MOLECULAR ECOLOGY

Molecular Ecology (2011) **20**, 4550–4563 doi: 10.1111/j.1365-294X.2011.05294.x

Andean uplift promotes lowland speciation through vicariance and dispersal in *Dendrocincla* woodcreepers

JASON T. WEIR*† and MOMOKO PRICE*‡

*Department of Biological Sciences, University of Toronto Scarborough, Toronto, ON, Canada M1C 1A4, †Department of Ecology and Evolution Biology, University of Toronto, Toronto, ON, Canada M5S 3G5, ‡Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

Abstract

Andean uplift contributed importantly to the build-up of high Neotropical diversity. Final uplift of the Eastern Cordillera of Colombia separated once-contiguous lowland faunas east and west of the Andes between 5 and 3.5 million years ago (Ma hereafter). We used DNA sequences from several moderate- to fast-evolving mitochondrial and two slow-evolving nuclear genes to generate a well-supported phylogeny of *Dendrocincla* woodcreepers, a genus with multiple species endemic to lowland regions both east and west of the Andes. A time-calibrated phylogeny and dispersal–vicariance analysis indicated that uplift of the Eastern Cordillera of Colombia resulted in the initial vicariant separation of a widespread lowland form east and west of the Andes at *c.* 3.6 Ma. This was followed by two separate east-to-west dispersal events over or around the completed Andes, each producing a genetically distinct lineage. Our analysis suggests that Andean uplift promoted the build-up of biodiversity in lowland Neotropical faunas both through vicariance-based speciation during uplift and through dispersal-based speciation following uplift. In contrast to the multiple colonizations of the trans-Andean region by *Dendrocincla*, the Atlantic Forest was colonized from the Amazon only once, followed by *in situ* diversification.

Keywords: Andes, Atlantic Forest, *Dendrocincla*, dispersal, Eastern Cordillera, speciation, vicariance

Received 4 February 2011; revision received 10 August 2011; accepted 16 August 2011

Introduction

Neotropical humid forests possess the highest diversity on the planet (Rosenzweig 1995; Newton 2003; Kreft & Jetz 2007), yet our understanding of the historical processes that helped forge this diversity continues to develop. Andean uplift is widely recognized as having fostered a highly diverse and species-rich fauna in the highlands of the Neotropics (Burns & Naoki 2004; Hughes & Eastwood 2006; Ribas *et al.* 2007; Sedano & Burns 2009; Weir 2006, 2009; Weir *et al.* 2008). What is less well understood is the role played by Andean uplift to the build-up of diversity in the Neotropical lowlands.

Correspondence: Jason T. Weir, Fax: 416 287 7676;
E-mail: jason.weir@utoronto.ca

The orogenic sequence of the Andes proceeded in a south-to-north fashion (Gregory-Wodzicki 2000; Hartley 2003; Garzione *et al.* 2008). Between 5 and 3.5 Ma, the Eastern Cordillera of Colombia was rapidly uplifted, completing an otherwise unbroken Andean chain from temperate regions in the south of the continent, north to the Caribbean coast in Venezuela. Prior to this completion, lowland wet forests are believed to have stretched unbroken from the Pacific to Atlantic (Hoorn *et al.* 1995; Hooghiemstra & van der Hammen 1998), but were bisected by Andean completion into *cis-* and *trans-*Andean components, each comprising a high degree of endemism (e.g. Haffer 1967; Cracraft 1985). This endemism led past authors to propose that final Andean uplift promoted vicariance of once-widespread species into eastern and western components, resulting in an increase in lowland species diversity (Chapman 1917). If correct, then splitting events between *cis-* and

trans-Andean sister clades should date to the final period of uplift in the Eastern Cordillera of Colombia. Following uplift, speciation resulting from rare dispersal events over the Andes via low-elevation passes, or around the northern Andes through temporary wet-forest corridors, are also thought to have contributed to the build-up of faunas and floras (Chapman 1917, 1926; Haffer 1967, 1969), and such dispersal-based splitting events should date to the past 3.5 million years (Ma) following completion of the Andes. The relative contribution of these two processes—initial vicariance at uplift and subsequent dispersal after uplift—in generating lowland diversity are poorly understood (see Brumfield & Capparella 1996).

We investigated the contribution of Andean uplift to the diversification of *Dendrocincla* woodcreepers. We chose *Dendrocincla* because the genus comprises two species largely endemic to the *trans*-Andean region (*D. anabatina* and *D. homochroa*), two to the *cis*-Andean region (*D. merula* and *D. turdina*), one that straddles both *cis*- and *trans*-Andean regions (*D. fuliginosa*), and a sixth species restricted to high altitudes in the tropical Andes (*D. tyrannina*) (Fig. 1). The presence of three species in *cis*-Andean and three in *trans*-Andean regions suggests Andean uplift may have promoted multiple low-elevation speciation events in this group. Lowland species in this genus actively forage at swarms of the army ant *Eciton burchellii* and several species are obligate army ant followers (Willis 1972; Hilty 1972; Marantz *et al*. 2003). Given that the temperature-dependent *E. burchellii* becomes rare above 1000 m (Hilty 1972), *Dendrocincla* may have been especially prone to population fragmentation mediated by Andean uplift.

We investigate the phylogenetic history within *Dendrocincla* using four mitochondrial genes and two slowly evolving nuclear genes. We used this phylogenetic reconstruction along with a dated relaxed-clock tree and dispersal–vicariance analysis to determine the number and dates of divergence events between *cis*- and *trans*-Andean regions. Our results suggest the Andes played a complex role in driving diversification in *Dendrocincla*, promoting both vicariant- and dispersal-based speciation.

Material and methods

Taxon sampling

Tissues were collected by JTW in Panama or were obtained from museum collections (Field Museum of Natural History, University of Kansas Natural History, Museum of Vertebrate Zoology at the University of California, and the Smithsonian Tropical Research Institute; see Table 1). We obtained tissue samples for all species and included multiple subspecies if tissues were available: six of 12 subspecies (and all subspecies groups, Fig. 1) for *Dendrocincla fuliginosa*, one of two for *Dendrocincla tyrannina*, two of three for *Dendrocincla anabatina*, five of seven for *Dendrocincla merula* and two of four for *Dendrocincla homochroa*. A total of 43 *Dendrocincla*

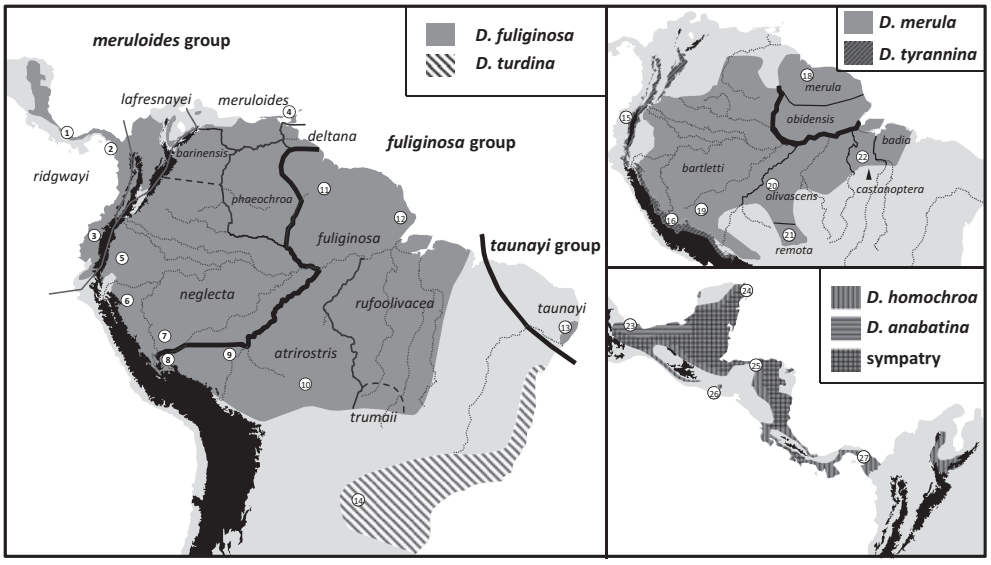

Fig. 1 Geographic range of *Dendrocincla* species and sampling localities. Altitudes in the Andes and Central America above 1800 m are shown in black. Rivers are shown by dotted grey lines. Approximate borders between subspecies in *Dendrocincla fuliginosa* and *Dendrocincla merula* are shown by thin black lines and subspecies groups shown by thick black lines. Numbered collecting localities (white circles) correspond to samples in Table 1.

