) exhibited a *cis*- to *trans*-Andean pattern of gene flow. In *Xenops*, gene flow patterns are from the Chocó west (Figure 4.5.B). As was shown in Chapter 2 using cyt *b*, estimated timing of divergence (*t*, scaled to μ) varied widely with *Attila* exhibiting the shallowest divergence (Figure 4.6.C) when accounting for the basal western Mexico clade. *Automolus* (Figure 4.4.C) was approximately twice the estimated *t* of *Attila*. The within *trans*-Andes break in *Xenops* was the deepest divergence estimated (Figure 4.5.C) despite being a relatively shallow split on the mitochondrial gene tree (Figure 4.2.B).

DISCUSSION

Both the phylogeographic data and demographic estimations using IM suggest the variance in across-taxa divergences reflects a history of staggered isolation versus a simultaneous event. Despite any shared mitochondrial haplotypes across *cis*- and *trans*-Andean populations, the nuclear data reveal evidence of asymmetrical gene flow in two species of lowland rainforest birds marked by relatively shallow cross-Andean divergence. In all three study taxa, there are phylogeographic breaks across the Isthmus of Panama, that in *Automolus*, pre-date cross-Andean divergences.

Table 4.2 Levels of nucleotide diversity.

		BF7		*16214*		*17483*	
		N	π	*N*	π	*N*	π
Automolus ochrolaemus	All	180	0.00362	152	0.00930	174	0.00453
	Cis-Andes	146	0.00338	122	0.00666	130	0.00218
	Trans-Andes	34	0.00380	30	0.00943	44	0.00414
Xenops minutus	All	196	0.01630	174	0.00844	196	0.00955
	Cis-Andes	152	0.01225	146	0.00717	150	0.00877
	Trans-Andes	44	0.00889	28	0.00513	46	0.00391
Attila spadiceus	All	154	0.00621	142	0.00050	140	0.00525
	Cis-Andes	74	0.00688	68	0.00076	66	0.00474
	Trans-Andes	80	0.00520	74	0.00026	74	0.00520

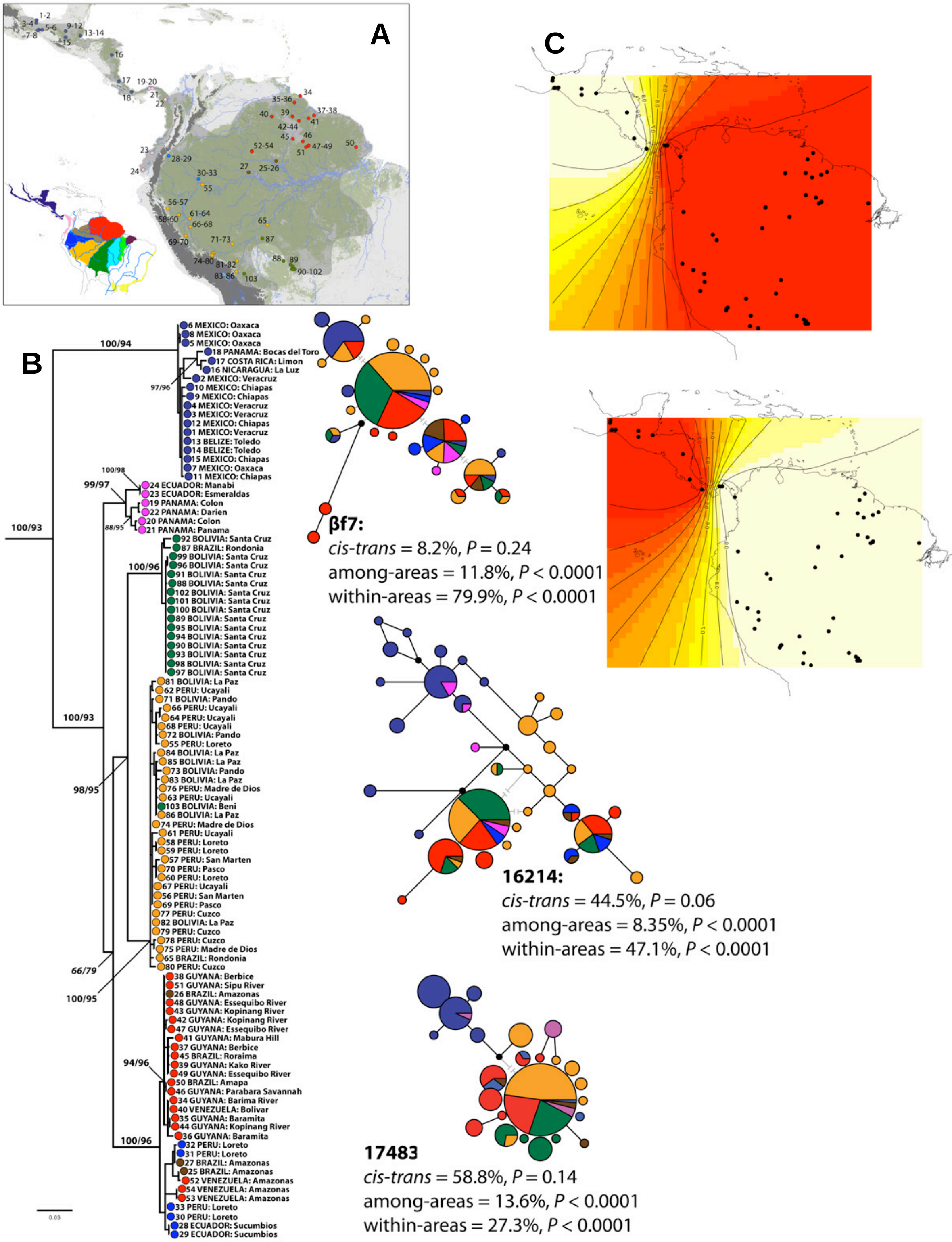


Figure 4.1 *Automolus ochrolaemus.* A) Sampling localities and areas of endemism, B) Maximum-likelihood mitochondrial gene tree (see Chapter 3) and networks/AMOVAs of nuclear markers, C) Clusters estimated using GENELAND.

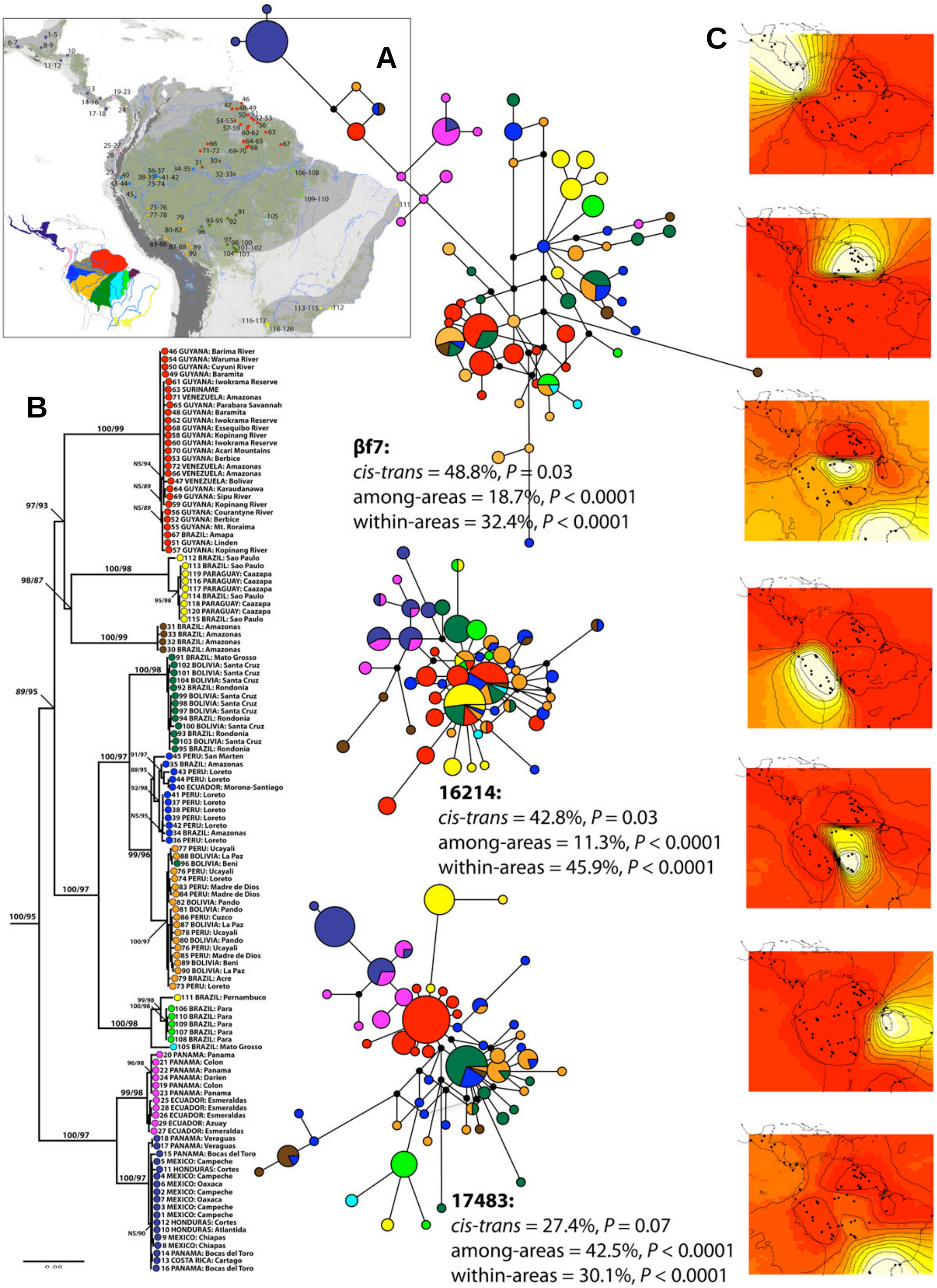


Figure 4.2 *Xenops minutus.* A) Sampling localities and areas of endemism, B) Maximum-likelihood mitochondrial gene tree (see Chapter 3) and networks/AMOVAs of nuclear markers, C) Clusters estimated using GENELAND.

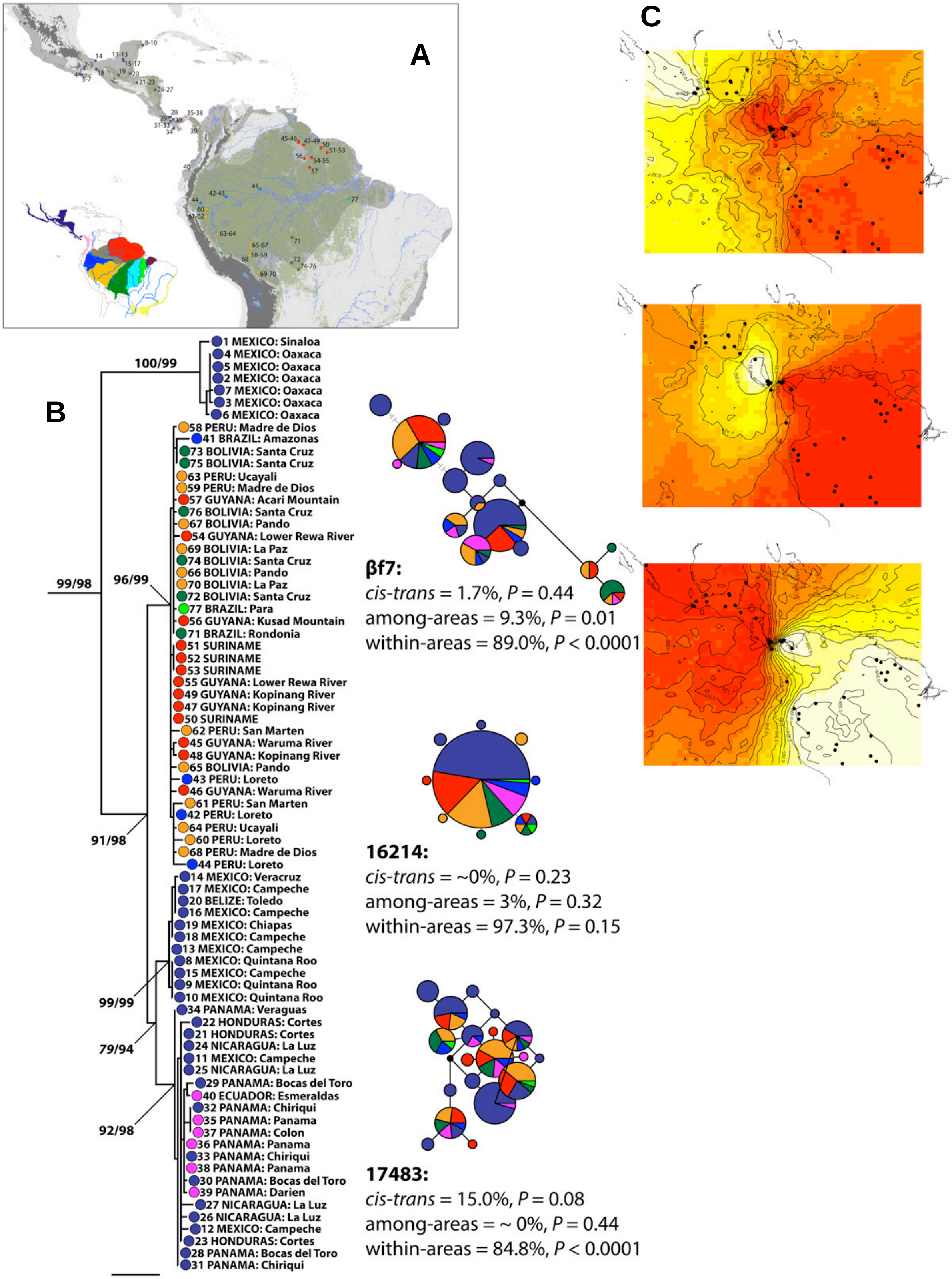


Figure 4.3 *Attila spadiceus.* A) Sampling localities and areas of endemism, B) Maximum-likelihood mitochondrial gene tree (see Chapter 3) and networks/AMOVAs of nuclear markers, C) Clusters estimated using GENELAND.

A) Posterior distribution of theta

B) Posterior distribution of gene flow estimates

C) Posterior distribution of divergences

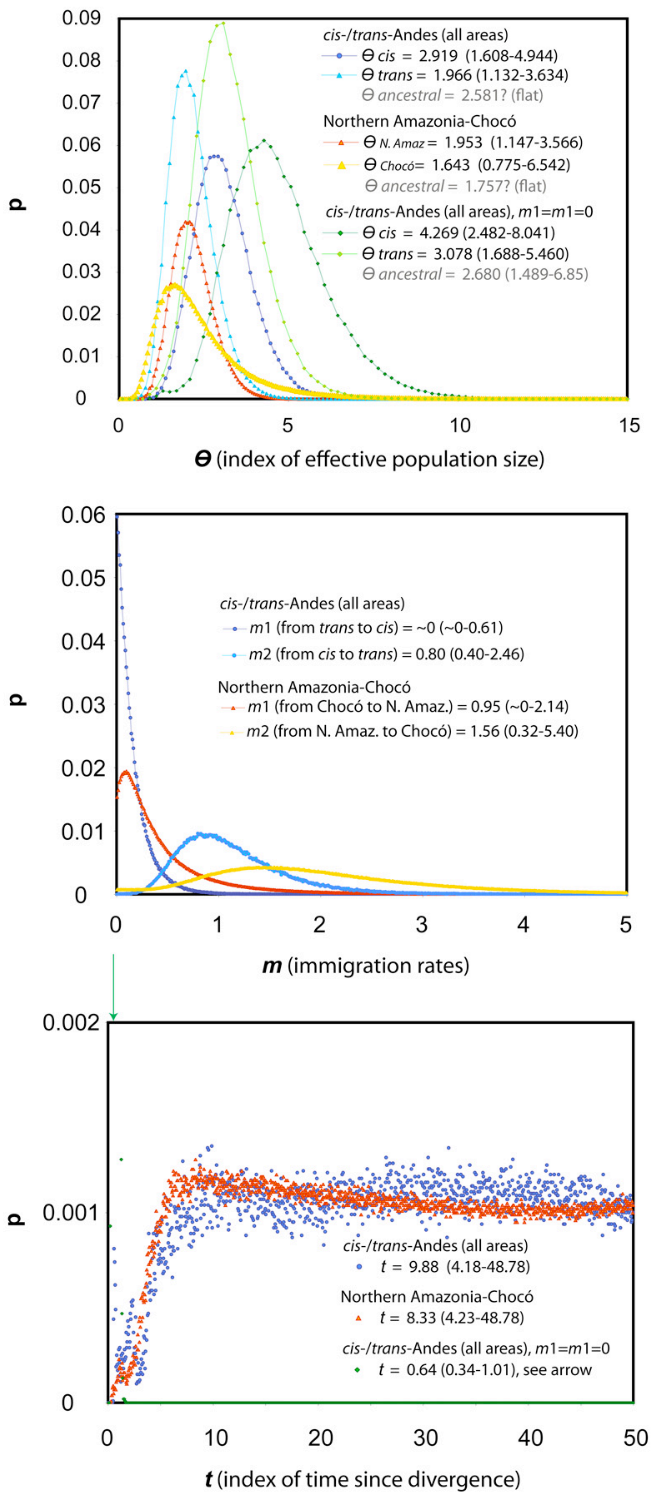


Figure 4.4 IM analyses for *Automolus ochrolaemus*.

A) Posterior distribution of theta

B) Posterior distribution of gene flow estimates

C) Posterior distribution of divergences

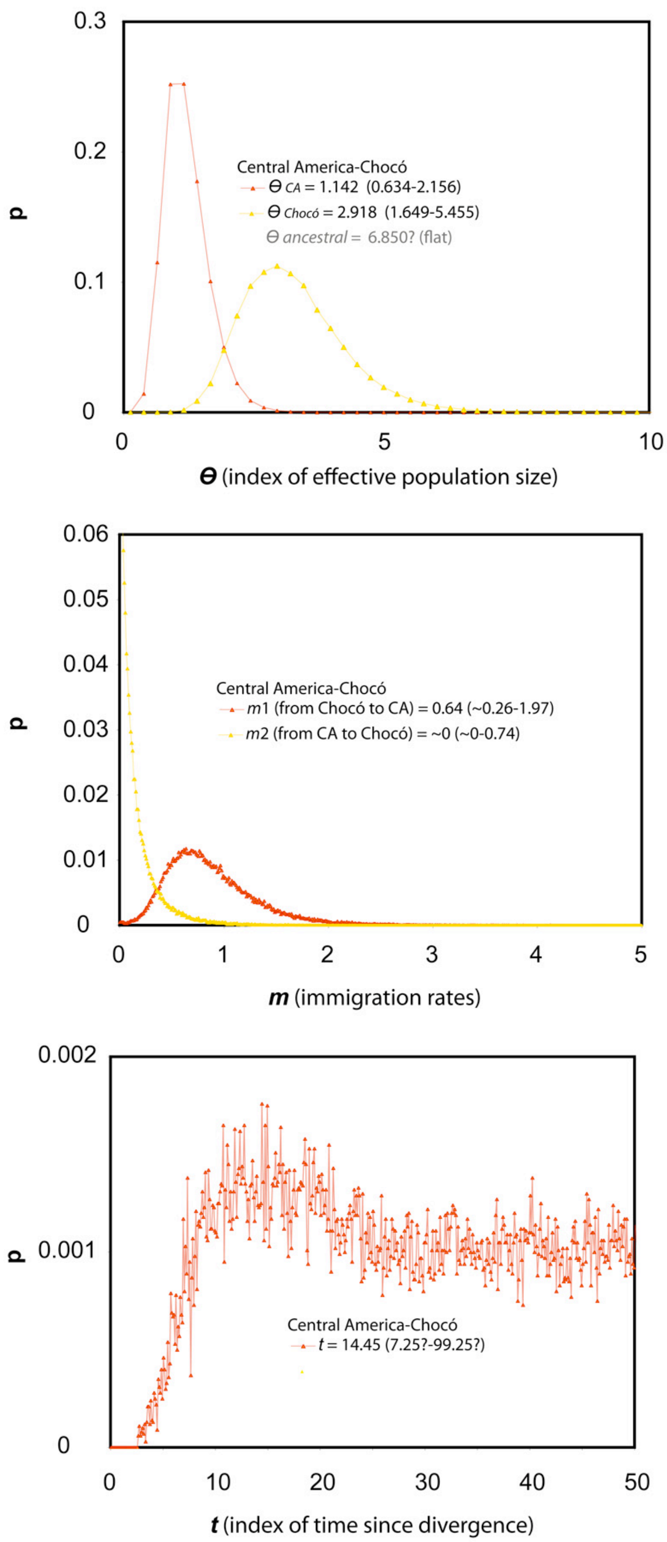
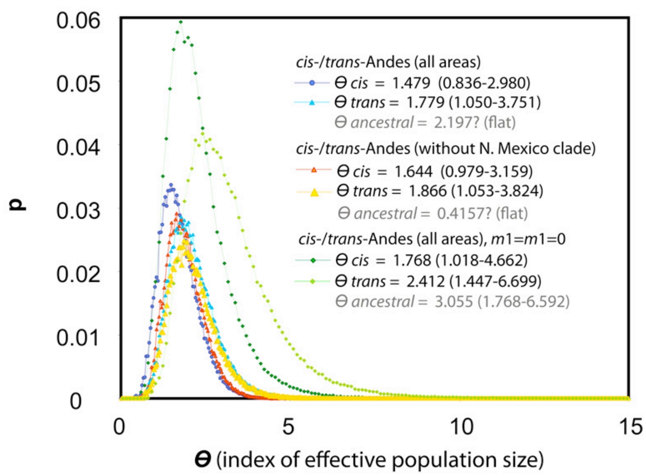
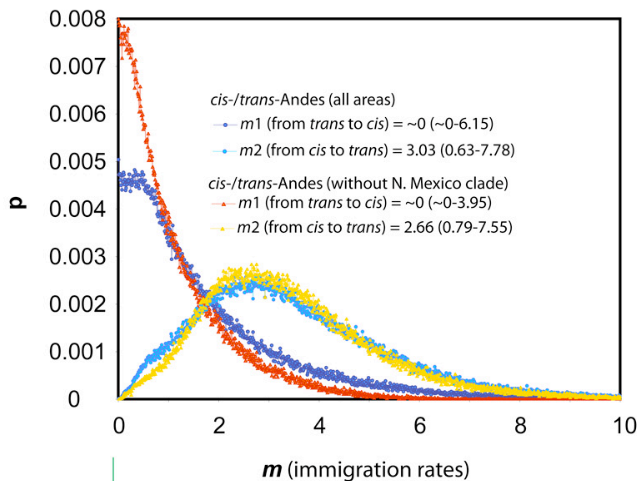


Figure 4.5 IM analyses for *Xenops minutus.*

A) Posterior distribution of theta



B) Posterior distribution of gene flow estimates



C) Posterior distribution of divergences

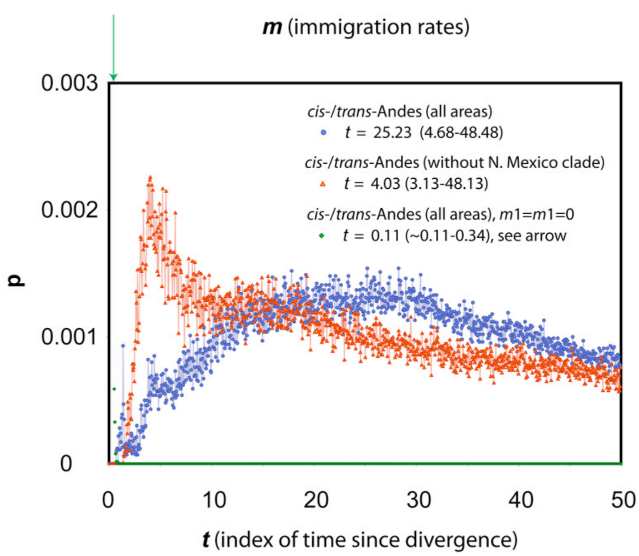


Figure 4.6 IM analyses for *Attila spadiceus.*

Staggered Isolation across the Andes

Since the Andes are approximately 2000 m or higher where ranges flank lowland rainforest, it is widely thought the Andes form an effective barrier to gene flow for lowland biota (Chapman 1917; Chapman 1926; Cracraft and Prum 1988). Published molecular studies of species complexes or populations distributed from either side of the Andes have highlighted the importance of the Andean uplift (Hackett 1996; Burns 1997; Zamudio and Greene 1997; Slade and Moritz 1998; Richardson et al. 2001; Cortes-Ortiz et al. 2003; Dick et al. 2003; Dick et al. 2004; Flanagan et al. 2004; Eberhard and Bermingham 2005; Whinnett et al. 2005; Camargo et al. 2006; Roberts et al. 2006). Levels of divergence in these studies are wide-ranging suggesting isolation was not simultaneous across co-distributed taxa (see Chapter 2). However, support for staggered isolation remains equivocal given the comparison, in many cases, involves disparate taxa and that most studies incorporated a single-locus approach in estimates of divergence.

My results using a multi-locus approach to address coalescent and demographic uncertainty suggest the variance in cross-Andean divergences across three species of lowland rainforest birds is the result of staggered isolation. This corroborates a preliminary result using approximate Bayesian computation (ABC) in the computer program MsBayes that showed the 40-taxa cyt *b* sequence data fit a scenario involving multiple isolation events (Hickerson et al. 2006b). My results suggest the effective population sizes and level of population structuring between *Attila* and *Automolus* are comparable, and thus, the difference in levels of divergence are likely due to differences in the timing of isolation. Using a substitution rate rather than a true mutation rate, the tentative IM divergence estimate in years (~1.4Mya) for *Attila* are comparable with a mtDNA divergence estimate (~1.3Mya) based on 2% sequencer divergence per million years. Although the cross-Andes divergence of *Xenops* could not be inferred using IM, it is worth noting that the timing of a more recent divergence across the *trans*-Andean phylogeographic break between the Chocó and regions west of the Panamanian Isthmus (~4.6Mya) is roughly twice the cross-Andes divergence in *Automolus.*

Historical *cis*- to *trans*-Andean Gene Flow

The *across-Andes dispersal* hypothesis states *cis*-/*trans*-Andean distributions were derived after the uplift of the Andes via dispersal (Chapman 1926; Haffer 1967). An additional prediction of the hypothesis is a dispersal bias from east (*cis*-) to west (*trans*-) since the tropical zone reaches elevations of 1500 m on the eastern slope and 600-1200 m on the western slope (Chapman 1926). My results provide support for the second prediction in both *Attila* and *Automolus*. However, the origin of cross-Andean lineages, via recent dispersal or vicariance, remains equivocal. It is worth noting that, in both taxa, no mitochondrial haplotypes are shared across the Andes and all haplogroups are represented solely by either *cis*- or *trans*-Andean individuals. IM estimates of migration are measures of gene exchange since population splitting. Thus, the signal of asymmetrical gene flow across nuclear loci in both *Attila* and *Automolus* must represent historical, rather than current migration.

Isthmus of Panama

My results reveal deep phylogeographic breaks across the Isthmus of Panama in both *Automolus* and *Xenops*. Clustering analyses of nuclear loci suggest structuring in *Attila* across this region as well. The uplift of the Panamanian Isthmus approximately 3 million years ago is thought to have united tracts of lowland tropical rainforest of the North and South American continents (Duque-Caro 1990; Coates and Obando 1996; Coates et al. 2004) providing a dispersal corridor for terrestrial organisms into and out of South America. However, molecular studies are showing this relatively confined region has a complex history (Witt 2004; Crawford et al. 2007; Dacosta and

Klicka 2008; Dick and Heuertz 2008). The paleobotanical record is inconclusive regarding the late Tertiary and Pleistocene history of this region in terms of forest cover (Burnham and Graham 1999). The fossil mammal record is composed of ungulates and supports periods of open-land savanna, however, the pollen analyses support a mixed forest landscape.

To better understand the rich diversity of South American fauna, evolutionary biologists must gain insight into mechanisms of diversification. As seen in *Xenops*, phylogeographic patterns in the Neotropics may involve complicated and deep patterns of divergence. The biogeographical history of this region is almost certainly complex, and potentially species-specific (Bush 1994). Teasing apart this history will require a thorough understanding of past geology and climate in order to generate explicit tests of long-standing process-level hypotheses (Bush 1994; Bates et al. 1998; Marks et al. 2002; Ribas et al. 2005). Lastly, new population genetic models and statistical methods are needed to more accurately estimate the timing of divergence between populations, particularly those represented by reciprocally monophyletic lineages (Arbogast et al. 2002), as well as deal with complex models of population history that include population structuring.

CHAPTER 5: CONCLUSIONS

An important goal in evolutionary biology has been to link the spatiotemporal genetic patterns within species to processes related to their ecology and life history. To this aim, researchers have employed the comparative approach to investigate whether taxa with contrasting ecologies have coinciding disagreement in one or more population genetic measures. These types of studies have traditionally focused on small assemblages and, consequently, a limited number of comparisons are made. In this dissertation, I compared patterns of genetic differention for a large number of co-distributed species, thus, permitting the use of statistical analyses in determining ecological correlates of across-taxa variance in genetic divergence and other measures.