Table 1 List of *Dendrocincla* and outgroup samples used in this study. GenBank accession numbers are given for each gene

No.*	Taxon	Museum (tissue no)	Locality	Cyt B	ND2	COI	16s	RAG1	c-myc
1	*Dendrocincla fuliginosa ridgwayi*	STRI JTW253	Panama; Bocas del Toro; Valle de Risco	DQ364135	GU215373	JN622066	JN622041	GU215453	GU215438
1	*D. fuliginosa ridgwayi*	STRI IJL064	Panama; Bocas del Toro; Cerro Chalite	JN622097					
1	*D. fuliginosa ridgwayi*	STRI JTW172	Panama; Bocas del Toro; above Chiriqui Grande	JN622098					
1	*D. fuliginosa ridgwayi*	STRI JTW269	Panama; Bocas del Toro; Valle de Risco	JN622096					
2	*D. fuliginosa ridgwayi*	STRI JTW744	Panama; Darien; Puerto Pina	GU215180	GU215374	JN622070	JN622045	GU215450	GU215435
3	*D. fuliginosa ridgwayi*	LSUMZ 11927	Ecuador; Esmeraldas; El Placer	FJ899287†					
4	*Dendrocincla fuliginosa meruloides*	STRI TR_DFU1	Trinidad	GU215182	GU215371	JN622067	JN622042	GU215452	GU215437
4	*D. fuliginosa meruloides*	STRI TR_DFU9	Trinidad	JN622095					
5	*Dendrocincla fuliginosa neglecta*	STRI EC_DFU1	Ecuador; Jatun Sacha	GU215179	GU215372	JN622068	JN622043	GU215449	GU215434
6	*D. fuliginosa neglecta*	LSUMZ 5478	Peru; San Martin	FJ899294†					
7	*D. fuliginosa neglecta*	LSUMZ 10499	Peru; Ucayali	FJ899291†					
7	*D. fuliginosa neglecta*	LSUMZ 10694	Peru; Ucayali	FJ899284†					
8	*Dendrocincla fuliginosa atrirostris*	FMNH 429948	Peru; Cuzco; Paucartambo	GU215181	GU215369	JN622069	JN622044	GU215451	GU215436
9	*D. fuliginosa atrirostris*	LSUMZ 8947	Bolivia; Pando; Nicolas Suarez	FJ899283†					
10	*D. fuliginosa atrirostris*	LSUMZ 12326	Bolivia; Santa Cruz; Velasco	FJ899285†					
10	*D. fuliginosa atrirostris*	LSUMZ 14452	Bolivia; Santa Cruz; Serrania de Huanchaca	FJ899282†					
11	*D. fuliginosa fuliginosa*	UKNH 5752	Guyana	JN622093					
11	*D. fuliginosa fuliginosa*	UKNH 5780	Guyana	JN622094					
12	*D. fuliginosa fuliginosa*	FMNH 391298	Brazil; Amapa	GU215178	GU215370	JN622064	JN622039	GU215448	GU215433
12	*D. fuliginosa fuliginosa*	FMNH 391301	Brazil; Amapa	DQ364136					
13	*Dendrocincla fuliginosa taunayi*	FMNH 399181	Brazil; Alagoas, Ibateouara	GU215177	GU215375	JN622065	JN622040	GU215447	GU215432
13	*D. fuliginosa taunayi*	FMNH 399182	Brazil; Alagoas, Ibateouara	JN622099					
13	*D. fuliginosa taunayi*	FMNH 399178	Brazil; Alagoas	DQ364139					
14	*Dendrocincla turdina*	UKNH 3698	Paraguay	GU215185	GU215379	JN622071	JN622046	GU215456	GU215442
14	*D. turdina*	NRM 976662	Paraguay	AY065713†					
14	*D. turdina*	UKNH 3783	Paraguay	JN622100					
14	*D. turdina*	UKNH 296	Paraguay	JN622108					
14	*D. turdina*	UKNH 250	Paraguay	JN622107					
15	*Dendrocincla tyrannina tyrannina*	LSUMZ 12108	Ecuador; Pichincha; Mindo	JN622106					
16	*D. tyrannina tyrannina*	FMNH 429946	Peru; Cuzco; Paucartambo	GU215186	GU215380	JN622079	JN622054	GU215457	GU215443
17	*D. tyrannina tyrannina*	ZMUC 1110	Unknown	AY443985†					
18	*Dendrocincla merula merula*	UKNH 1307	Guiana	JN622104	JN622089	JN622075	JN622050	JN622084	JN622059
19	*D. merula bartletti*	MVZ 169483	Peru; Madre de Dios; near Puerto Maldonado	JN622102	JN622091	JN622078	JN622053	JN622086	JN622061
20	*D. merula olivascens*	FMNH 389810	Brazil; Rodonia; Cachoeira Nazare, W bank Rio Jiparana	GU215184	GU215378	JN622076	JN622051	GU215455	GU215441
21	*D. merula remota*	FMNH 391081	Bolivia; La Paz; Rio Manupari	JN622105	JN622090	JN622077	JN622052	JN622085	JN622060
22	*D. merula castanoptera*	FMNH 391306	Brazil; Para; Serra dos Carajas	JN622103	JN622088	JN622074	JN622049	JN622083	JN622058
23	*Dendrocincla anabatina anabatina*	FMNH 343230	Mexico; Veracruz; El Bastonal	DQ364137					

Table 1 *Continued*

No.*	Taxon	Museum (tissue no)	Locality	Cyt B	ND2	COI	16s	RAG1	c-myc
24	*D. anabatina typhla*	UKNH 536	Mexico; Quintana Roo; Puerto Morelos	GU215176	GU215368	JN622063	JN622038	GU215446	GU215431
25	*D. anabatina anabatina*	STRI HO_DEA71	Honduras	JN622092					
27	*Dendrocincla homochroa ruficeps*	STRI DHO_PA671	Panama	GU215183	GU215377	JN622073	JN622048		GU215439
27	*D. homochroa ruficeps*	STRI DHO_PA558	Panama	JN622101					
26	*D. homochroa homochroa*	FMNH 434035	El Salvador; Parque Nacional El Imposible	DQ364138	GU215376	JN622072	JN622047	GU215454	GU215440
	Sittasoma griseicapillus	FMNH 343231	Mexico; Veracruz; El Bastonal	DQ364140	GU215383	JN622080	JN622055		GU215444
	Deconychura longicauda	STRI CR_DLO2761	Costa Rica	GU215173	GU215367	JN622081	JN622056	GU215445	GU215430
	Xiphorhynchus lachrymosus	STRI JTW317	Panama; Bocas del Toro; Cerro Chalite	GU215202	GU215384	JN622082	JN622057	JN622087	JN622062

FMNH, Field Museum of Natural History; STRI, Smithsonian Tropical Research Institute; UKNH, University of Kansas Natural History; MVZ, Museum of Vertebrate Zoology; LSUMZ, Louisiana Museum of Natural History; ZMUC, Zoological Museum, University of Copenhagen; NRM, Swedish Museum of Natural History; COI, cytochrome oxidase I.
*Locality of sample in Fig. 1.
†GenBank samples obtained from other authors (Irestedt *et al.* 2002, 2004; Burney & Brumfield 2009).

individuals were sampled. A molecular phylogeny of all dendrocolaptid genera placed *Dendrocincla* as sister to a clade containing *Deconychura longicauda* and *Sittasomus griseicapillus* (Weir *et al.* 2009; Derryberry *et al.* 2010). We included these two species as outgroups in addition to a more distant relative, *Xiphorhynchus lachrymosus*.

Laboratory protocols

Genomic DNA was isolated from pectoral muscle using phenol–chloroform extraction. We sequenced 1005 bp of mitochondrial cytochrome b (cyt b) for all individuals using primers S-14987 (Weir & Schluter 2007) and S-16065 5'ACTCTTCAGTCTCTGGTTTACAAGAC'3 designed here for specificity to suboscines. We sequenced five additional genes (extended sequence data set hereafter) for a subset of 17 *Dendrocincla* individuals and three outgroups, with one representative individual per *Dendrocincla* subspecies. These genes included two additional protein-coding mitochondrial genes—partial NADH dehydrogenase subunit 2 gene (ND2: 876 bp) using primers L5215 (Hackett 1996) and H6313 (Johnson & Sorenson 1998) and partial cytochrome oxidase I gene (COI: 592 bp) using primers COIf and COIa (Palumbi 1996); partial sequences of one ribosomal RNA gene—small ribosomal unit 16 (16s: 588 bp) using primers 16sar and 16sbr (Palumbi 1996); and partial sequences of two nuclear genes—RAG 1 (RAG1: 893 bp) using primers R50 and R51, and c-myc (c-myc: 499 bp) using primers mycEX3A and RmycEX3A (Ericson *et al.* 2000; Irestedt *et al.* 2001). Amplification and sequencing of these genes followed standard protocols (mitochondrial genes: Weir *et al.* 2008; nuclear genes: Groth & Barrowclough 1999) with annealing temperatures ranging from 48 to 56 °C. Sequences were aligned and edited in BioEdit (Hall 1999).

Phylogenetic analysis

We used four partitions for our extended data set: (i) mtDNA protein-coding genes (cyt b, ND2 and COI), (ii) 16s, (iii) RAG 1 and (iv) c-myc. A partition homogeneity test conducted in PAUP* v4.0b10 (Swofford 2002) (1000 heuristic replicates with 100 stepwise addition replicates) showed no significant differences in phylogenetic signal across partitions ($P = 0.99$) and trees generated for each data set had similar topologies (although only the mtDNA protein-coding data set was well resolved). MrModelTest (Nylander 2004) was used to determine the best-supported models of sequence evolution for both the cyt b data set and the extended data set with four partitions. Akaike information criterion was used to choose the model with the best fit to the data for

each partition. The GTR-Γ-I model was chosen for the cyt b data set. For the four partition data set, GTR-Γ-I best fit the mtDNA protein-coding genes and 16s, and HKY+I best fit RAG 1 and c-myc.

Bayesian analyses were conducted in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001) on the cyt b and concatenated data set of all genes using the best-supported model of sequence evolution for each partition, as well as individually on each nuclear gene as well as a combined data set of both nuclear genes. Heterozygous sites were coded using ambiguity codes for nuclear genes. Model parameters were estimated for each partition by MrBayes. To aid in mixing, the temperature parameter for heating the chains was reduced from its default value of 0.2–0.05 and a total of eight chains were run, seven heated and one cold. A total of six (cyt b and extended sequence data sets) or two runs (individual nuclear genes and the combined nuclear data set), each starting from a different random starting tree, were performed. Analysis were run for 40 (cyt b and extended sequence data sets) or 100 million generations (individual nuclear genes and the combined nuclear data set), with trees sampled every 1000 generations. Convergence of overall tree likelihoods and individual model parameters was analysed in Tracer v1.5.0 (Rambaut & Drummond 2009). Convergence of the tree topology was analysed in AWTY (Nylander *et al.* 2008b). For each analysis, likelihoods and model parameters converged before 3 million generations in all runs, but the tree topology took up to 8 million generations to reach convergence (as assessed by lack of trends in plots of cumulative split frequencies through the course of individual simulations; see Nylander *et al.* 2008b). We deleted the first 8 million generations as the burnin. Following the burnin, bivariate plots of node posterior probabilities (not shown) for separate pairwise runs showed little scatter around the 1:1 line, suggesting all runs had converged on similar topologies (see Nylander *et al.* 2008b). Majority-rule consensus trees were generated in MrBayes from samples generated after the burnin period.

A Bayesian analysis was also used to estimate a species tree (Edwards *et al.* 2007) in BEST 2.3 (Liu 2008) for our three unlinked data sets (all mtDNA genes, RAG1 and c-myc), allowing each data set to have its own model as in the concatenated data set analysis. Individuals with multiple heterozygous sites within a nuclear gene were phased probabilistically for the BEST analysis using the Stephens & Donnelly (2003) model of haplotype reconstruction in PHASE 2.1 (Stephens *et al.* 2001) with default settings. Subspecies within *D. fuliginosa, D. homochroa* and *D. merula* were deeply diverged genetically and/or were reciprocally monophyletic in the cyt b analysis (Fig. 3) and these are treated as distinct units for species tree analysis. *Deconychura* was used as the only outgroup. In BEST, we used the default value of 3 for the mean of the inverse gamma distribution prior on the effective population size, but changed its standard deviation from 0.003 to 0.03 to help aid in mixing. The prior on mutation rates was set conservatively as a uniform distribution ranging from 0.001 to 5, to allow for potentially large differences in rate between nuclear and mitochondrial loci. The analysis was run for 100 million generations and with six independent chains. Other parameters (number of runs, temperature, etc.) of the BEST analysis were identical to the MrBayes analyses. Likelihoods and model parameters converged in <10 million generations in the first four runs but took 20 million generations in the fifth and 50 million in the sixth runs. The tree topology of the last two runs failed to converge, and we deleted them from the analysis. Tree topology converged well within 50 million generations in the other four runs (assessed using plots of cumulative split frequencies and bivariate plots of node posterior probabilities as in the MrBayes analyses), and we used a conservative burnin of 50 million generations. Majority-rule consensus trees were generated in BEST from samples generated after the burnin period.

Equally weighted parsimony trees were also generated in PAUP* for the concatenated data set of all genes. The parsimony analysis used a neighbour joining starting tree, a stepwise heuristic search using tree bisection–reconnection branch swapping and 100 random addition sequence replicates. Ten trees were held at each cycle of the stepwise addition procedure. One thousand bootstraps were performed with the conLevel option set to 50.

Molecular dating

We produced a relaxed-clock tree (with rate variation following a log-normal distribution and Yule speciation prior) in BEAST 1.5.4 (Drummond & Rambaut 2007) using the GTR-Γ model of sequence evolution for our protein-coding mtDNA data set (cyt b, ND2 and COI). We use the GTR-Γ rather than the GTR-Γ-I for dating purposes to utilize published molecular rates from Weir & Schluter (2008), which used the GTR-Γ model. The topology was fixed (following the majority-rule consensus topology uncovered for the combined analysis of all genes) and only branch lengths were optimized. The analysis was run for 100 million generations; trees were sampled every 1000 generations, and mean node ages were calculated for sampled trees following a 10-million year burnin. We placed uniform priors (limits: 0 to infinity) on relative rate parameters between nucleotides, as the null priors in BEAST failed to mix well.

Thirty-six cross-validated calibrations from the order Passeriformes yielded an average per lineage rate of 0.0104 (standard deviation = 0.0031, calculated directly from the online data set of Weir & Schluter 2008 because the value reported in their Table 1 for Passeriformes was incorrect) mutations per site per million years for cyt b (Weir & Schluter 2008). To determine the validity of applying this rate for cyt b to our data set of three mitochondrial protein-coding genes, we performed a major axis regression of maximum-likelihood GTR-Γ-corrected distances for cyt b vs. combined distances of all mtDNA protein-coding genes. The slope of the major axis regression is 1.10 ($P < 0.0001$, $r^2 = 0.94$), indicating that the protein-coding mtDNA data set is evolving 10% faster than just cyt b (Fig. 2). We multiplied the cyt b rate by 1.1 to yield a rate of 0.0114 with a standard deviation of 0.0034 and fixed BEAST's 'meanRate' prior to follow a normal distribution with this mean and standard deviation.