In Chapter 2, this approach revealed that ecological differences among species of lowland Neotropical rainforest birds explain much of the interspecific variance in population genetic differentiation across three biogeographic barriers in South America. These findings are conservative given the underlying uncertainty inherent in single-locus estimates of population divergence. I suggest that habitat-mediated differences in dispersal propensity between canopy and understory species of lowland rainforest birds have affected historical patterns of gene flow and/or effective population sizes to generate the interspecific variance in across-barrier divergences.

To explore the role of biogeography on range-wide patterns of genetic variation, in Chapter 3, I examined the phylogeographic pattern of four species (two canopy and two understory) with broad distributions. I found that patterns of within-species genetic variation reflect contrasting regional biogeographic histories between *trans*-Andean and Amazonian populations. Levels of genetic diversity and partitioning of genetic variation were comparable among species of the same foraging stratum. While both canopy and understory birds exhibited marked divergence between cross-Andean populations, understory species were structured at smaller spatial scales, particularly across riverine barriers of the Amazon basin. Surprisingly, estimates of isolation by distance, a proxy for dispersal propensity, are similar through contiguous habitat for all study taxa. Lastly, unique patterns of population structuring were observed for each of the four study taxa suggesting demographic histories within the Neotropics are undoubtedly complex and largely species specific (Bush 1994).

For Chapter 4, I compared the multilocus phylogeography of three species with differing mtDNA patterns revealed in Chapter 3. Incorporating additional loci addresses the coalescent and demographic uncertainty associated with single-locus approaches. Both the phylogeographic data and demographic estimations using the coalescent-based program, Isolation with Migration (IM), suggest the variance in across-taxa divergences reflects a history of staggered isolation versus a simultaneous event. Despite the lack of shared mitochondrial haplotypes across *cis*- and *trans*-Andean populations, the nuclear sequence data reveal evidence of asymmetrical gene flow in two species of lowland rainforest birds marked by relatively shallow cross-Andean divergence. In all three study taxa, there are phylogeographic breaks across the Isthmus of Panama, and, in *Automolus ochrolaemus*, this break pre-dates the observed cross-Andean divergence.

Species' demographic histories within western Amazonia are complex, as previous phylogeographic studies have revealed (Marks et al. 2002; Cheviron et al. 2005b). Increased sampling of additional taxa, both at large and small spatial scales using a multilocus approach, are needed to evaluate general patterns of divergence across Amazonia as well as *trans*-Andean regions. My dissertation provides a glimpse of the genetic variation housed in the Neotropics.

The relationships found in this study add support to previous arguments that low dispersal propensity facilitates geographic isolation and divergence (Slatkin 1987; Bohonak 1999; Belliure et al. 2000). Studies using patterns assessed at the family-level in birds have shown the opposite trend, linking greater dispersal to higher diversification rates (Owens et al. 1999; Phillimore et al. 2006). This conflict is likely the result of differences in the phylogenetic scale at which questions regarding ecological correlates of diversity are being addressed. In my approach, I assessed within-species patterns of diversification. Insights gained at the population-level may better address the factors, including ecology, pertinent to speciation that could be overlooked in studies examining patterns at deeper phylogenetic levels. To my knowledge this is the first large-scale comparative avian study to document a significant association between ecological traits of a species and its level of genetic differentiation. My dissertation highlights the importance of basic natural history information in generating and testing associations between ecological and genetic parameters.

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APPENDIX A: LIST OF TAXA

Bird Family	Species	Max. Elevation (Meters)	Occupy *Várzea*	Habitat Use[a] (Stotz Et Al. 1996)	Habitat Breadth	Occupy Forest Edge	Strata[b] (Stotz et al. 1996)	Strata[b] (This Study)	Feeding Guild[c]	Relative Abundance[d]	Mass (g)	Primers[e,f]
Tinamidae	*Crypturellus soui*	1500	No	F1E, F15, F3	Three+	Yes	T	U	F	C	200	E1, E2, I1, I2
Columbidae	*Patagioenas subvinacea*	1800	Yes	F1,F2,F4	Three+	No	C	C	F	FC	172	E1, E2, I1, I2
Columbidae	*Geotrygon saphirina*	1100	No	F1,F4	Two	No	T	U	O	U	160.4	E1, E2, I1, I2
Psittacidae	*Pyrrhura melanura*	1500	No	F1,F4	Two	No	C	C	F	FC	83	E1, E2, I1, I2
Psittacidae	*Pionus menstruus*	1200	No	F3,F8,F1E,F15	Three+	Yes	C	C	F	C	252	E1, E2, I1, I2
Psittacidae	*Amazona farinosa*	1200	No	F1	One	No	C	C	F	FC	649.5	E1, E2, I1, I2
Cuculidae	*Piaya cayana*	2500	Yes	F1,F7,F15,F8. F2	Three+	No	C	C	I	C	98	E1, E2, I1, I2
Trogonidae	*Trogon collaris*	2500	Yes	F1,F4,F2,F7	Three+	No	M/C	C	O	C	55.5	E1, E2, I1, I2
Trogonidae	*Trogon rufus*	900	No	F1,F15	Two	No	U/M	U	O	U	52.5	E1, E2, I1, I2
Momotidae	*Baryphthengus martii*	1400	No	F1	One	No	U/M	U	I	FC	153	E1, E2, I1, I2
Furnariidae	*Automolus ochrolaemus*	1400	Yes	F1,F2	Two	No	U	U	I	C	38	E1, E2, I3, I4
Furnariidae	*Automolus rubiginosus*	2400	No	F4,F1	Two	No	U/M	U	I	U	47.5	E1, E2, I3, I4
Furnariidae	*Sclerurus mexicanus*	1800	No	F1,F4	Two	No	T	U	I	U	27	E1, E2, I3, I4
Furnariidae	*Xenops minutus*	1500	Yes	F1,F2	Two	No	U/M	U	I	FC	11	E1, E2, I3, I4
Furnariidae	*Dendrocincla fuliginosa*	1200	No	F1	One	No	U/M	U	I	FC	35.5	E1, E2, I3, I4
Furnariidae	*Glyphorynchus spirurus*	1250	No	F1,F4	Two	No	U/M	U	I	FC	16	E1, E2, I3, I4
Thamnophilidae	*Cymbilaimus lineatus*	1000	No	F1	One	No	C	C	I	FC	37.5	E1, E2, I1, I2

Appendix A cont.

Thamnophilidae	*Taraba major*	1400	No	F1E,F15,F8,N 11,N14	Three+	Yes	U	U	I	C	60	E1, E2, I1, I2
Thamnophilidae	*Myrmotherula ignota*	900	Yes	F1E,F15/F1E, F2	Three+	Yes	C	C	I	FC	7	E1, E2, I1, I2
Thamnophilidae	*Myrmotherula axillaris*	1100	Yes	F1,F2,F15	Three+	No	U/M	U	I	C	8	E1, E2, I1, I2
Tyrannidae	*Colonia colonus*	1800	No	F4E,F1E,F15	Three+	Yes	C	C	I	FC	16.5	E1, E2, I1, I2
Tyrannidae	*Attila spadiceus*	1800	No	F1,F7,F4	Three+	No	M/C	C	I	FC	38	E1, E2, I1, I2
Cotingidae	*Querula purpurata*	1050	No	F1	One	No	C	C	O	FC	101	E1, E2, I1, I2
Pipridae	*Lepidothrix coronata*	1400	No	F1,F15	Two	No	U/M	U	F	C	8.5	E1, E2, I1, I2
Tityridae	*Tityra inquisitor*	1200	No	F1,F15	Two	No	C	C	F	FC	45	E1, E2, I1, I2
Tityridae	*Tityra semifasciata*	1200	No	F1,F4,F15	Three+	No	C	C	F	C	82.5	E1, E2, I1, I2
Tityridae	*Schiffornis turdina*	1500	No	F1,F4	Two	No	U	U	O	FC	31	E1, E2, I1, I2
Vireonidae	*Hylophilus ochraceiceps*	1200	No	F1	One	No	U/M	U	I	FC	11	E1, E2, I1, I2
Troglodytidae	*Microcerculus marginatus*	1200	No	F1	One	No	T/U	U	I	FC	19.5	E3, E2, I1, I2
Troglodytidae	*Henicorhina leucosticta*	1100	No	F1,F4	Two	No	U	U	I	FC	15.7	E3, E2, I1, I2
Polioptilidae	*Microbates cinereiventris*	1200	No	F1	One	No	U	U	I	FC	10.4	E1, E2, I1, I2
Thraupidae	*Tangara gyrola*	1800	No	F4,F1	Two	No	C	C	I	FC	22.3	E1, E2, I1, I2
Thraupidae	*Tangara cyanicollis*	2400	No	F4,F1,F15	Three+	No	C	C	I	FC	17.4	E1, E2, I1, I2
Thraupidae	*Tersina viridis*	1600	No	F1E,F15,F3,F8	Three+	Yes	C	C	F	FC	28.4	E1, E2, I1, I2
Thraupidae	*Cyanerpes caeruleus*	1100	Yes	F1,F2,F15,F4	Three+	No	C	C	I	C	11.1	E1, E2, I1, I2
Thraupidae	*Chlorophanes spiza*	1600	Yes	F1,F2,F8,F15	Three+	No	C	C	O	FC	16.8	E1, E2, I1, I2

Appendix A cont.

Emberizidae	*Arremon aurantiirostris*	1200	No	F1	One	No	T	U	O	FC	25	E1, E2, I1, I2
Cardinalidae	*Saltator grossus*	1200	No	F1	One	No	M/C	C	F	FC	47.3	E1, E2, I1, I2
Parulidae	*Phaeothlypis fulvicauda*	1100	No	F1	One	No	T	U	I	FC	13.6	E1, E2, I1, I2
Icteridae	*Psarocolius angustifrons*	2400	Yes	F3,F2,F4E,F1 E,F15	Three+	Yes	C	C	F	C	306.7	E1, E2, I1, I2

[a] Habitats: F1 - Tropical lowland evergreen forest; F2 - Flooded tropical evergreen forest; F3 - River-edge forest; F4 - Montane evergreen forest; F7 - Tropical deciduous forest; F8 - Gallery forest; F15 - Secondary forest; N11 - Riparian thickets; N14 - Second-growth scrub; E - Edge (added to habitat type above)

[b] Strata: T – Terrestrial; T/U – Terrestrial/Understory; U – Understory; U/M – Understory/Midstory; M/C – Midstory/Canopy; C – Canopy

[c] Feeding Guild: F – Frugivore; I – Insectivore; O – Omnivore

[d] Relative Abundance: U – Uncommon; FC – Fairly common; C – Common

[e] External Primers: E1 - L14990 5'-CCA TCC AAC ATC TCA GCA TGA TGA AA-3'; E2 - H15915 5'-AAC TGC AGT CAT CTC CGG TTT ACA AGA C-3'; E3 - ND5emb1 5'-AGG ATC ATT CGC CCT ATC CAT-3'

[f] Internal Primers: I1 - cytb.mtf 5'-CAC GAR ACY GGR TCY AAY AAY CC-3'; I2 - cytb.intr 5'-GGR TTR TTR GAY CCR GTY TCG TG-3'; I3 - P5L 5'-CCT TCC TCC ACG AAA CAG GCT CAA ACA ACC C-3'; I4 - H658 5'-TCT TTG ATG GAG TAG TAG GGG TGG AAT GG-3'

APPENDIX B: LIST OF SAMPLES

Species	Collection	Tissue Number	Outside Source (Genbank)	Side of Andes	Area of Endemism (Cracraft 1985)	Country	State/Province/ Department	Latitude	Longitude
Crypturellus soui	ANSP	4690		*trans*	Choco	Ecuador	Esmeraldas	0.670000	-78.860000
Crypturellus soui	LSUMZ	5065		*cis*	Inambari	Peru	Loreto	-3.498869	-72.716158
Crypturellus soui	LSUMZ	6048		*cis*	Napo	Ecuador	Morona-Santiago	-2.750000	-78.000000
Crypturellus soui	LSUMZ	15073		*cis*	Rondonia	Bolivia	Santa Cruz	-13.770000	-61.950000
Crypturellus soui	LSUMZ	15170		*cis*	Rondonia	Bolivia	Santa Cruz	-13.770000	-61.950000
Crypturellus soui	LSUMZ	100031		*cis*	Rondonia	Bolivia	Santa Cruz	-13.770000	-61.950000
Patagioenas subvinacea	ANSP	3118		*trans*	Choco	Ecuador	Manabi	-1.583333	-80.666667
Patagioenas subvinacea	FMNH	SML10 45		*cis*	Inambari	Peru	Madres De Dios	-12.877300	-71.386500
Patagioenas subvinacea	LSUMZ	33054		*cis*	Napo	Peru	Cajamarca	-5.071667	-78.881667
Patagioenas subvinacea	LSUMZ	33062		*cis*	Napo	Peru	Cajamarca	-5.071667	-78.881667
Patagioenas subvinacea	LSUMZ	12314		*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
Patagioenas subvinacea	LSUMZ	12362		*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
Geotrygon saphirina	LSUMZ	11835		*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Geotrygon saphirina	LSUMZ	10770		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Geotrygon saphirina	ANSP	2638		*cis*	Napo	Ecuador	Morona-Santiago	-2.420000	-77.520000
Pyrrhura melanura	LSUMZ	11845		*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Pyrrhura melanura	LSUMZ	29972		*trans*	Choco	Ecuador	Pichincha	0.266667	-79.200000
Pyrrhura melanura	ANSP	5111	(AY751651)	*cis*	Napo	Ecuador	Sucumbios	0.166667	-77.300000
Pyrrhura melanura	ANSP	5112	(AY751652)	*cis*	Napo	Ecuador	Sucumbios	0.166667	-77.300000
Pyrrhura melanura	LSUMZ	6946		*cis*	Napo	Peru	Loreto	-3.142222	-72.721111
Pionus menstruus	ANSP	2300		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Pionus menstruus	IBUSP	2087	(EF517605)	*cis*	Inambari	Brazil	Acre	-11.000000	-68.733330
Pionus menstruus	LSUMZ	10513		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Pionus menstruus	IBUSP	2938	(EF517604)	*cis*	Rondonia	Brazil	Mato Grosso	-9.900000	-55.900000
Pionus menstruus	LSUMZ	6804		*cis*	Rondonia	Bolivia	Beni	-14.750000	-67.070000
Amazona farinosa	ANSP	2128		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Amazona farinosa	ANSP	2233		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Amazona farinosa	LSUMZ	10625		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Piaya cayana	LSUMZ	12177		*trans*	Choco	Ecuador	Pichincha	0.033300	-78.800000
Piaya cayana	LSUMZ	4718		*cis*	Inambari	Peru	Loreto	-3.498869	-72.716158
Piaya cayana	LSUMZ	12390		*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
Piaya cayana	LSUMZ	12469		*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000

Appendix B cont.

Piaya cayana	LSUMZ	14529		*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
Piaya cayana	LSUMZ	18359		*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Piaya cayana	LSUMZ	36770		*cis*	Rondonia	Brazil	Rondönia	-10.760000	-64.750000
Piaya cayana	LSUMZ	37524		*cis*	Rondonia	Bolivia	Santa Cruz	-17.333333	-59.683333
Trogon collaris	ANSP	2032		*trans*	Choco	Ecuador	Manabi	-1.583333	-80.666667
Trogon collaris	LSUMZ	10760		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Trogon collaris	LSUMZ	10657		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Trogon collaris	LSUMZ	913		*cis*	Inambari	Bolivia	La Paz	-15.290000	-67.590000
Trogon collaris	LSUMZ	22702		*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
Trogon collaris	LSUMZ	18342		*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Trogon rufus	ANSP	2380		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Trogon rufus	ANSP	2305		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Trogon rufus	LSUMZ	5060		*cis*	Inambari	Peru	Loreto	-3.489722	-72.791667
Trogon rufus	LSUMZ	27391		*cis*	Inambari	Peru	Loreto	-7.150000	-75.733333
Trogon rufus	LSUMZ	4256		*cis*	Napo	Peru	Loreto	-2.967500	-73.297500
Baryphthengus martii	ANSP	2281		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Baryphthengus martii	ANSP	2260		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Baryphthengus martii	LSUMZ	22906	Witt	*cis*	Inambari	Bolivia	La Paz	-15.180000	-68.420000
Baryphthengus martii	LSUMZ	9657	Witt	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Baryphthengus martii	LSUMZ	27572	Witt	*cis*	Inambari	Peru	Loreto	-7.133333	-75.683333
Baryphthengus martii	LSUMZ	11256	Witt	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Baryphthengus martii	ANSP	2680		*cis*	Napo	Ecuador	Morona-Santiago	-2.420000	-77.520000
Baryphthengus martii	LSUMZ	2817		*cis*	Napo	Peru	Loreto	-2.433056	-73.708056
Baryphthengus martii	LSUMZ	15241	Witt	*cis*	Rondonia	Bolivia	Santa Cruz	-13.760000	-61.910000
Automolus ochrolaemus	ANSP	3436		*trans*	Choco	Ecuador	Manabi	-1.583333	-80.666667
Automolus ochrolaemus	ANSP	4306		*trans*	Choco	Ecuador	Esmeraldas	0.660000	-79.440000
Automolus ochrolaemus	LSUMZ	8952		*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Automolus ochrolaemus	LSUMZ	9255		*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Automolus ochrolaemus	LSUMZ	10655		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Automolus ochrolaemus	LSUMZ	11048		*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Automolus ochrolaemus	LSUMZ	11164		*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Automolus ochrolaemus	LSUMZ	11244		*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Automolus ochrolaemus	LSUMZ	22613		*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
Automolus ochrolaemus	LSUMZ	22633		*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
Automolus ochrolaemus	LSUMZ	22841		*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
Automolus ochrolaemus	LSUMZ	31359		*cis*	Inambari	Brazil	Rondönia	-8.942933	-64.084047
Automolus ochrolaemus	LSUMZ	39944		*cis*	Inambari	Peru	Loreto	-7.566667	-75.891944
Automolus ochrolaemus	LSUMZ	40504		*cis*	Inambari	Peru	Loreto	-7.594444	-75.916111
Automolus ochrolaemus	LSUMZ	40554		*cis*	Inambari	Peru	Loreto	-7.561111	-75.916111

Appendix B cont.

Automolus ochrolaemus	LSUMZ	46009	*cis*	Inambari	Peru	San Marten	-6.733333	-77.383333
Automolus ochrolaemus	LSUMZ	46133	*cis*	Inambari	Peru	San Marten	-6.733333	-77.383333
Automolus ochrolaemus	ANSP	5854	*cis*	Napo	Ecuador	Sucumbios	0.250000	-77.250000
Automolus ochrolaemus	ANSP	5856	*cis*	Napo	Ecuador	Sucumbios	0.250000	-77.250000
Automolus ochrolaemus	LSUMZ	4159	*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
Automolus ochrolaemus	LSUMZ	4264	*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
Automolus ochrolaemus	LSUMZ	4353	*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
Automolus ochrolaemus	LSUMZ	12479	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
Automolus ochrolaemus	LSUMZ	12537	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
Automolus ochrolaemus	LSUMZ	14488	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
Automolus ochrolaemus	LSUMZ	14655	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
Automolus ochrolaemus	LSUMZ	18161	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Automolus ochrolaemus	LSUMZ	18197	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Automolus ochrolaemus	LSUMZ	18244	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Automolus ochrolaemus	LSUMZ	18444	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Automolus ochrolaemus	LSUMZ	18522	*cis*	Rondonia	Bolivia	Santa Cruz	-14.840000	-60.730000
Automolus ochrolaemus	LSUMZ	36699	*cis*	Rondonia	Brazil	Rondönia	-10.760000	-64.750000
Automolus rubiginosus	LSUMZ	11736	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Automolus rubiginosus	LSUMZ	11807	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Automolus rubiginosus	LSUMZ	11818	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Automolus rubiginosus	LSUMZ	5388	*cis*	Inambari	Peru	San Marten	-6.394444	-76.340278
Automolus rubiginosus	LSUMZ	10684	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Automolus rubiginosus	LSUMZ	11246	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Automolus rubiginosus	LSUMZ	28056	*cis*	Inambari	Peru	Loreto	-7.133333	-75.683333
Sclerurus mexicanus	ANSP	2410	*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Sclerurus mexicanus	LSUMZ	11742	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Sclerurus mexicanus	LSUMZ	11813	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Sclerurus mexicanus	LSUMZ	5452	*cis*	Inambari	Peru	San Marten	-6.394444	-76.340278
Sclerurus mexicanus	LSUMZ	1991	*cis*	Inambari	Peru	Pasco	-10.410833	-74.964722
Sclerurus mexicanus	LSUMZ	1078	*cis*	Inambari	Bolivia	La Paz	-15.290000	-67.590000
Sclerurus mexicanus	LSUMZ	8897	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Sclerurus mexicanus	LSUMZ	40524	*cis*	Inambari	Peru	Loreto	-7.594444	-75.916111
Sclerurus mexicanus	ANSP	4877	*cis*	Napo	Ecuador	Napo	-0.660000	-77.316600
Sclerurus mexicanus	ANSP	4454	*cis*	Napo	Ecuador	Zamora-Chinchipe	-3.625000	-78.586900
Sclerurus mexicanus	LSUMZ	6765	*cis*	Rondonia	Bolivia	Cochabamba	-17.458611	-65.395556
Xenops minutus	ANSP	2227	*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Xenops minutus	ANSP	4331	*trans*	Choco	Ecuador	Esmeraldas	0.660000	-79.440000
Xenops minutus	ANSP	3542	*trans*	Choco	Ecuador	Azuay	-2.500000	-79.416667
Xenops minutus	ANSP	2315	*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000

Appendix B cont.

Xenops minutus	LSUMZ	11948		*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Xenops minutus	LSUMZ	10510		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Xenops minutus	LSUMZ	10854		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Xenops minutus	LSUMZ	11276		*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Xenops minutus	LSUMZ	22778		*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
Xenops minutus	LSUMZ	4706		*cis*	Inambari	Peru	Loreto	-3.498869	-72.716158
Xenops minutus	LSUMZ	5442		*cis*	Inambari	Peru	San Marten	-6.394444	-76.340278
Xenops minutus	LSUMZ	6761		*cis*	Inambari	Bolivia	Beni	-14.250000	-67.600000
Xenops minutus	LSUMZ	8988		*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Xenops minutus	LSUMZ	9026		*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Xenops minutus	LSUMZ	9452		*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Xenops minutus	ANSP	1484		*cis*	Napo	Ecuador	Morona-Santiago	-3.400000	-78.550000
Xenops minutus	LSUMZ	4244		*cis*	Napo	Peru	Loreto	-2.967500	-73.297500
Xenops minutus	LSUMZ	2754		*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Xenops minutus	LSUMZ	42756		*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
Xenops minutus	LSUMZ	42810		*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
Xenops minutus	LSUMZ	4328		*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
Xenops minutus	LSUMZ	6862		*cis*	Napo	Peru	Loreto	-3.313722	-72.519992
Xenops minutus	LSUMZ	7127		*cis*	Napo	Peru	Loreto	-3.313722	-72.519992
Xenops minutus	LSUMZ	12264		*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
Xenops minutus	LSUMZ	12378		*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
Xenops minutus	LSUMZ	12760		*cis*	Rondonia	Bolivia	Santa Cruz	-13.566600	-61.233300
Xenops minutus	LSUMZ	14683		*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
Xenops minutus	LSUMZ	14752		*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
Xenops minutus	LSUMZ	15114		*cis*	Rondonia	Bolivia	Santa Cruz	-13.770000	-61.950000
Xenops minutus	LSUMZ	18175		*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Xenops minutus	LSUMZ	36719		*cis*	Rondonia	Brazil	Rondönia	-10.760000	-64.750000
Xenops minutus	LSUMZ	36696		*cis*	Rondonia	Brazil	Rondönia	-10.760000	-64.750000
Xenops minutus	LSUMZ	36779		*cis*	Rondonia	Brazil	Rondönia	-10.760000	-64.750000
Dendrocincla fuliginosa	LSUMZ	11927	Perez	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Dendrocincla fuliginosa	LSUMZ	11754	Perez	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Dendrocincla fuliginosa	LSUMZ	12096	Perez	*trans*	Choco	Ecuador	Pichincha	0.033300	-78.800000
Dendrocincla fuliginosa	LSUMZ	11175	Perez	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Dendrocincla fuliginosa	LSUMZ	10499	Perez	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Dendrocincla fuliginosa	LSUMZ	5478	Perez	*cis*	Inambari	Peru	San Marten	-6.328889	-76.303611
Dendrocincla fuliginosa	LSUMZ	27822	Perez	*cis*	Inambari	Peru	Loreto	-7.083333	-75.650000
Dendrocincla fuliginosa	LSUMZ	5438	Perez	*cis*	Inambari	Peru	San Marten	-6.394444	-76.340278
Dendrocincla fuliginosa	LSUMZ	10694	Perez	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Dendrocincla fuliginosa	LSUMZ	8947	Perez	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611

Appendix B cont.

Dendrocincla fuliginosa	LSUMZ	9193	Perez	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Dendrocincla fuliginosa	LSUMZ	6059	Perez	*cis*	Napo	Ecuador	Morona-Santiago	-2.750000	-78.000000
Dendrocincla fuliginosa	LSUMZ	12326	Perez	*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
Dendrocincla fuliginosa	LSUMZ	14452	Perez	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
Glyphorynchus spirurus	LSUMZ	11916		*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Glyphorynchus spirurus	LSUMZ	11976		*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Glyphorynchus spirurus	LSUMZ	11131		*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Glyphorynchus spirurus	LSUMZ	2042		*cis*	Inambari	Peru	Pasco	-10.410833	-74.964722
Glyphorynchus spirurus	LSUMZ	22619		*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
Glyphorynchus spirurus	LSUMZ	22842		*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
Glyphorynchus spirurus	LSUMZ	8836		*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Glyphorynchus spirurus	LSUMZ	7227		*cis*	Napo	Peru	Loreto	-3.313722	-72.519992
Glyphorynchus spirurus	LSUMZ	7233		*cis*	Napo	Peru	Loreto	-3.313722	-72.519992
Glyphorynchus spirurus	LSUMZ	7234		*cis*	Napo	Peru	Loreto	-3.313722	-72.519992
Glyphorynchus spirurus	LSUMZ	4549		*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
Glyphorynchus spirurus	LSUMZ	5967		*cis*	Napo	Ecuador	Morona-Santiago	-2.750000	-78.000000
Glyphorynchus spirurus	LSUMZ	12267		*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
Cymbilaimus lineatus	ANSP	4686		*trans*	Choco	Ecuador	Esmeraldas	0.670000	-78.860000
Cymbilaimus lineatus	LSUMZ	11156		*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Cymbilaimus lineatus	ANSP	1630		*cis*	Napo	Ecuador	Morona-Santiago	-3.400000	-78.550000
Cymbilaimus lineatus	ANSP	2641		*cis*	Napo	Ecuador	Morona-Santiago	-2.420000	-77.520000
Cymbilaimus lineatus	LSUMZ	4157		*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
Cymbilaimus lineatus	LSUMZ	6890		*cis*	Napo	Peru	Loreto	-3.313722	-72.519992
Cymbilaimus lineatus	LSUMZ	18168		*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Taraba major	ANSP	3438		*trans*	Choco	Ecuador	Manabi	-1.583333	-80.666667
Taraba major	ANSP	3432		*trans*	Choco	Ecuador	Manabi	-1.583333	-80.666667
Taraba major	LSUMZ	10797		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Taraba major	LSUMZ	10831		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Taraba major	ANSP	1567		*cis*	Napo	Ecuador	Morona-Santiago	-3.400000	-78.550000
Taraba major	LSUMZ	37544		*cis*	Rondonia	Bolivia	Santa Cruz	-17.333333	-59.683333
Taraba major	LSUMZ	37956		*cis*	Rondonia	Bolivia	Santa Cruz	-17.200000	-59.333333
Taraba major	LSUMZ	38086		*cis*	Rondonia	Bolivia	Santa Cruz	-16.666667	-58.500000
Taraba major	LSUMZ	38909		*cis*	Rondonia	Bolivia	Santa Cruz	-18.770778	-63.092694
Myrmotherula ignota	LSUMZ	29954		*trans*	Choco	Ecuador	Pichincha	0.132667	-79.132500
Myrmotherula obscura	LSUMZ	4908		*cis*	Inambari	Peru	Loreto	-3.489722	-72.791667
Myrmotherula obscura	LSUMZ	10704		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Myrmotherula axillaris	ANSP	2115		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Myrmotherula axillaris	ANSP	2271		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Myrmotherula axillaris	LSUMZ	5468		*cis*	Inambari	Peru	San Marten	-6.394444	-76.340278