A previous study used multiple nuclear and mitochondrial genes to date major clades in the radiation of the Dendrocolaptidae and Furnariidae (Irestedt *et al.* 2009). This phylogeny was calibrated using the basal passerine split between *Acanthisitta* (endemic to New Zealand) and other passerines with the age when New Zealand split off from Gondwana 82–65 Ma. Because the lineage leading to *Acanthisitta* could have colonized New Zealand any time after its separation, this calibration point provides only a maximum age constraint and we consider the node ages in Irestedt *et al.* (2009) as representing maximum possible ages of nodes. The node connecting *Xiphorhynchus* to the clade that includes *Dendrocincla*, *Deconychura* and *Sittasomus* was dated at 20 Ma. We use this as a maximum age calibration for this node in our phylogeny (i.e. the root node) and implement this with a uniform distribution from 0 to 20 Ma. Eliminating this constraint on the root node age did not alter mean node ages but did increase the upper end of the 95% highest posterior density interval for node ages.

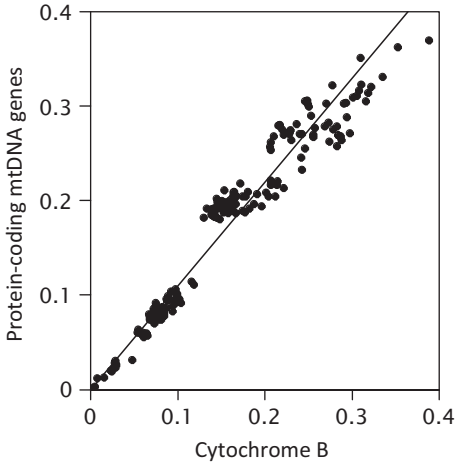

Fig. 2 Relationship between GTR-Γ distances calculated for cytochrome b only and for all mitochondrial protein-coding genes. The slope of the major axis regression is 1.1, indicating that the mitochondrial protein-coding data set is evolving 10% faster than the rate for just cytochrome b.

Biogeographic analysis

We reconstructed the biogeographic history of *Dendrocincla* using Bayes dispersal–vicariance analysis (BayesDIVA; Nylander *et al.* 2008a) as implemented in RASP (Yu *et al.* 2010), a method that accounts for phylogenetic uncertainty by integrating over a sample of trees from a Bayesian MCMC analysis. We used a random sample of 5000 post-burnin trees from our Bayesian analysis of the concatenated data set of all genes. We reconstructed three geographic areas along this sample of trees: *cis*-Andean, *trans*-Andean and Andean. The three outgroup genera occur in both *cis*- and *trans*-Andean regions (almost all *Xiphorhynchus* are lowland) and were coded as occurring in both *cis*- and *trans*-Andean regions. Coding of all ingroup taxa is illustrated in Fig. 4.

Results

For the cyt b analysis of all individuals, 300 of 1005 bp were variable. The extended sequence data set contained a total of 4453 bp, 886 of which were variable in ingroup sequences. In the extended data set, uncorrected distances for ingroup taxa (excluding distances between the two individuals of *Dendrocincla fuliginosa ridgwayi*) ranged from 0.5% to 6.8% for cyt b, 0.11–9.0% for ND2, 0.17–6.5% for COI, 0–3.7% for 16s, 0–0.72% for RAG1 and 0–1.21% for c-myc.

Our Bayesian analysis of the cyt b data set (Fig. 3 and Dataset S1) strongly supported (posterior probability of 1.0) reciprocal monophyly for all subspecies for which two or more individuals were sampled. The uncovered cyt b topology was poorly supported at several nodes (Fig. 3) and was not able to verify the monophly of *Dendrocincla* with respect to outgroups *Deconychura* and *Sittasomus*. Despite poor support at some nodes, the cyt b phylogeny yielded a topology almost identical to that uncovered in the well-supported phylogeny for the extended genetic data set (compare Figs 3 and 4).

For the concatenated data set of all genes, the Bayesian consensus tree and parsimony (a single most parsimonious tree was uncovered) yielded identical topologies (Fig. 4) with at least moderate support (0.7–0.95 posterior probability, 60–70% bootstrap support) for all but one node, and strong support (>0.95 posterior probability, >70% bootstrap support) for all but

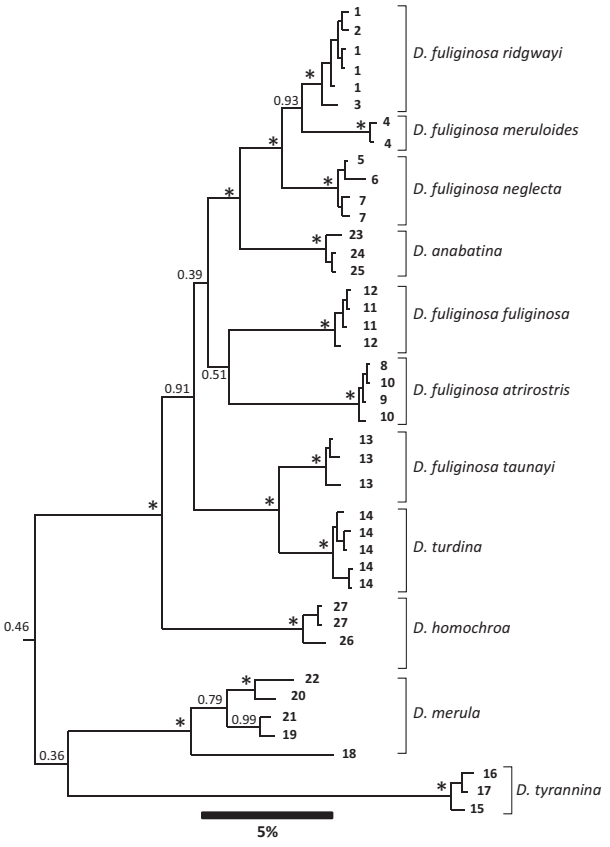

Fig. 3 Bayesian majority-rule consensus phylogeny generated under the GTR-Γ-I model for *Dendrocincla* for cytochrome b. Numbers at tips refer to sampling localities in Fig. 1 and Table 1. Numbers at nodes indicate posterior probabilities and are not shown for nodes connecting samples within a subspecies. Posterior probability of 1.0 is indicated by *. Scale bar is per cent divergence.

three nodes. The key topological uncertainty involved placement of *f. atrirostris* as sister to a clade that included *f. fuliginosa*, *f. neglecta*, *f. meruloides*, *f. ridgwayi* and *anabatina* (posterior probability = 0.65, bootstrap support = 58%). The next best-supported placements grouped *f. atrirostris* and *f. fuliginosa* as sister taxa (parsimony bootstrap support = 27%) or placed *Dendrocincla fuliginosa atrirostris* as sister to a clade containing *Dendrocincla turdina* and *Dendrocincla fuliginosa taunayi* (bootstrap support = 19%). Shimodaira–Hasegawa tests failed to reject these alternative topology placements ($P = 0.20$ and 0.25, respectively, using a one-tailed bootstrap test of 1000 permutations; Shimodaira & Hasegawa 1999). Regardless of the uncertainty in placing *f. atrirostris*, the uncovered topology demonstrates that *D. fuliginosa* is not a monophyletic species. Both *Dendrocincla anabatina* and *D. turdina* are phylogenetically nested within *D. fuliginosa*. A Shimodaira–Hasegawa test comparing the topology in Fig. 4 to one forcing *D. fuliginosa* to be reciprocally monophyletic rejected monophyly of *D. fuliginosa* ($P < 0.0001$). All other species were monophyletic.

Bayesian topologies for individual nuclear genes were poorly supported (Fig. S1, Supporting information), which is not surprising given their low levels of ingroup uncorrected distances compared to the mitochondrial genes. Nevertheless, the topology uncovered from the combined nuclear data set (Fig. S1, Supporting information), although receiving only weak to moderate nodal support, was similar to the topology of the concatenated data set of all genes (Fig. 4). The only differences between the topologies of these data sets occurred between recently diverged taxa within two clades: (i) the clade comprised of *merula castanoptera*, *m. olivascens*, *m. remota* and *m. bartletti* and (ii) the clade comprised of *fuliginosa fuliginosa*, *f. ridgwayi*, *f. neglecta*, *f. meruloides* and *anabatina* (compared Fig. S1, Supporting information and Fig. 4). The topological similarity at deeper levels suggests that the two data sets are congruent but that the nuclear data set does not have sufficient variability to resolve recently diverged taxa.