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Myrmotherula axillaris	LSUMZ	27895	*cis*	Inambari	Peru	Loreto	-7.083333	-75.650000
Myrmotherula axillaris	LSUMZ	42520	*cis*	Inambari	Peru	Loreto	-5.313333	-76.275556
Myrmotherula axillaris	LSUMZ	2512	*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Myrmotherula axillaris	LSUMZ	2644	*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Myrmotherula axillaris	LSUMZ	4319	*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
Myrmotherula axillaris	LSUMZ	7051	*cis*	Napo	Peru	Loreto	-3.313722	-72.519992
Myrmotherula axillaris	LSUMZ	42872	*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
Myrmotherula axillaris	LSUMZ	12700	*cis*	Rondonia	Bolivia	Santa Cruz	-13.566600	-61.233300
Myrmotherula axillaris	LSUMZ	14916	*cis*	Rondonia	Bolivia	Santa Cruz	-13.770000	-61.950000
Myrmotherula axillaris	LSUMZ	15145	*cis*	Rondonia	Bolivia	Santa Cruz	-13.770000	-61.950000
Myrmotherula axillaris	LSUMZ	18408	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Colonia colonus	LSUMZ	11941	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Colonia colonus	LSUMZ	5945	*cis*	Napo	Ecuador	Morona-Santiago	-2.666600	-78.200000
Attila spadiceus	LSUMZ	29986	*trans*	Choco	Ecuador	Esmeraldas	1.090861	-78.690611
Attila spadiceus	LSUMZ	1013	*cis*	Inambari	Bolivia	La Paz	-15.290000	-67.590000
Attila spadiceus	LSUMZ	5419	*cis*	Inambari	Peru	San Marten	-6.394444	-76.340278
Attila spadiceus	LSUMZ	5429	*cis*	Inambari	Peru	San Marten	-6.394444	-76.340278
Attila spadiceus	LSUMZ	9353	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Attila spadiceus	LSUMZ	9506	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Attila spadiceus	LSUMZ	10613	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Attila spadiceus	LSUMZ	10639	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Attila spadiceus	LSUMZ	21231	*cis*	Inambari	Bolivia	La Paz	-15.290000	-67.590000
Attila spadiceus	LSUMZ	42434	*cis*	Inambari	Peru	Loreto	-5.330000	-76.275556
Attila spadiceus	LSUMZ	2843	*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Attila spadiceus	LSUMZ	2913	*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Attila spadiceus	LSUMZ	42724	*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
Attila spadiceus	LSUMZ	12532	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
Attila spadiceus	LSUMZ	12575	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
Attila spadiceus	LSUMZ	12599	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
Attila spadiceus	LSUMZ	12619	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
Attila spadiceus	LSUMZ	15008	*cis*	Rondonia	Bolivia	Santa Cruz	-13.770000	-61.950000
Querula purpurata	ANSP	4628	*trans*	Choco	Ecuador	Esmeraldas	0.670000	-78.860000
Querula purpurata	LSUMZ	40407	*cis*	Inambari	Peru	Loreto	-7.586111	-75.933611
Querula purpurata	LSUMZ	103546	*cis*	Inambari	Peru	Loreto	-5.083333	-74.583333
Querula purpurata	LSUMZ	27363	*cis*	Inambari	Peru	Loreto	-7.150000	-75.733333
Querula purpurata	LSUMZ	27975	*cis*	Inambari	Peru	Loreto	-7.133333	-75.683333
Querula purpurata	LSUMZ	42317	*cis*	Inambari	Peru	Loreto	-5.330000	-76.275556
Querula purpurata	LSUMZ	42318	*cis*	Inambari	Peru	Loreto	-5.330000	-76.275556
Querula purpurata	LSUMZ	42632	*cis*	Inambari	Peru	Loreto	-5.313333	-76.275556

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Querula purpurata	LSUMZ	5511	*cis*	Inambari	Peru	San Marten	-6.328889	-76.303611
Querula purpurata	LSUMZ	9495	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Querula purpurata	LSUMZ	9648	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Querula purpurata	LSUMZ	4375	*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
Querula purpurata	LSUMZ	2785	*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Querula purpurata	LSUMZ	2542	*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Querula purpurata	LSUMZ	2824	*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Lepidothrix coronata	ANSP	2140	*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Lepidothrix coronata	LSUMZ	10492	*cis*	Inambari	Peru	Ucayali	-8.130000	-74.040000
Lepidothrix coronata	LSUMZ	27832	*cis*	Inambari	Peru	Loreto	-7.130000	-75.670000
Lepidothrix coronata	LSUMZ	31333	*cis*	Inambari	Brazil	Rondönia	-9.250000	-64.400000
Lepidothrix coronata	ANSP	2490	*cis*	Napo	Ecuador	Morona-Santiago	-2.370000	-77.500000
Lepidothrix coronata	ANSP	5859	*cis*	Napo	Ecuador	Sucumbios	0.250000	-77.250000
Lepidothrix coronata	LSUMZ	2836	*cis*	Napo	Peru	Loreto	-3.270000	-73.080000
Tityra inquisitor	ANSP	4671	*trans*	Choco	Ecuador	Esmeraldas	0.670000	-78.860000
Tityra inquisitor	ANSP	4632	*trans*	Choco	Ecuador	Esmeraldas	0.670000	-78.860000
Tityra inquisitor	LSUMZ	40288	*cis*	Inambari	Peru	Loreto	-7.586111	-75.933611
Tityra inquisitor	LSUMZ	9626	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Tityra inquisitor	LSUMZ	18568	*cis*	Rondonia	Bolivia	Santa Cruz	-14.840000	-60.730000
Tityra inquisitor	LSUMZ	18569	*cis*	Rondonia	Bolivia	Santa Cruz	-14.840000	-60.730000
Tityra semifasciata	ANSP	2377	*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Tityra semifasciata	ANSP	2326	*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Tityra semifasciata	LSUMZ	12007	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Tityra semifasciata	LSUMZ	10608	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Tityra semifasciata	LSUMZ	40861	*cis*	Inambari	Peru	Loreto	-7.586167	-75.900333
Tityra semifasciata	LSUMZ	1990	*cis*	Inambari	Peru	Pasco	-10.410833	-74.964722
Tityra semifasciata	LSUMZ	22812	*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
Tityra semifasciata	LSUMZ	42582	*cis*	Inambari	Peru	Loreto	-5.313333	-76.275556
Tityra semifasciata	LSUMZ	9434	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Tityra semifasciata	ANSP	1546	*cis*	Napo	Ecuador	Morona-Santiago	-3.400000	-78.550000
Tityra semifasciata	LSUMZ	14748	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
Tityra semifasciata	LSUMZ	18171	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Tityra semifasciata	LSUMZ	18275	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
Tityra semifasciata	LSUMZ	38928	*cis*	Rondonia	Bolivia	Cochabamba	-17.146389	-65.779444
Schiffornis turdina	LSUMZ	11889	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Schiffornis turdina	LSUMZ	6028	*cis*	Napo	Ecuador	Morona-Santiago	-2.750000	-78.000000
Hylophilus ochraceiceps	ANSP	2242	*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Hylophilus ochraceiceps	LSUMZ	4952	*cis*	Inambari	Peru	Loreto	-3.498869	-72.716158
Hylophilus ochraceiceps	LSUMZ	11173	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722

Appendix B cont.

Hylophilus ochraceiceps	LSUMZ	106764		*cis*	Inambari	Bolivia	Beni	-14.250000	-67.600000
Hylophilus ochraceiceps	LSUMZ	5480		*cis*	Inambari	Peru	San Marten	-6.328889	-76.303611
Hylophilus ochraceiceps	LSUMZ	9357		*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Hylophilus ochraceiceps	ANSP	4880		*cis*	Napo	Ecuador	Napo	-0.660000	-77.316600
Hylophilus ochraceiceps	LSUMZ	7010		*cis*	Napo	Peru	Loreto	-3.313722	-72.519992
Hylophilus ochraceiceps	LSUMZ	2534		*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Hylophilus ochraceiceps	LSUMZ	42609		*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
Hylophilus ochraceiceps	LSUMZ	42694		*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
Hylophilus ochraceiceps	LSUMZ	42701		*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
Hylophilus ochraceiceps	LSUMZ	42765		*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
Hylophilus ochraceiceps	LSUMZ	36633		*cis*	Rondonia	Brazil	Rondönia	-10.760000	-64.750000
Hylophilus ochraceiceps	LSUMZ	36752		*cis*	Rondonia	Brazil	Rondönia	-10.760000	-64.750000
Microcerculus marginatus	ANSP	2408		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Microcerculus marginatus	ANSP	2248		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Microcerculus marginatus	LSUMZ	11839		*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Microcerculus marginatus	LSUMZ	10697		*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
Microcerculus marginatus	LSUMZ	11053		*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Microcerculus marginatus	LSUMZ	4734		*cis*	Inambari	Peru	Loreto	-3.498869	-72.716158
Microcerculus marginatus	LSUMZ	9146		*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Microcerculus marginatus	ANSP	2518		*cis*	Napo	Ecuador	Morona-Santiago	-2.420000	-77.520000
Microcerculus marginatus	ANSP	1556		*cis*	Napo	Ecuador	Morona-Santiago	-3.400000	-78.550000
Microcerculus marginatus	LSUMZ	2640		*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Microcerculus marginatus	LSUMZ	2513		*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Microcerculus marginatus	LSUMZ	42842		*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
Microcerculus marginatus	LSUMZ	4459		*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
Microcerculus marginatus	LSUMZ	7077		*cis*	Napo	Peru	Loreto	-3.313722	-72.519992
Microcerculus marginatus	FMNH	JH-014	(AY612516)	*cis*	Rondonia	Brazil	Mato Grosso	-9.904000	-55.881000
Microcerculus marginatus	FMNH	JH-260	(AY612515)	*cis*	Rondonia	Brazil	Mato Grosso	-9.904000	-55.881000
Microcerculus marginatus	FMNH	JH-124	(AY612514)	*cis*	Rondonia	Brazil	Mato Grosso	-9.904000	-55.881000
Microcerculus marginatus	FMNH	JH-052	(AY612513)	*cis*	Rondonia	Brazil	Mato Grosso	-9.904000	-55.881000
Microcerculus marginatus	FMNH	JH-395	(AY612512)	*cis*	Rondonia	Brazil	Mato Grosso	-9.904000	-55.881000
Microcerculus marginatus	FMNH	JH-376	(AY612511)	*cis*	Rondonia	Brazil	Mato Grosso	-9.904000	-55.881000
Microcerculus marginatus	LSUMZ	106784		*cis*	Rondonia	Bolivia	Beni	-15.500000	-67.116600
Microcerculus marginatus	LSUMZ	1092		*cis*	Rondonia	Bolivia	La Paz	-15.290000	-67.590000
Henicorhina leucosticta	ANSP	2396		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Henicorhina leucosticta	ANSP	2426		*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Henicorhina leucosticta	LSUMZ	12005		*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Henicorhina leucosticta	LSUMZ	11738		*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
Henicorhina leucosticta	LSUMZ	11868		*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000

Appendix B cont.

Henicorhina leucosticta	LSUMZ	5391	*cis*	Inambari	Peru	San Marten	-6.394444	-76.340278
Henicorhina leucosticta	ANSP	2482	*cis*	Napo	Ecuador	Morona-Santiago	-2.420000	-77.520000
Henicorhina leucosticta	ANSP	2630	*cis*	Napo	Ecuador	Morona-Santiago	-2.420000	-77.520000
Henicorhina leucosticta	ANSP	2653	*cis*	Napo	Ecuador	Morona-Santiago	-2.420000	-77.520000
Henicorhina leucosticta	LSUMZ	42803	*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
Henicorhina leucosticta	LSUMZ	43060	*cis*	Choco	Peru	Loreto	-4.280833	-77.237778
Henicorhina leucosticta	LSUMZ	6019	*cis*	Inambari	Ecuador	Morona-Santiago	-2.750000	-78.000000
Microbates cinereiventris	ANSP	2283	*trans*	Napo	Ecuador	Esmeraldas	1.030000	-78.580000
Microbates cinereiventris	LSUMZ	11812	*trans*	Rondonia	Ecuador	Esmeraldas	0.866667	-78.550000
Microbates cinereiventris	LSUMZ	11750	*trans*	Rondonia	Ecuador	Esmeraldas	0.866667	-78.550000
Microbates cinereiventris	ANSP	2589	*cis*	Rondonia	Ecuador	Morona-Santiago	-2.420000	-77.520000
Tangara gyrola	ANSP	4337	*trans*	Choco	Ecuador	Esmeraldas	0.660000	-79.440000
Tangara gyrola	LSUMZ	34886	*trans*	Inambari	Ecuador	Pichincha	0.300000	-78.900000
Tangara gyrola	LSUMZ	34861	*trans*	Napo	Ecuador	Pichincha	0.150000	-79.200000
Tangara gyrola	LSUMZ	34869	*trans*	Napo	Ecuador	Pichincha	0.216667	-79.033333
Tangara gyrola	LSUMZ	34911	*trans*	Rondonia	Ecuador	Pichincha	0.333333	-79.016667
Tangara gyrola	LSUMZ	22850	*cis*	Rondonia	Bolivia	La Paz	-15.188056	-68.255000
Tangara gyrola	LSUMZ	11294	*cis*	Choco	Peru	Ucayali	-8.090833	-74.444722
Tangara gyrola	LSUMZ	11150	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
Tangara gyrola	LSUMZ	22706	*cis*	Napo	Bolivia	La Paz	-15.188056	-68.255000
Tangara gyrola	LSUMZ	27563	*cis*	Choco	Peru	Loreto	-7.133333	-75.683333
Tangara gyrola	LSUMZ	28002	*cis*	Choco	Peru	Loreto	-7.083333	-75.650000
Tangara gyrola	LSUMZ	28004	*cis*	Napo	Peru	Loreto	-7.083333	-75.650000
Tangara gyrola	LSUMZ	5397	*cis*	Napo	Peru	San Marten	-6.394444	-76.340278
Tangara gyrola	ANSP	2677	*cis*	Napo	Ecuador	Morona-Santiago	-2.420000	-77.520000
Tangara gyrola	LSUMZ	4258	*cis*	Choco	Peru	Loreto	-2.819997	-73.273803
Tangara gyrola	LSUMZ	6838	*cis*	Inambari	Peru	Loreto	-3.313722	-72.519992
Tangara gyrola	LSUMZ	34925	*cis*	Inambari	Ecuador	Napo	-0.685300	-77.865600
Tangara gyrola	LSUMZ	14862	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
Tangara gyrola	LSUMZ	12295	*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
Tangara gyrola	LSUMZ	12604	*cis*	Choco	Bolivia	Santa Cruz	-14.810000	-60.810000
Tangara gyrola	LSUMZ	13020	*cis*	Choco	Bolivia	Santa Cruz	-13.566600	-61.233300
Tangara gyrola	LSUMZ	6793	*cis*	Inambari	Bolivia	Beni	-15.500000	-67.116600
Tangara gyrola	LSUMZ	936	*cis*	Choco	Bolivia	La Paz	-15.290000	-67.590000
Tangara cyanicollis	LSUMZ	34904	*trans*	Inambari	Ecuador	Pichincha	0.150000	-79.200000
Tangara cyanicollis	LSUMZ	35010	*cis*	Rondonia	Ecuador	Pichincha	0.000000	-78.900000
Tangara cyanicollis	LSUMZ	5613	*cis*	Rondonia	Peru	San Marten	-6.050000	-76.733333
Tangara cyanicollis	LSUMZ	22724	*cis*	Rondonia	Bolivia	La Paz	-15.188056	-68.255000
Tangara cyanicollis	LSUMZ	34824	*cis*	Rondonia	Peru	Cajamarca	-4.991667	-78.905000

Appendix B cont.

Tangara cyanicollis	LSUMZ	15351	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
Tangara cyanicollis	LSUMZ	14423	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
Tangara cyanicollis	LSUMZ	15097	*cis*	Choco	Bolivia	Santa Cruz	-13.770000	-61.950000
Tangara cyanicollis	LSUMZ	18102	*cis*	Inambari	Bolivia	Santa Cruz	-14.833333	-60.416667
Tersina viridis	LSUMZ	11788	*trans*	Inambari	Ecuador	Esmeraldas	0.866667	-78.550000
Tersina viridis	LSUMZ	9680	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Tersina viridis	LSUMZ	5527	*cis*	Inambari	Peru	San Marten	-6.050000	-76.733333
Tersina viridis	LSUMZ	9132	*cis*	Rondonia	Bolivia	Pando	-11.470278	-68.778611
Tersina viridis	LSUMZ	9640	*cis*	Choco	Bolivia	Pando	-11.470278	-68.778611
Tersina viridis	LSUMZ	944	*cis*	Choco	Bolivia	La Paz	-15.290000	-67.590000
Tersina viridis	LSUMZ	27997	*cis*	Inambari	Peru	Loreto	-7.133333	-75.683333
Tersina viridis	LSUMZ	2914	*cis*	Inambari	Peru	Loreto	-3.179269	-72.903511
Tersina viridis	LSUMZ	2632	*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Tersina viridis	LSUMZ	14819	*cis*	Choco	Bolivia	Santa Cruz	-13.770000	-61.950000
Tersina viridis	LSUMZ	14912	*cis*	Choco	Bolivia	Santa Cruz	-13.770000	-61.950000
Tersina viridis	LSUMZ	12855	*cis*	Inambari	Bolivia	Santa Cruz	-13.566600	-61.233300
Tersina viridis	LSUMZ	37911	*cis*	Inambari	Bolivia	Santa Cruz	-17.200000	-59.333333
Tersina viridis	LSUMZ	37912	*cis*	Inambari	Bolivia	Santa Cruz	-17.200000	-59.333333
Cyanerpes caeruleus	LSUMZ	11825	*trans*	Inambari	Ecuador	Esmeraldas	0.866667	-78.550000
Cyanerpes caeruleus	LSUMZ	5404	*cis*	Napo	Peru	San Marten	-6.394444	-76.340278
Cyanerpes caeruleus	LSUMZ	2730	*cis*	Napo	Peru	Loreto	-3.179269	-72.903511
Cyanerpes caeruleus	LSUMZ	12906	*cis*	Rondonia	Bolivia	Santa Cruz	-13.566600	-61.233300
Chlorophanes spiza	ANSP	2453	*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
Chlorophanes spiza	LSUMZ	5431	*cis*	Choco	Peru	San Marten	-6.394444	-76.340278
Chlorophanes spiza	LSUMZ	9048	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
Chlorophanes spiza	LSUMZ	22731	*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
Chlorophanes spiza	LSUMZ	27666	*cis*	Inambari	Peru	Loreto	-7.133333	-75.683333
Chlorophanes spiza	LSUMZ	28014	*cis*	Inambari	Peru	Loreto	-7.083333	-75.650000
Chlorophanes spiza	LSUMZ	42292	*cis*	Inambari	Peru	Loreto	-5.330000	-76.275556
Chlorophanes spiza	LSUMZ	42349	*cis*	Inambari	Peru	Loreto	-5.330000	-76.275556
Chlorophanes spiza	LSUMZ	42539	*cis*	Inambari	Peru	Loreto	-5.313333	-76.275556
Chlorophanes spiza	LSUMZ	2727	*cis*	Inambari	Peru	Loreto	-3.179269	-72.903511
Chlorophanes spiza	LSUMZ	2783	*cis*	Inambari	Peru	Loreto	-3.179269	-72.903511
Chlorophanes spiza	LSUMZ	2838	*cis*	Inambari	Peru	Loreto	-3.179269	-72.903511
Chlorophanes spiza	LSUMZ	2861	*cis*	Inambari	Peru	Loreto	-3.179269	-72.903511
Chlorophanes spiza	LSUMZ	12296	*cis*	Inambari	Bolivia	Santa Cruz	-14.270000	-60.990000
Chlorophanes spiza	LSUMZ	12339	*cis*	Inambari	Bolivia	Santa Cruz	-14.270000	-60.990000
Chlorophanes spiza	LSUMZ	12486	*cis*	Inambari	Bolivia	Santa Cruz	-14.810000	-60.810000
Arremon aurantiirostris	ANSP	3148	*trans*	Inambari	Ecuador	Manabi	-1.583333	-80.666667

Appendix B cont.

Arremon aurantiirostris	ANSP	3508		*trans*	Napo	Ecuador	Azuay	-2.500000	-79.416667
Arremon aurantiirostris	ANSP	3627		*trans*	Napo	Ecuador	Azuay	-2.500000	-79.416667
Arremon aurantiirostris	LSUMZ	12044		*trans*	Napo	Ecuador	Pichincha	0.033300	-78.800000
Arremon aurantiirostris	LSUMZ	5495		*cis*	Napo	Peru	San Marten	-6.328889	-76.303611
Arremon aurantiirostris	ANSP	4857		*cis*	Napo	Ecuador	Napo	-0.660000	-77.316600
Arremon aurantiirostris	LSUMZ	5983		*cis*	Rondonia	Ecuador	Morona-Santiago	-2.750000	-78.000000
Arremon aurantiirostris	LSUMZ	5994		*cis*	Rondonia	Ecuador	Morona-Santiago	-2.750000	-78.000000
Saltator grossus	ANSP	2398		*trans*	Rondonia	Ecuador	Esmeraldas	1.030000	-78.580000
Saltator grossus	ANSP	2457		*trans*	Rondonia	Ecuador	Esmeraldas	1.030000	-78.580000
Saltator grossus	LSUMZ	11942		*trans*	Rondonia	Ecuador	Esmeraldas	0.866667	-78.550000
Saltator grossus	LSUMZ	11943		*trans*	Rondonia	Ecuador	Esmeraldas	0.866667	-78.550000
Saltator grossus	LSUMZ	11197		*cis*	Rondonia	Peru	Ucayali	-8.090833	-74.444722
Saltator grossus	LSUMZ	11169		*cis*	Rondonia	Peru	Ucayali	-8.090833	-74.444722
Saltator grossus	LSUMZ	5439		*cis*	Rondonia	Peru	San Marten	-6.394444	-76.340278
Saltator grossus	LSUMZ	9662		*trans*	Rondonia	Bolivia	Pando	-11.470278	-68.778611
Saltator grossus	LSUMZ	2873		*cis*	Choco	Peru	Loreto	-3.179269	-72.903511
Saltator grossus	LSUMZ	18432		*cis*	Choco	Bolivia	Santa Cruz	-14.833333	-60.416667
Saltator grossus	LSUMZ	35254		*cis*	Choco	Brazil	Mato Grosso	-9.830833	-56.092500
Saltator grossus	LSUMZ	948		*cis*	Inambari	Bolivia	La Paz	-15.290000	-67.590000
Phaeothlypis fulvicauda	LSUMZ	11873	(AY340210)	*trans*	Inambari	Ecuador	Esmeraldas	0.866667	-78.550000
Phaeothlypis rivularis	LSUMZ	1146	(AY340209)	*cis*	Inambari	Bolivia	La Paz	-15.290000	-67.590000
Phaeothlypis rivularis	LSUMZ	2050	(AY340215)	*cis*	Inambari	Peru	Pasco	-10.410833	-74.964722
Phaeothlypis fulvicauda	ANSP	1527	(AY340211)	*cis*	Choco	Ecuador	Morona-Santiago	-3.400000	-78.550000
Phaeothlypis rivularis	LSUMZ	7061	(AY340216)	*cis*	Choco	Peru	Loreto	-3.142222	-72.721111
Phaeothlypis fulvicauda	LSUMZ	42908		*cis*	Choco	Peru	Loreto	-4.280833	-77.237778
Phaeothlypis fulvicauda	LSUMZ	36701		*cis*	Inambari	Brazil	Rondönia	-10.760000	-64.750000
Psarocolius angustifrons	LSUMZ	7776	(AF472365)	*trans*	Inambari	Ecuador	Pichincha	0.030000	-78.810000
Psarocolius angustifrons	LSUMZ	7790		*trans*	Inambari	Ecuador	Pichincha	0.030000	-78.810000
Psarocolius angustifrons	FMNH	324068	(AF472362)	*cis*	Inambari	Peru	Madres De Dios	-12.877300	-71.386500
Psarocolius angustifrons	LSUMZ	32967	(AF472363)	*cis*	Inambari	Peru	Cajamarca	-5.383333	-78.771667
Psarocolius angustifrons	LSUMZ	7273	(AF472364)	*cis*	Napo	Peru	Loreto	-3.386197	-72.632553
Psarocolius angustifrons	LSUMZ	7241		*cis*	Napo	Peru	Loreto	-3.386197	-72.632553

APPENDIX C: LIST OF INDIVIDUAL SAMPLES OF *AUTOMOLUS OCHROLAEMUS*

Sample ID	Collection	Tissue Number	Side of Andes	Area of Endemism (da Silva 2005)	Country	State/Province/ Department	Latitude	Longitude
1	FIELD	393900	*trans*	North CA & W Pan	Mexico	Veracruz	18.362000	-94.838000
2	FIELD	393901	*trans*	North CA & W Pan	Mexico	Veracruz	18.362000	-94.838000
3	FIELD	343240	*trans*	North CA & W Pan	Mexico	Veracruz	18.000000	-94.900000
4	FIELD	343241	*trans*	North CA & W Pan	Mexico	Veracruz	18.000000	-94.900000
5	MZFC	CHIMA027	*trans*	North CA & W Pan	Mexico	Oaxaca	17.066819	-94.118333
6	MZFC	CHIMA107	*trans*	North CA & W Pan	Mexico	Oaxaca	17.066819	-94.118333
7	MZFC	CHIMA175	*trans*	North CA & W Pan	Mexico	Oaxaca	17.066667	-94.583333
8	MZFC	OMVP562	*trans*	North CA & W Pan	Mexico	Oaxaca	17.006667	-94.689444
9	MZFC	YACH354	*trans*	North CA & W Pan	Mexico	Chiapas	16.905833	-90.982778
10	MZFC	YACH072	*trans*	North CA & W Pan	Mexico	Chiapas	16.901667	-90.973333
11	MZFC	YACH238	*trans*	North CA & W Pan	Mexico	Chiapas	16.901667	-90.973333
12	MZFC	YACH400	*trans*	North CA & W Pan	Mexico	Chiapas	16.901667	-90.973333
13	LSUMZ	3774	*trans*	North CA & W Pan	Belize	Toledo	16.290000	-89.020000
14	LSUMZ	8766	*trans*	North CA & W Pan	Belize	Toledo	16.290000	-89.020000
15	MZFC	YACH368	*trans*	North CA & W Pan	Mexico	Chiapas	16.084167	-90.976667
16	BARR	4376	*trans*	North CA & W Pan	Nicaragua		13.701667	-84.851669
17	LSUMZ	16279	*trans*	North CA & W Pan	Costa Rica	Limon	10.208333	-83.880556
18	LSUMZ	51424	*trans*	North CA & W Pan	Panama	Bocas del Toro	8.791389	-82.209844
19	LSUMZ	26528	*trans*	Choco	Panama	Colon	9.250833	-79.781111
20	LSUMZ	26537	*trans*	Choco	Panama	Colon	9.250833	-79.781111
21	BARR	15332	*trans*	Choco	Panama	Panama	9.237500	-79.412333
22	LSUMZ	2241	*trans*	Choco	Panama	Darien	7.756000	-77.684000
23	ANSP	4306	*trans*	Choco	Ecuador	Esmeraldas	0.660000	-79.440000
24	ANSP	3436	*trans*	Choco	Ecuador	Manabi	-1.583333	-80.666667
25	AMNH	14519	*cis*	Imeri	Brazil	Amazonas	-0.416667	-62.933333
26	AMNH	14626	*cis*	Imeri	Brazil	Amazonas	-0.416667	-62.933333
27	FIELD	457890	*cis*	Imeri	Brazil	Amazonas	-1.936700	-66.605000
28	ANSP	5854	*cis*	Napo	Ecuador	Sucumbios	0.250000	-77.250000
29	ANSP	5956	*cis*	Napo	Ecuador	Sucumbios	0.250000	-77.250000
30	LSUMZ	4159	*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
31	LSUMZ	4234	*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
32	LSUMZ	4264	*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
33	LSUMZ	4353	*cis*	Napo	Peru	Loreto	-2.819997	-73.273803
34	USNM	14589	*cis*	Guiana	Guyana		8.250000	-59.733333
35	USNM	9415	*cis*	Guiana	Guyana	Northwest	7.366667	-60.483333

Appendix C cont.

36	USNM	9513	*cis*	Guiana	Guyana	Northwest	7.366667	-60.483333
37	USNM	4185	*cis*	Guiana	Guyana	Berbice	5.666667	-57.883333
38	USNM	4187	*cis*	Guiana	Guyana	Berbice	5.666667	-57.883333
39	USNM	14298	*cis*	Guiana	Guyana		5.516667	-60.733333
40	AMNH	2950	*cis*	Guiana	Venezuela	Bolivar	5.500000	-63.500000
41	ANSP	5716	*cis*	Guiana	Guyana		5.283330	-58.633330
42	LSUMZ	48382	*cis*	Guiana	Guyana		4.932778	-59.893611
43	LSUMZ	48396	*cis*	Guiana	Guyana		4.932778	-59.893611
44	LSUMZ	48411	*cis*	Guiana	Guyana		4.932778	-59.893611
45	FIELD	389199	*cis*	Guiana	Brazil	Roraima	2.540500	-60.710800
46	USNM	12563	*cis*	Guiana	Guyana		2.200000	-59.366667
47	USNM	11390	*cis*	Guiana	Guyana		1.650000	-58.616667
48	USNM	11935	*cis*	Guiana	Guyana		1.650000	-58.616667
49	USNM	11630	*cis*	Guiana	Guyana		1.583333	-58.633333
50	FIELD	391345	*cis*	Guiana	Brazil	Amapa	1.429200	-52.279700
51	USNM	10423	*cis*	Guiana	Guyana		1.416667	-58.950000
52	AMNH	12394	*cis*	Guiana	Venezuela	Amazonas	0.916667	-66.166667
53	AMNH	12407	*cis*	Guiana	Venezuela	Amazonas	0.916667	-66.166667
54	AMNH	12688	*cis*	Guiana	Venezuela	Amazonas	0.834167	-66.166667
55	LSUMZ	5123	*cis*	Inambari	Peru	Loreto	-3.552193	-72.749257
56	LSUMZ	46009	*cis*	Inambari	Peru	San Marten	-6.733333	-77.383333
57	LSUMZ	46133	*cis*	Inambari	Peru	San Marten	-6.733333	-77.383333
58	LSUMZ	40554	*cis*	Inambari	Peru	Loreto	-7.561111	-75.916111
59	LSUMZ	39944	*cis*	Inambari	Peru	Loreto	-7.566667	-75.891944
60	LSUMZ	40504	*cis*	Inambari	Peru	Loreto	-7.594444	-75.916111
61	LSUMZ	11048	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
62	LSUMZ	11164	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
63	LSUMZ	11187	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
64	LSUMZ	11244	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
65	LSUMZ	31359	*cis*	Inambari	Brazil	Rondonia	-8.942933	-64.084047
66	LSUMZ	10514	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
67	LSUMZ	10655	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
68	LSUMZ	10864	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
69	LSUMZ	2027	*cis*	Inambari	Peru	Pasco	-10.410833	-74.964722
70	LSUMZ	2063	*cis*	Inambari	Peru	Pasco	-10.410833	-74.964722
71	LSUMZ	8921	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
72	LSUMZ	8952	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
73	LSUMZ	9255	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
74	FIELD	397967	*cis*	Inambari	Peru	Madre de Dios	-12.666944	-71.270556

Appendix C cont.