The species tree generated in BEST had an almost identical topology (although with lower posterior probabilities at several nodes) to the concatenated data set of all genes generated in MrBayes (Fig. 4) and the parsimony tree. The only difference in the BEST topology was that it placed *Dendrocincla tyrannina* as sister to the clade including *Dendrocincla homochroa, Dendrocincla fuliginsa, D. anabatina* and *Dendrocincla turdina* (with very low support, posterior probability = 0.42), while MrBayes and parsimony placed it as sister to *Dendrocincla merula* with moderate support (posterior probability = 0.92, bootstrap support = 61%).

The topologies uncovered by the concatenated data set of all genes and the species tree analysis resolve a number of taxonomic uncertainties that have plagued this genus: (i) *D. f. atrirostris* does not belong to *D. turdina* as suggested by some authors (Willis 1992; Marantz *et al.* 2003); (ii) *D. f. taunayi*, which is morphologically intermediate between *D. turdina* and Amazonian forms of *D. fuliginosa* (Zimmer & Mayr 1943; Marantz *et al.* 2003), is the sister taxon to *D. turdina*, and not closely related to other taxa in the *D. fuliginosa* complex; (iii) *Dendrocincla fuliginosa meruloides* has at times been considered conspecific with *D. merula* (see Marantz *et al.* 2003), but our topology clearly placed it within the *D. fuliginosa* complex; (iv) *D. anabatina* was thought to be the sister of *D. tyrannina* (Raikow 1994), but our topology suggests these two species are not closely related. Our analysis also indicates that current taxonomic practice of recognizing *D. fuliginosa* as a single polytypic species needs re-evaluation because two other species, *D. turdina* and *D. anabatina*,

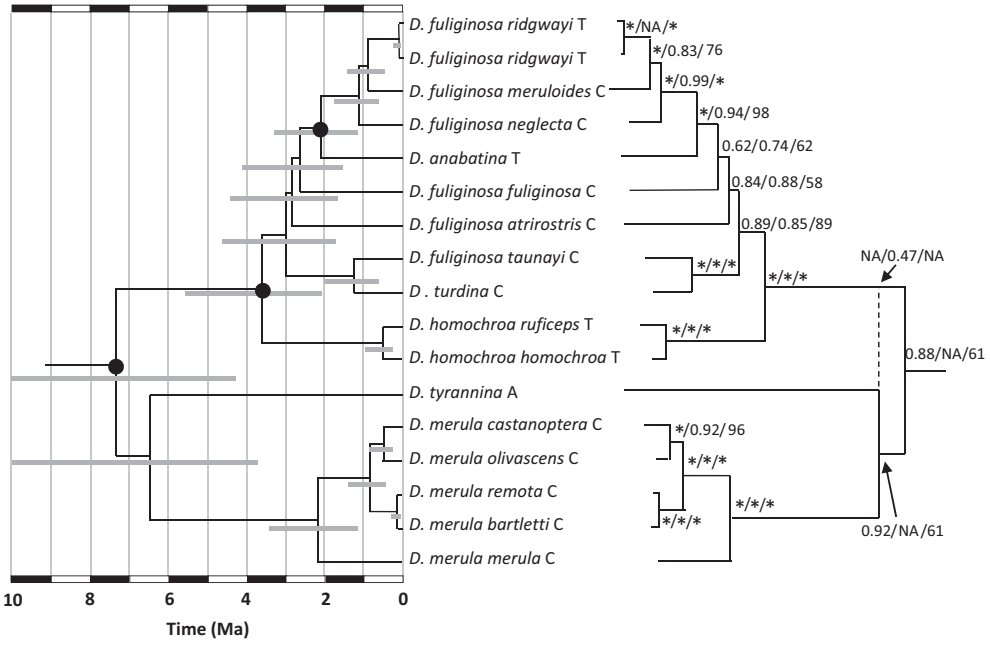

Fig. 4 Phylogenetic analyses generated for *Dendrocincla* from the extended sequence data set. (Right) Bayesian majority-rule consensus phylogeny generated for the concatenated data set of all genes. The most parsimonious tree yielded an identical topology. The species tree yielded a topology identical in all respects except the placement of *Dendrocincla tyrannina* as sister to the *Dendrocincla homochroa* and *Dendrocincla fuliginosa* complex (dashed line). Numbers at nodes indicate posterior probabilities for the concatenated analysis (left), species tree analysis (middle) and per cent bootstrap support (right). Posterior probability of 1.0% and 100% bootstrap support each are indicated by *. NA, not applicable because the node in question does not appear in the analysis. (Left) Time-calibrated phylogeny using the relaxed-clock model of BEAST with a mean molecular rate of 1.14% (±0. 34% SD; see text) per lineage and topology fixed to that estimated for the concatenated Bayesian analysis of all genes. Grey bars show the 95% highest posterior density interval for node ages (which for the most basal split extends beyond the graph to 11.3 Ma). T, *trans*-Andean; C, *cis*-Andean; A, Andean. Black circles at nodes indicate that taxa descending from that node have sympatric overlap in geographic ranges.

are phylogenetically nested within *D. fuliginosa*, rendering that species paraphyletic. We suggest that *D. f. taunayi* be recognized as a subspecies of *D. turdina* (vocalizations are similar between these taxa, but highly distinct from Amazonian members of the *D. fuliginosa* complex, suggesting that together they comprise a separate biological species, Weir unpublished data). *D. anabatina* is sympatric with *D. f. ridgwayi* (Figs 1 and 5), demonstrating its status as a unique biological species. Further analysis of contact zones and vocalizations are needed to determine whether other taxa in the *D. fuliginosa* complex should be separated into multiple species level taxa or whether it should be retained as a paraphyletic species with respect to *D. anabatina* (an option acceptable under the biological species concept).

Dated phylogenies are shown in Figs 4 and 5. The basal split within *Dendrocincla* was estimated to be 7.3 Ma. The first split between *cis*- and *trans*-Andean clades (*D. homochroa* vs. the clade comprising *D. fuliginosa*, *D. anabatina* and *D. turdina*) occurred at 3.6 Ma.

The Bayes-DIVA analysis produced a single most parsimonious reconstruction across the random sample of 5000 trees, providing a strongly supported (reconstruction at all ingroup nodes had a probability of 1.0) reconstruction despite topology uncertainties in a few parts of the tree which appear not to have affected the reconstructions. The basal node of *Dendrocincla* was reconstructed as occurring in the *cis*-Andean region with four nested nodes originating through vicariance or dispersal into other regions: *tyrannina* into the Andes (not shown), and three independent events (labelled event 1–3 in Fig. 5c), resulting in separation of sister clades into *cis*-Andean and *trans*-Andean regions. The first *cis/trans*-Andean splitting event occurred at 3.6 Ma towards the end of the 5–3.5 Ma uplift of the eastern Cordillera of Colombia. We interpret this splitting as a vicariant event, with Andean uplift bisecting the range of a widespread ancestor distributed in both *cis*- and *trans*-Andean regions to produce the lineages that would become the *trans*-Andean *D. homochroa* and the *cis*-Andean *D. fuliginosa* complex. The next two *cis*- to *trans*-events postdate Andean uplift and we interpret them as dispersal-based speciation events, either around the northern end of the Andes or over them. During the second event, *trans*-Andean *D. anabatina* originated following dispersal of

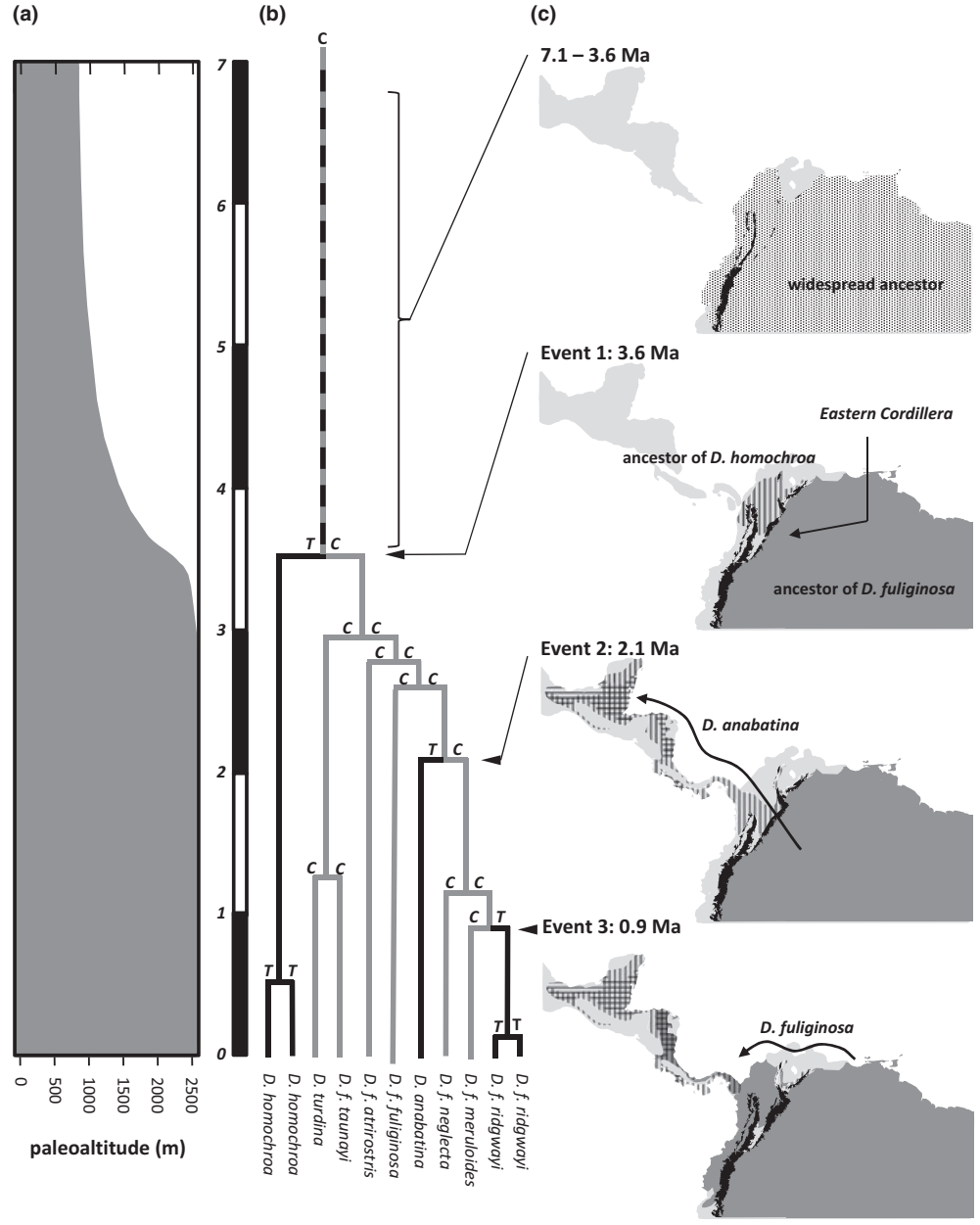

Fig. 5 The role of Andean uplift in the biogeographic history of lowland *Dendrocincla homochroa* and *Dendrocincla fuliginosa* complexes. (a) Reconstructed palaeoelevations for one transect across the Eastern Cordillera of Colombia based on data presented in Mora *et al*. 2008 (Fig. 12). Scale bar shows time in millions of years. (b) Dated phylogeny showing the Bayes-DIVA reconstruction of geographic distribution. *T* (black lines) = *trans*-Andean distribution, *C* (grey lines) = *cis*-Andean. Nodes with a *T* and *C* represent dispersal or vicariant splitting events. The dashed black and grey lines indicate our interpretation that a widespread ancestor was distributed in both geographic regions along a branch before vicariantly splitting into *cis*- and *trans*- regions (see text). Probabilities of the Bayes-DIVA reconstruction were 1.0 at each node and are not shown. (c) Reconstructed biogeographic history in relation to uplift of the Andes and formation of the Central America landbridge (see text for details). Palaeoelevations above 1800 m in the Andes shown by black are approximate and are presented for illustrative purposes only. Range of *D. fuliginosa* is shown by dark grey, *Dendrocincla anabatina* by horizontal barring, and *D. homochroa* by vertical barring. All three species occur sympatrically in parts of Central America.

D. fuliginosa stock around or across the completed Andes at *c.* 2.1 Ma. During the third event, *D. fuliginosa* dispersed around or across the northern Andes a second time at *c.* 0.9 Ma, producing *trans*-Andean *D. f. ridgwayi* (and probably also *D. f. lafresnayei* that was not sampled).

Discussion

Uplift of the northern Andes strongly influenced diversification of lowland *Dendrocincla* with all three reconstructed divergence events between *cis-* and *trans-*Andean lowland regions dating to the period during or following final Andean uplift. In contrast, Andean uplift resulted in a single highland species, *Dendrocincla tyrannina*. This species split off from other *Dendrocincla* 6–7 Ma, suggesting that highland and lowland clades have existed in South America for much of the history of the genus (Fig. 4). Despite the extended presence of *Dendrocincla* in highland and lowland regions, almost all subsequent diversification occurred within the lowlands. Here, we discuss the contribution of Andean uplift and other barriers to diversification within lowland *Dendrocincla*.

Role of Andean uplift

Our reconstruction suggests that the ancestor of the *Dendrocincla fuliginosa* and *Dendrocincla homochroa* clades probably had a widespread distribution prior to the completion of the Andean chain (Fig. 5c). The date of divergence between *D. homochroa* and the *D. fuliginosa* complex occurred towards the end of the uplift phase at *c.* 3.6 Ma (Fig. 5c, event 1). By 3.6 Ma, the Eastern Cordillera had achieved palaeo-altitudes of 2200 m or greater in most regions (Fig. 5a) (Gregory-Wodzicki 2000). Given *D. fuliginosa* occurs primarily below 1300 m (not known to exceed 2000 m) and *D. homochroa* below 800 m (not known to exceed 1800 m) in Colombia and Venezuela (Hilty & Brown 1986; Hilty 2003; Marantz *et al.* 2003), the Eastern Cordillera would probably have provided a formidable barrier to gene flow by 3.6 Ma. This barrier may have been strengthened by the close association of lowland *Dendrocincla* species with army ant swarms (mostly *Eciton burchellii* and to a lesser extent *Labidus praedator*; Willis 1972; Hilty 1972; Marantz *et al.* 2003) as *E. burchellii* becomes scarce at elevations above 1000 m in the northern Andes (Hilty 1972). The correspondence of this date of splitting to the uplift phase of the Eastern Cordillera suggests the widespread ancestor of these species was vicariantly separated by Andean uplift to produce the *trans*-Andean *D. homochroa* and *cis*-Andean *D. fuliginosa* complex at this time.

Following the final phase of Andean uplift, our reconstruction supports two dispersal events from *cis*-Andean to *trans*-Andean regions, either over or around the northern Andes. The first dispersal event produced *Dendrocincla anabatina* at 2.1 Ma. *Dendrocincla anabatina* is endemic to Central America, and its origin from *cis*-Andean, *D. fuliginosa* stock (i.e. it is nested within a paraphyletic *D. fuliginosa*; Figs 3 and 4) occurred slightly after the completion of the Central American land bridge in the mid-Pliocene. Likewise, phylogenetic reconstruction of colonization of South American woodcreepers (and other forest-restricted South American-derived groups) into Central America supported colonization at or after completion of the Central American land bridge, but not prior (Weir *et al.* 2009). The second dispersal event occurred *c.* 0.9 Ma, producing the endemic *trans*-Andean *Dendrocincla fuliginosa ridgwayi* and probably also the unsampled but closely related *D. f. lafresnayei* from northern Colombia, which we assume is sister to *D. f. ridgwayi* (alternatively, *D. f. lafresnayei* could represent an independent colonization from *cis*-Andean stock; sampling of this range-restricted taxon is necessary for confirmation). Given the recent divergence between *D. f. ridgwayi* and the *cis*-Andean *Dendrocincla fuliginosa meruloides* from north Venezuela and Trinidad, we suggest this final dispersal event likely occurred around the northern Andes, rather than over them. The timing of this dispersal event in the mid-Pleistocene, near the beginning of severe glacial cycles in the Andes, suggests that climate change–mediated dispersal corridors suggested by Haffer (1967) may have facilitated dispersal through what are currently arid regions north of the Andes. Elevational descent of montane forest into lowland regions and lower sea levels during glacial maxima may have facilitated the formation of temporary dispersal corridors around the northern Andes at this time.