75	FIELD	433309	*cis*	Inambari	Peru	Madre de Dios	-12.766667	-71.383333
76	FIELD	433310	*cis*	Inambari	Peru	Madre de Dios	-12.766667	-71.383333
77	FIELD	433308	*cis*	Inambari	Peru	Cuzco	-13.016667	-71.483333
78	FIELD	433311	*cis*	Inambari	Peru	Cuzco	-13.016667	-71.483333
79	FIELD	433312	*cis*	Inambari	Peru	Cuzco	-13.016667	-71.483333
80	FIELD	433313	*cis*	Inambari	Peru	Cuzco	-13.016667	-71.483333
81	FIELD	391104	*cis*	Inambari	Bolivia	La Paz	-13.750000	-68.150000
82	FIELD	391105	*cis*	Inambari	Bolivia	La Paz	-13.750000	-68.150000
83	LSUMZ	22613	*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
84	LSUMZ	22633	*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
85	LSUMZ	22733	*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
86	LSUMZ	22841	*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
87	LSUMZ	36699	*cis*	Rondonia	Brazil	Rondonia	-10.760000	-64.750000
88	LSUMZ	15160	*cis*	Rondonia	Bolivia	Santa Cruz	-13.770000	-61.950000
89	LSUMZ	12375	*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
90	LSUMZ	13829	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
91	LSUMZ	14484	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
92	LSUMZ	14488	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
93	LSUMZ	14655	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
94	LSUMZ	12479	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
95	LSUMZ	12537	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
96	LSUMZ	18161	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
97	LSUMZ	18197	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
98	LSUMZ	18225	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
99	LSUMZ	18244	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
100	LSUMZ	18444	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
101	LSUMZ	18522	*cis*	Rondonia	Bolivia	Santa Cruz	-14.840000	-60.730000
102	LSUMZ	18550	*cis*	Rondonia	Bolivia	Santa Cruz	-14.840000	-60.730000
103	LSUMZ	6785	*cis*	Rondonia	Bolivia	Beni	-15.447222	-67.166111

APPENDIX D: LIST OF INDIVIDUAL SAMPLES OF *XENOPS MINUTUS*

Sample ID	Collection	Tissue Number	Side of Andes	Area of Endemism (da Silva 2005)	Country	State/Province/ Department	Latitude	Longitude
1	MZFC	1901	*trans*	North CA & W Pan	Mexico	Campeche	18.592778	-90.256111
2	MZFC	1966	*trans*	North CA & W Pan	Mexico	Campeche	18.592778	-90.256111
3	MZFC	2044	*trans*	North CA & W Pan	Mexico	Campeche	18.592778	-90.256111
4	MZFC	2166	*trans*	North CA & W Pan	Mexico	Campeche	18.592778	-90.256111
5	KU	1901	*trans*	North CA & W Pan	Mexico	Campeche	18.446043	-90.270887
6	MZFC	238	*trans*	North CA & W Pan	Mexico	Oaxaca	17.066667	-94.583333
7	MZFC	480	*trans*	North CA & W Pan	Mexico	Oaxaca	17.051667	-94.673333
8	MZFC	51	*trans*	North CA & W Pan	Mexico	Chiapas	16.901667	-90.973333
9	MZFC	68	*trans*	North CA & W Pan	Mexico	Chiapas	16.901667	-90.973333
10	BARR	8686	*trans*	North CA & W Pan	Honduras	Atlantida	15.716667	-86.866667
11	LSUMZ	60935	*trans*	North CA & W Pan	Honduras	Cortés	14.872833	-87.905000
12	LSUMZ	60945	*trans*	North CA & W Pan	Honduras	Cortés	14.872833	-87.905000
13	LSUMZ	35767	*trans*	North CA & W Pan	Costa Rica	Cartago	9.783333	-83.750000
14	USNM	1283	*trans*	North CA & W Pan	Panama	Bocas Del Toro	9.021536	-81.762039
15	USNM	1302	*trans*	North CA & W Pan	Panama	Bocas Del Toro	9.021536	-81.762039
16	USNM	1400	*trans*	North CA & W Pan	Panama	Bocas Del Toro	9.021536	-81.762039
17	ANSP	7207	*trans*	North CA & W Pan	Panama	Veraguas	7.383333	-80.883333
18	BARR	16144	*trans*	North CA & W Pan	Panama	Veraguas	7.241667	-80.905667
19	LSUMZ	28753	*trans*	Choco	Panama	Colon	9.280000	-79.710000
20	BARR	15267	*trans*	Choco	Panama	Panama	9.250000	-79.583333
21	LSUMZ	26497	*trans*	Choco	Panama	Colon	9.190000	-79.790000
22	LSUMZ	26932	*trans*	Choco	Panama	Panama	9.058333	-79.650833
23	LSUMZ	28628	*trans*	Choco	Panama	Panama	9.030000	-79.700000
24	LSUMZ	2209	*trans*	Choco	Panama	Darien	7.756000	-77.684000
25	ANSP	2227	*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
26	ANSP	2315	*trans*	Choco	Ecuador	Esmeraldas	1.030000	-78.580000
27	LSUMZ	11948	*trans*	Choco	Ecuador	Esmeraldas	0.866667	-78.550000
28	ANSP	4331	*trans*	Choco	Ecuador	Esmeraldas	0.660000	-79.440000
29	ANSP	3542	*trans*	Choco	Ecuador	Azuay	-2.500000	-79.416667
30	AMNH	14435	*cis*	Imeri	Brazil	Amazonas	-0.783333	-63.166667
31	FIELD	456907	*cis*	Imeri	Brazil	Amazonas	-1.730000	-65.879200
32	AMNH	14231	*cis*	Imeri	Brazil	Amazonas	-2.850000	-60.866667
33	AMNH	14232	*cis*	Imeri	Brazil	Amazonas	-2.850000	-60.866667
34	FIELD	456908	*cis*	Napo	Brazil	Amazonas	-2.049700	-67.263100
35	FIELD	456909	*cis*	Napo	Brazil	Amazonas	-2.049700	-67.263100

Appendix D cont.

36	LSUMZ	4244	*cis*	Napo	Peru	Loreto	-2.916670	-73.083330
37	LSUMZ	4328	*cis*	Napo	Peru	Loreto	-2.916670	-73.083330
38	LSUMZ	2571	*cis*	Napo	Peru	Loreto	-3.266670	-72.933333
39	LSUMZ	2754	*cis*	Napo	Peru	Loreto	-3.266670	-72.933333
40	ANSP	1484	*cis*	Napo	Ecuador	Morona-Santiago	-3.400000	-78.550000
41	LSUMZ	6862	*cis*	Napo	Peru	Loreto	-3.416670	-72.583330
42	LSUMZ	7127	*cis*	Napo	Peru	Loreto	-3.416670	-72.583330
43	LSUMZ	42756	*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
44	LSUMZ	42810	*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
45	LSUMZ	5442	*cis*	Napo	Peru	San Marten	-6.394444	-76.340278
46	USNM	14628	*cis*	Guiana	Guyana		8.250000	-59.733333
47	AMNH	11942	*cis*	Guiana	Venezuela	Bolivar	7.383333	-61.216667
48	USNM	9164	*cis*	Guiana	Guyana	Northwest	7.366667	-60.483333
49	USNM	9333	*cis*	Guiana	Guyana	Northwest	7.366667	-60.483333
50	USNM	14183	*cis*	Guiana	Guyana		6.400000	-58.766667
51	USNM	14260	*cis*	Guiana	Guyana		5.933333	-58.233333
52	USNM	4266	*cis*	Guiana	Guyana	Berbice	5.666667	-57.883333
53	USNM	4331	*cis*	Guiana	Guyana	Berbice	5.666667	-57.883333
54	USNM	5132	*cis*	Guiana	Guyana	Essequibo	5.500000	-60.783333
55	USNM	15759	*cis*	Guiana	Guyana		5.283333	-60.750000
56	USNM	14525	*cis*	Guiana	Guyana		5.200000	-57.283333
57	LSUMZ	48433	*cis*	Guiana	Guyana		4.932778	-59.893611
58	LSUMZ	48452	*cis*	Guiana	Guyana		4.932778	-59.893611
59	LSUMZ	48478	*cis*	Guiana	Guyana		4.932778	-59.893611
60	KU	1225	*cis*	Guiana	Guyana		4.666667	-58.666667
61	KU	1276	*cis*	Guiana	Guyana		4.666667	-58.666667
62	ANSP	7407	*cis*	Guiana	Guyana	Potaro-Siparuni	4.333333	-58.850000
63	LSUMZ	45809	*cis*	Guiana	Suriname		3.731623	-55.983179
64	USNM	12223	*cis*	Guiana	Guyana		2.366667	-59.450000
65	USNM	12772	*cis*	Guiana	Guyana		2.200000	-59.366667
66	AMNH	8845	*cis*	Guiana	Venezuela	Amazonas	1.895400	-65.045600
67	FIELD	391346	*cis*	Guiana	Brazil	Amapa	1.821313	-53.650755
68	USNM	11810	*cis*	Guiana	Guyana		1.583333	-58.633333
69	USNM	10412	*cis*	Guiana	Guyana		1.416667	-58.950000
70	USNM	10887	*cis*	Guiana	Guyana	North West	1.383333	-58.933333
71	AMNH	12699	*cis*	Guiana	Venezuela	Amazonas	0.834167	-66.166667
72	AMNH	12700	*cis*	Guiana	Venezuela	Amazonas	0.834167	-66.166667
73	LSUMZ	4706	*cis*	Inambari	Peru	Loreto	-3.552193	-72.749257
74	LSUMZ	4746	*cis*	Inambari	Peru	Loreto	-3.552193	-72.749257

Appendix D cont.

75	LSUMZ	11186	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
76	LSUMZ	11276	*cis*	Inambari	Peru	Ucayali	-8.090833	-74.444722
77	LSUMZ	10510	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
78	LSUMZ	10854	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
79	FIELD	395561	*cis*	Inambari	Brazil	Acre	-10.248282	-69.377749
80	LSUMZ	8988	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
81	LSUMZ	9026	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
82	LSUMZ	9452	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
83	FIELD	433363	*cis*	Inambari	Peru	Madre de Dios	-12.766667	-71.383333
84	FIELD	433365	*cis*	Inambari	Peru	Madre de Dios	-12.766667	-71.383333
85	FIELD	321726	*cis*	Inambari	Peru	Madre de Dios	-12.877300	-71.386500
86	FIELD	433364	*cis*	Inambari	Peru	Cuzco	-13.016667	-71.483333
87	FIELD	391107	*cis*	Inambari	Bolivia	La Paz	-13.750000	-68.150000
88	FIELD	391110	*cis*	Inambari	Bolivia	La Paz	-13.750000	-68.150000
89	LSUMZ	6761	*cis*	Inambari	Bolivia	Beni	-14.250000	-67.600000
90	LSUMZ	22778	*cis*	Inambari	Bolivia	La Paz	-15.188056	-68.255000
91	SAOPAULO	91	*cis*	Rondonia	Brazil	Mato Grosso do Norte	-9.179311	-60.630630
92	FIELD	389826	*cis*	Rondonia	Brazil	Rondonia	-9.733333	-61.883333
93	LSUMZ	36696	*cis*	Rondonia	Brazil	Rondönia	-10.760000	-64.750000
94	LSUMZ	36719	*cis*	Rondonia	Brazil	Rondönia	-10.760000	-64.750000
95	LSUMZ	36779	*cis*	Rondonia	Brazil	Rondönia	-10.760000	-64.750000
96	FIELD	391109	*cis*	Rondonia	Bolivia	El Beni	-11.009163	-65.995241
97	LSUMZ	15114	*cis*	Rondonia	Bolivia	Santa Cruz	-13.770000	-61.950000
98	LSUMZ	12264	*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
99	LSUMZ	12378	*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
100	LSUMZ	12760	*cis*	Rondonia	Bolivia	Santa Cruz	-14.270000	-60.990000
101	LSUMZ	14683	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
102	LSUMZ	14752	*cis*	Rondonia	Bolivia	Santa Cruz	-14.486667	-60.675278
103	LSUMZ	18175	*cis*	Rondonia	Bolivia	Santa Cruz	-14.833333	-60.416667
104	LSUMZ	18534	*cis*	Rondonia	Bolivia	Santa Cruz	-14.840000	-60.730000
105	FIELD	392023	*cis*	Tapajos	Brazil	Mato Grosso do Norte	-9.904000	-55.881000
106	FIELD	456904	*cis*	Xingu	Brazil	Para	-1.950000	-51.600000
107	FIELD	456905	*cis*	Xingu	Brazil	Para	-1.950000	-51.600000
108	FIELD	456906	*cis*	Xingu	Brazil	Para	-1.950000	-51.600000
109	FIELD	391347	*cis*	Xingu	Brazil	Para	-6.078295	-50.246776
110	FIELD	391348	*cis*	Xingu	Brazil	Para	-6.078295	-50.246776
111	FIELD	399212	*cis*	Atlantic Forest	Brazil	Pernambuco	-7.616667	-35.500000
112	FIELD	395738	*cis*	Atlantic Forest	Brazil	Sao Paulo	-23.634273	-45.866654
113	SAOPAULO	1667	*cis*	Atlantic Forest	Brazil	Sao Paulo	-23.711392	-47.418759

Appendix D cont.