Several other avian phylogeographic studies have also recovered multiple splitting events between *cis-* and *trans*-Andean regions in lowland wet-forest-restricted clades (e.g. Nyári 2007; DaCosta & Klicka 2008; Miller *et al.* 2008; Patane *et al.* 2009). The earliest *cis/trans* splits in *Ramphastos* at 3.3 Ma (Patane *et al.* 2009), *Trogon* at 3.4 Ma (DaCosta & Klicka 2008) and *Dendrocincla* at 3.6 Ma probably correspond to vicariant events of widespread ancestors separated into *cis-* and *trans*-Andean populations by uplift of the Eastern Cordillera of Colombia. In contrast to these groups, all *cis-* to *trans*-Andean splits in *Mionectes* occurred after 1.9 Ma (Miller *et al.* 2008) and thus greatly postdate the completion of uplift of the Eastern Cordillera of Colombia at 3.5 Ma. *Dendrocincla, Ramphastos, Trogon* and *Mionectes* all possessed multiple dispersal events between *cis-* and *trans*-regions that postdate final Andean uplift, supporting the role of the Andes in commonly promoting dispersal-based speciation.

Diversification within cis-Andean regions

Dendrocincla turdina and *Dendrocincla fuliginosa taunayi* occur in the Atlantic forest of Brazil, and previous authors suggested these represented a double invasion

from the Amazon (Willis 1992; Marantz *et al.* 2003) as found for a number of endemic Atlantic forest groups of mammals (Costa 2003). Our phylogeny unambiguously rejects the double invasion hypothesis in favour of a single invasion (or vicariant event) at 3.0 Ma (a similar date of colonization occurred in the Atlantic forest woodcreeper *Xiphorhynchus fuscus* which split from its Amazonian sister at about 3.1–3.7 Ma assuming a 2.1% clock; see Aleixo 2002; Cabanne *et al.* 2008), followed by an *in situ* divergence event at 1.3 Ma, which resulted in the formation of *D. turdina* and *D. f. taunayi*. The Rio São Francisco appears to separate the ranges of these taxa. Deeply diverged phylogroups of *X. fuscus,* and the sister species pair *Tangara seledon* and *T. fastuosa* also diverged across the Rio São Francisco, and levels of sequence divergence (*Xiphorhynchus,* uncorrected divergence = 2.6% for three protein-coding mitochondrial genes; *Tangara,* GTR-Γ distance = 3.18% for cyt B) suggest a divergence event at *c.* 1.2–1.5 Ma (assuming a 2.1% clock), similar to that for *turdina* and *taunayi*. The correspondence of these dates across multiple bird groups suggests a common biogeographic event may have affected each simultaneously. For example, formation of the current course of the Rio São Francisco may have simultaneously fragmented the ancestors of both these taxa pairs, or dispersal-based speciation across this barrier may have been facilitated by climate change or some other factor at this time. Alternatively, palaeoclimate modelling suggests that during Pleistocene glacial advances, separate forest refugia occurred to the north (Pernambuco refugium) and south (Bahia refugium) of the Rio São Francisco and could have promoted divergence (Carnaval *et al.* 2009). The mid-Pleistocene dates for *Dendrocincla*, *Xiphorhynchus* and *Tangara* are consistent with the refugium hypothesis. Multiple species of anurans (Carnaval *et al.* 2009) and other groups (Pellegrino *et al.* 2005) also show differentiation between these regions, suggesting that *in situ* diversification within the northern half of the Atlantic forest was taxonomically widespread.

Within Amazonia, the modern Amazon River became deeply entrenched in the late Miocene and early Pliocene (Figueiredo *et al.* 2009; Mora *et al.* 2010) following uplift of the northern Andes and blockage of the northward-flowing drainage pattern. The major tributaries flowing into the Amazon River probably obtained their current drainage patterns within the past 5–6 Ma (Figueiredo *et al.* 2009). This time period corresponds with extensive Amazonian diversification of lineages, both within *Dendrocincla merula*, over the past 2.2 Ma; *D. fuliginosa*, over the past 2.8 Ma; and other Amazonian woodcreeper groups (e.g. *Glyphorynchus*, Marks *et al.* 2002; *Xiphorhynchus,* Aleixo 2004). Major Amazonian rivers form boundaries between many subspecies within each of these species, suggesting they may have been instrumental in their diversification (river refuge hypothesis; Sick 1967). However, detailed analyses of the role of Amazonian river barriers in promoting diversification in *Dendrocincla* require more extensive phylogeographic sampling than provided here.

Patterns of sympatry

Species richness at the local and regional scales are often strongly correlated (e.g. MacArthur & Wilson 1967; Ricklefs 1987; Harrison & Cornell 2008), a pattern that does not hold true for *Dendrocinla*. Local species richness is highest in *trans*-Andean regions where all three *trans*-Andean species are broadly sympatric in Honduras and Nicaragua (Figs 1 and 5c; though, *D. homochroa* tends to higher elevations in sympatry; Ridgely & Tudor 1994; Marantz *et al.* 2003). In contrast, only two *cis*-Andean species (*D. fuliginosa* and *D. merula*) are broadly sympatric despite the greater regional pool of taxa there (17 *cis*- vs. nine *trans*-Andean taxa). The three sympatric trans-Andean species also share more recent common ancestors (*c.* 3.6 and 2.1 Ma) than the sympatric cis-Andean species (*c.* 7.3 Ma; Fig. 4), suggesting they have achieved sympatry despite less time for evolutionary and ecological divergence. One explanation is that completion of the Isthmus of Panama between 3 and 3.5 Ma allowed cis-Andean taxa to colonize into a relatively depauperate Middle American community (see Weir *et al.* 2009). The absence of competitors and availability of underutilized niches may have allowed for faster rates of sympatry in those lineages that were able to colonize Middle America. For example, as many as eight species of obligate army ant following antbirds co-occur in Amazonia and presumably compete with army ant following *Dendrocincla*. In Nicaragua and Honduras, where all three *trans*-Andean *Dendrocincla* are sympatric, only two species of obligate army-ant following antbirds occur (Brumfield *et al.* 2007). Fewer competing antbirds and other species of woodcreeper many have allowed for more rapid attainment of sympatry in Middle America compared to Amazonia. Alternatively, geographic barriers to sympatry in *cis*-Andean regions may be less permeable to range expansions and taxa there have simply had less opportunity to expand their ranges into sympatry compared to *trans*-Andean regions. For example, *Dendrocincla* may have been less prone to cross major Amazonian river barriers—which often separate taxa and prevent sympatry—than they were to colonize over or around the Andes. This seems unlikely given several Amazonian taxa appear to be in geographic contact without sympatry (e.g. *Dendrocincla fuliginosa atrirostris* and *Dendrocincla fuliginosa neglecta* which diverged from a

common ancestor *c.* 2.8 Ma appear to be broadly parapatric; Fig. 1).

Conclusions

The molecular phylogenetic hypothesis for *Dendrocincla* confirms the importance of Andean uplift in contributing to lowland diversification. Our reconstruction support three separate divergence events of lowland taxa across the Andes, with the first representing a vicariant event caused by Andean uplift, followed by two dispersal events over or around the northern Andes from *cis-* to *trans*-Andean regions. Molecular phylogenetic data suggest Andean uplift has similarly affected other lowland wet-forest groups (e.g. DaCosta & Klicka 2008; Patane *et al.* 2009), with Andean uplift promoting both vicariant- and dispersal-based speciation. Together, these studies confirm the important role of Andean uplift in driving lowland diversification in northern South America. In contrast to predictions of a double invasion of the Atlantic Forest from the Amazon, our data support a single colonization, followed by *in situ* diversification across the Rio São Francisco. River barriers may have also played a key role in diversification within Amazonia, but finer-scale sampling is required.