114	SAOPAULO	685	*cis*	Atlantic Forest	Brazil	Sao Paulo	-23.711392	-47.418759
115	SAOPAULO	689	*cis*	Atlantic Forest	Brazil	Sao Paulo	-23.711392	-47.418759
116	KU	254	*cis*	Atlantic Forest	Paraguay	Caazapa	-26.100000	-55.766667
117	LSUMZ	25938	*cis*	Atlantic Forest	Paraguay	Caazapa	-26.100000	-55.766667
118	KU	255	*cis*	Atlantic Forest	Paraguay	Caazapa	-26.379579	-55.645614
119	KU	293	*cis*	Atlantic Forest	Paraguay	Caazapa	-26.379579	-55.645614
120	KU	342	*cis*	Atlantic Forest	Paraguay	Caazapa	-26.379579	-55.645614

APPENDIX E: LIST OF INDIVIDUAL SAMPLES OF *ATTILA SPADICEUS*

Sample ID	Collection	Tissue Number	Side of Andes	Area of Endemism (da Silva 2005)	Country	State/Province/ Department	Latitude	Longitude
1	BURKE	81460	*trans*	North CA & W Pan	Mexico	Sinaloa	24.303333	-106.763336
2	MZFC	689	*trans*	North CA & W Pan	Mexico	Oaxaca	17.080559	-96.762841
3	MZFC	690	*trans*	North CA & W Pan	Mexico	Oaxaca	17.080559	-96.762841
4	MZFC	1029	*trans*	North CA & W Pan	Mexico	Oaxaca	16.243611	-97.498889
5	FIELD	394276	*trans*	North CA & W Pan	Mexico	Oaxaca	16.100000	-97.183333
6	FIELD	394277	*trans*	North CA & W Pan	Mexico	Oaxaca	16.100000	-97.183333
7	FIELD	394278	*trans*	North CA & W Pan	Mexico	Oaxaca	16.100000	-97.183333
8	KU	530	*trans*	North CA & W Pan	Mexico	Quintana Roo	20.833333	-86.900000
9	KU	551	*trans*	North CA & W Pan	Mexico	Quintana Roo	20.833333	-86.900000
10	MZFC	532	*trans*	North CA & W Pan	Mexico	Quintana Roo	20.833333	-86.900000
11	MZFC	2153	*trans*	North CA & W Pan	Mexico	Campeche	18.592778	-90.256111
12	MZFC	2185	*trans*	North CA & W Pan	Mexico	Campeche	18.592778	-90.256111
13	MZFC	2168	*trans*	North CA & W Pan	Mexico	Campeche	18.592778	-90.256111
14	FIELD	393989	*trans*	North CA & W Pan	Mexico	Veracruz	18.362000	-94.838000
15	KU	1937	*trans*	North CA & W Pan	Mexico	Campeche	18.316667	-90.133333
16	KU	1976	*trans*	North CA & W Pan	Mexico	Campeche	18.316667	-90.133333
17	KU	2150	*trans*	North CA & W Pan	Mexico	Campeche	18.316667	-90.133333
18	MZFC	493	*trans*	North CA & W Pan	Mexico	Oaxaca	17.006667	-94.689444
19	MZFC	193	*trans*	North CA & W Pan	Mexico	Chiapas	16.084167	-90.976667
20	LSUMZ	8802	*trans*	North CA & W Pan	Belize	Toledo	16.290000	-89.020000
21	LSUMZ	55049	*trans*	North CA & W Pan	Honduras	Cortés	14.872833	-87.905000
22	LSUMZ	60697	*trans*	North CA & W Pan	Honduras	Cortés	14.872833	-87.905000
23	LSUMZ	60798	*trans*	North CA & W Pan	Honduras	Cortés	14.872833	-87.905000
24	BURKE	56335	*trans*	North CA & W Pan	Nicaragua		13.701667	-84.851669
25	BURKE	56336	*trans*	North CA & W Pan	Nicaragua		13.701667	-84.851669
26	BURKE	70012	*trans*	North CA & W Pan	Nicaragua		13.701667	-84.851669
27	BURKE	70059	*trans*	North CA & W Pan	Nicaragua		13.701667	-84.851669
28	USNM	1797	*trans*	North CA & W Pan	Panama	Bocas del Toro	9.400000	-82.266700
29	USNM	1918	*trans*	North CA & W Pan	Panama	Bocas del Toro	9.385000	-82.516000
30	USNM	1279	*trans*	North CA & W Pan	Panama	Bocas del Toro	9.021536	-81.762039
31	KU	5326	*trans*	North CA & W Pan	Panama	Chiriqui	8.733333	-82.250000
32	KU	5364	*trans*	North CA & W Pan	Panama	Chiriqui	8.733333	-82.250000
33	LSUMZ	28208	*trans*	North CA & W Pan	Panama	Chiriqui	8.729000	-82.246000
34	LSUMZ	46698	*trans*	North CA & W Pan	Panama	Veraguas	7.599500	-81.723000
35	BURKE	77019	*trans*	Choco	Panama	Panama	9.357333	-79.319664

Appendix E cont.

36	LSUMZ	28398	*trans*	Choco	Panama	Panama	9.240000	-79.350000
37	LSUMZ	28779	*trans*	Choco	Panama	Colon	9.208300	-79.995500
38	LSUMZ	26882	*trans*	Choco	Panama	Panama	9.058333	-79.650833
39	LSUMZ	2238	*trans*	Choco	Panama	Darien	7.756000	-77.684000
40	LSUMZ	29986	*trans*	Choco	Ecuador	Esmeraldas	1.090861	-78.690611
41	FIELD	457497	*cis*	Napo	Brazil	Amazonas	-2.049700	-67.263100
42	LSUMZ	2843	*cis*	Napo	Peru	Loreto	-3.266670	-72.933333
43	LSUMZ	2913	*cis*	Napo	Peru	Loreto	-3.266670	-72.933333
44	LSUMZ	42724	*cis*	Napo	Peru	Loreto	-4.280833	-77.237778
45	USNM	5026	*cis*	Guiana	Guyana	Essequibo	5.500000	-60.783333
46	USNM	16000	*cis*	Guiana	Guyana	Essequibo	5.383333	-60.766667
47	LSUMZ	48372	*cis*	Guiana	Guyana		4.932778	-59.893611
48	USNM	19048	*cis*	Guiana	Guyana		4.932778	-59.893611
49	USNM	19091	*cis*	Guiana	Guyana		4.932778	-59.893611
50	LSUMZ	55279	*cis*	Guiana	Suriname		4.479444	-57.057778
51	LSUMZ	45775	*cis*	Guiana	Suriname		3.731623	-55.983179
52	LSUMZ	45776	*cis*	Guiana	Suriname		3.731623	-55.983179
53	LSUMZ	45851	*cis*	Guiana	Suriname		3.731623	-55.983179
54	USNM	22289	*cis*	Guiana	Guyana	Upper Takutu - Essequibo	2.971389	-58.593611
55	USNM	22320	*cis*	Guiana	Guyana	Upper Takutu - Essequibo	2.971389	-58.593611
56	USNM	14105	*cis*	Guiana	Guyana		2.816667	-59.816667
57	USNM	10787	*cis*	Guiana	Guyana	North West	1.383333	-58.933333
58	MVZ	169640	*cis*	Inambari	Peru	Madre de Dios	-12.578500	-69.074820
59	MVZ	169642	*cis*	Inambari	Peru	Madre de Dios	-12.578500	-69.074820
60	LSUMZ	42434	*cis*	Inambari	Peru	Loreto	-5.313333	-76.275556
61	LSUMZ	5419	*cis*	Inambari	Peru	San Marten	-6.394444	-76.340278
62	LSUMZ	5429	*cis*	Inambari	Peru	San Marten	-6.394444	-76.340278
63	LSUMZ	10613	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
64	LSUMZ	10639	*cis*	Inambari	Peru	Ucayali	-9.193056	-74.383333
65	LSUMZ	9353	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
66	LSUMZ	9413	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
67	LSUMZ	9506	*cis*	Inambari	Bolivia	Pando	-11.470278	-68.778611
68	KU	466	*cis*	Inambari	Peru	Madre de Dios	-12.550000	-69.050000
69	LSUMZ	1013	*cis*	Inambari	Bolivia	La Paz	-15.290000	-67.590000
70	LSUMZ	21231	*cis*	Inambari	Bolivia	La Paz	-15.290000	-67.590000
71	FIELD	389961	*cis*	Rondonia	Brazil	Rondonia	-9.733333	-61.883333
72	LSUMZ	15008	*cis*	Rondonia	Bolivia	Santa Cruz	-13.770000	-61.950000
73	LSUMZ	12532	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
74	LSUMZ	12575	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000

Appendix E cont.

75	LSUMZ	12599	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
76	LSUMZ	12619	*cis*	Rondonia	Bolivia	Santa Cruz	-14.810000	-60.810000
77	USNM	6994	*cis*	Xingu	Brazil	Para	-3.650000	-52.366667

APPENDIX F: LIST OF INDIVIDUAL SAMPLES OF *TITYRA SEMIFASCIATA*

Sample ID	Collection	Tissue Number	Side of Andes	Area of Endemism (da Silva 2005)	Country	State/Province/ Department	Latitude	Longitude
1	BURKE	81149	*trans*	NCA	Mexico	Sinaloa	24.303333	-106.763336
2	MZFC	CONY308	*trans*	NCA	Mexico	San Luis Potosi	22.133333	-99.433333
3	MZFC	HGO147	*trans*	NCA	Mexico	Hidalgo	21.000000	-99.133333
4	FIELD	393861	*trans*	NCA	Mexico	Jalisco	19.550000	-104.230000
5	MZFC	B2203	*trans*	NCA	Mexico	Campeche	18.592778	-90.256111
6	LSUMZ	8754	*trans*	NCA	Belize	Toledo	16.290000	-89.020000
7	KU	6012	*trans*	NCA	El Salvador	Sonsonate	13.821000	-89.653000
8	BURKE	69160	*trans*	NCA	Nicarauga	Granada	11.766666	-85.958336
9	FIELD	393052	*trans*	NCA	Costa Rica		10.833333	-85.050000
10	LSUMZ	27268	*trans*	NCA	Costa Rica	Alajuela	10.833333	-85.050000
11	AMNH	3682	*trans*	NCA	Costa Rica	Puntarenas	9.450000	-84.150000
12	BURKE	76942	*trans*	NCA	Panama	Panama	9.387500	-79.343170
13	(GENBAN K)	EF212894	*trans*	NCA	Panama	Bocas del Toro	9.021536	-81.762039
14	LSUMZ	28203	*trans*	NCA	Panama	Chiriqui	8.729000	-82.246000
15	LSUMZ	28204	*trans*	NCA	Panama	Chiriqui	8.729000	-82.246000
16	LSUMZ	28667	*trans*	CHOC	Panama	Colon	9.208300	-79.995500
17	LSUMZ	28668	*trans*	CHOC	Panama	Colon	9.208300	-79.995500
18	LSUMZ	28670	*trans*	CHOC	Panama	Colon	9.208300	-79.995500
19	LSUMZ	28675	*trans*	CHOC	Panama	Colon	9.208300	-79.995500
20	LSUMZ	28677	*trans*	CHOC	Panama	Colon	9.208300	-79.995500
21	ANSP	2326	*trans*	CHOC	Ecuador	Esmeraldas	1.030000	-78.580000
22	ANSP	2377	*trans*	CHOC	Ecuador	Esmeraldas	1.030000	-78.580000
23	LSUMZ	12007	*trans*	CHOC	Ecuador	Esmeraldas	0.866667	-78.550000
24	ANSP	1546	*cis*	Napo	Ecuador	Morona-Santiago	-3.400000	-78.550000
25	FIELD	391534	*cis*	GUY	Brazil	Amapa	1.650000	-50.916667
26	FIELD	391535	*cis*	GUY	Brazil	Amapa	1.601667	-50.898333
27	LSUMZ	42582	*cis*	iNAM	Peru	Loreto	-5.313333	-76.275556
28	LSUMZ	40435	*cis*	INAM	Peru	Loreto	-7.594444	-75.916111
29	LSUMZ	40861	*cis*	INAM	Peru	Loreto	-7.594444	-75.916111
30	LSUMZ	10608	*cis*	INAM	Peru	Ucayali	-9.193056	-74.383333
31	LSUMZ	1990	*cis*	INAM	Peru	Pasco	-10.410833	-74.964722
32	LSUMZ	9434	*cis*	INAM	Bolivia	Pando	-11.470278	-68.778611
33	MVZ	169530	*cis*	INAM	Peru	Madre de Dios	-12.600000	-69.072890
34	FIELD	433665	*cis*	INAM	Peru	Cuzco	-13.016667	-71.483333

Appendix F cont.

35	FIELD	391193	*cis*	INAM	Bolivia	La Paz	-13.750000	-68.150000
36	LSUMZ	22812	*cis*	INAM	Bolivia	La Paz	-15.188056	-68.255000
37	LSUMZ	14748	*cis*	ROND	Bolivia	Santa Cruz	-14.486667	-60.675278
38	LSUMZ	18171	*cis*	ROND	Bolivia	Santa Cruz	-14.833333	-60.416667
39	LSUMZ	18275	*cis*	ROND	Bolivia	Santa Cruz	-14.833333	-60.416667
40	LSUMZ	38928	*cis*	ROND	Bolivia	Cochabamba	-17.146389	-65.766880

VITA

Curtis W. Burney was born in 1973 in West Point, New York, to Sam and Sandy Burney. As an army brat and young child, he moved several times and lived in California, Thailand, and Maryland before returning to West Point for 1st grade. During the next four years, he and his twin brother, Chris, spent the majority of their time hiking the woods and rocky creeks of the Hudson Highlands where they attempted to catalog all of the native fauna using their first set of binoculars and field guides. Upon his father retiring from the Army, Curtis moved to Auburn, Alabama, and was soon trouncing in slow moving, red mud creek beds in mixed pine forests listening to Hooded Warblers and catching Slimy Salamanders. During a visit to Florida to see his aunt and uncle, he was introduced to the Air Force and, specifically, the F-16 that his uncle was flying at the time. The trip to the airfield, with jets taking off and screaming overhead, made a lasting impression. After graduation from Auburn High School, Curt entered the United States Air Force Academy to pursue his interests, flying and biology. He graduated in 1996 with a major in biology. In the same summer, he married his high-school sweetheart, Melea Bardwell. Their first move as an Air Force couple was to Pensacola, Florida, where Curt began pilot training in a joint-service program with the Navy flying the T-34. Curt and Melea had their first son, Aidan, in Florida. After T-34s, the family moved to Enid, Oklahoma, where Curt began flying the T-38. Unfortunately, medical issues forced Curt out of the cockpit. In 1998, he was then assigned to a wildlife ecology position at the Air Force Safety Center in Albuquerque, New Mexico. Collin, Curt and Melea’s youngest son, was born in New Mexico. In 2001, Curt earned a Master of Science degree in ecology and evolutionary biology at Cornell University under the guidance of Dr. David Winkler. He then served as an instructor in the Biology Department at the United States Air Force Academy in Colorado Springs, Colorado, before entering the doctoral program at Louisiana State University in 2005.