Acknowledgements

This manuscript benefitted from comments by Nate Lovejoy, Devin Bloom and four anonymous reviewers. JTW acknowledges funding from an NSERC Discovery Grant and University of Toronto start-up funds. MP acknowledges NSERC funding awarded to D. Schluter.

References

Aleixo A (2002) Molecular systematics and the role of the ''varzea'' – ''Terra-firme'' ecotone in the diversification of *Xiphorhynchus* woodcreepers (Aves: Dendrocolaptidae). *The Auk*, **119**, 621–640.

Aleixo A (2004) Historical diversification of a terra-firme forest bird superspecies: a phylogeographic perspective on the role of different hypotheses of Amazonian diversification. *Evolution*, **58**, 1303–1317.

Brumfield RT, Capparella AP (1996) Historical diversification of birds in northwestern South America: a molecular perspective on the role of vicariant events. *Evolution*, **50**, 1607–1624.

Brumfield RT, Tello JG, Cheviron ZA, Carling MD, Crochet N, Rosenberg KV (2007) Phylogenetic conservatism and antiquity of a tropical specialization: army-ant-following in the typical antbirds (Thamnophilidae). *Molecular Phylogenetics and Evolution*, **45**, 1–13.

Burney CW, Brumfield RT (2009) Ecology predicts levels of genetic differentiation in Neotropical birds. *The American Naturalist*, **174**, 358–368.

Burns KJ, Naoki K (2004) Molecular phylogenetics and biogeography of Neotropical tanagers in the genus *Tangara*. *Molecular Phylogenetics and Evolution*, **32**, 838–854.

Cabanne GS, d'Horta FM, Sari HER, Santos FR, Miyaki CY (2008) Nuclear and mitochondrial phylogeography of the Atlantic forest endemic *Xiphorhynchus fuscus* (Aves: Dendrocolaptidae): biogeography and systematics implications. *Molecular Phylogenetics and Evolution*, **49**, 760–773.

Carnaval AC, Hickerson MJ, Haddad CFB, Rodrigues MT, Moritz C (2009) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science*, **323**, 785–789.

Chapman FM (1917) The distribution of bird-life in Colombia. *Bulletin of the American Museum of Natural History*, **36**, 347–355.

Chapman FM (1926) The distribution of bird-life in Ecuador. *Bulletin of the American Museum of Natural History*, **55**, 1–784.

Costa LP (2003) The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. *Journal of Biogeography*, **30**, 71–86.

Cracraft J (1985) Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Ornithological Monographs*, **36**, 49–84.

DaCosta JM, Klicka J (2008) The great American interchange in birds: a phylogenetic perspective with the genus Trogon. *Molecular Ecology*, **17**, 1328–1343.

Derryberry E, Claramunt S, Chesser RT *et al.* (2010) *Certhiasomus*, a new genus of woodcreeper (Aves: Passeriformes: Dendrocolatidae). *Zootaxa*, **2416**, 44–50.

Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**, 214.

Edwards SV, Lui L, Pearl DK (2007) High resolution species trees without concatenation. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 5936–5941.

Ericson PGP, Johansson US, Parsons TJ (2000) Major divisions in the oscines revealed by insertions in the nuclear gene c-myc: a novel gene in avian phylogenetics. *The Auk*, **117**, 1069–1078.

Figueiredo J, Hoorn C, van der Ven P, Soares E (2009) Late Miocene onset of the Amazon River and the Amazon deep-sea fan: evidence from the Foz do Amazonas Basin. *Geology*, **37**, 619–622.

Garzione CN, Hoke GD, Libarkin JC *et al.* (2008) Rise of the Andes. *Science*, **320**, 1304–1307.

Gregory-Wodzicki KM (2000) Uplift history of the central and northern Andes: a review. *Geological Society of America Bulletin*, **112**, 1091–1105.

Groth JC, Barrowclough GF (1999) Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. *Molecular Phylogenetics and Evolution*, **12**, 115–123.

Hackett S (1996) Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). *Molecular Phylogenetics and Evolution*, **5**, 368–382.

Haffer J (1967) Speciation in Colombian forest birds west of the Andes. *American Museum Novitates*, **294**, 1–57.

Haffer J (1969) Speciation in Amazonian forest birds. *Science*, **165**, 131–137.

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, **41**, 95–98.

Harrison S, Cornell H (2008) Towards a better understanding of the regional causes of local community richness. *Ecological Letters*, **11**, 969–979.

Hartley A (2003) Andean uplift and climate change. *Journal of the Geological Society*, **160**, 7–10.

Hilty SL (1972) Notes on birds at swarms of army ants in the highlands of Colombia. *Wilson Bulletin.*, **86**, 479–481.

Hilty SL (2003) *Birds of Venezuela*. Princeton University Press, Princeton, New Jersey.

Hilty SL, Brown WL (1986) *Birds of Colombia*. Princeton University Press, Princeton, New Jersey.

Hooghiemstra H, van der Hammen T (1998) Neogene and quaternary development of the neotropical rain forest: the forest refugia hypothesis, and a literature overview. *Earth-Science Reviews*, **44**, 147–183.

Hoorn C, Guerrero J, Sarmiento GA, Lorente MA (1995) Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology*, **23**, 237–240.

Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.

Hughes C, Eastwood R (2006) Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 10334–10339.

Irestedt M, Johansson US, Parsons TJ, Ericson PGP (2001) Phylogeny of major lineages of suboscines (Passeriformes) analysed by nuclear DNA sequence data. *Journal of Avian Biology*, **32**, 15–25.

Irestedt M, Fjeldså J, Johansson US, Ericson PGP (2002) Systematic relationships and biogeography of the tracheophone suboscines (Aves: Passeriformes). *Molecular Phylogenetics and Evolution*, **23**, 499–512.

Irestedt M, Fjeldså J, Ericson PGP (2004) Phylogenetic relationships of woodcreepers (Aves: Dendrocolaptinae)-incongruence between molecular and morphological data. *Journal of Avian Biology*, **35**, 280–288.

Irestedt M, Fjeldså J, Dalén L, Ericson PGP (2009) Convergent evolution, habitat shifts and variable diversification rates in the ovenbird-woodcreeper family (Furnariidae). *BMC Evolutionary Biology*, **9**, 268.

Johnson KJ, Sorenson MD (1998) Comparing molecular evolution in two mitochondrial protein coding genes (Cytochrome b and ND2) in the dabbling ducks (Tribe: Anatini). *Molecular Phylogenetics and Evolution*, **10**, 82–94.

Kreft H, Jetz W (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 5925–5930.

Liu L (2008) BEST: Bayesian estimation of species trees under the coalescent model. *Bioinformatics*, **24**, 2542–2543.

MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

Marantz CA, Aleixo A, Brevier LR, Patten MA (2003) Family Dendrocolaptidae (Woodcreepers). In: *Handbook of the Birds of the World Vol. 8. Broadbills to Tapaculos* (eds del Hoyo J, Elliott A, Christie DA), pp. 358–447. Lynx Edicions, Barcelona.

Marks BD, Hackett SJ, Capparella AP (2002) Historical relationships among Neotropical lowland forest areas of endemism as determined by mitochondrial DNA sequence variation within the wedge-billed woodcreeper (Aves: Dendrocolaptidae: *Glyphorynchus spirurus*). *Molecular Phylogenetics and Evolution*, **24**, 153–167.

Miller MJ, Bermingham E, Klicka J *et al.* (2008) Out of Amazonia again and again: episodic crossing of the Andes promotes diversification in a lowland forest flycatcher. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 1133–1142.

Mora A, Parra M, Strecker MR *et al.* (2008) Climatic forcing of asymmetric orogenic evolution in the Eastern Cordillera of Colombia. *Bulletin of the Geological Society of America*, **120**, 930–949.

Mora A, Baby P, Roddaz M *et al.* (2010) Tectonic history of the Andes and sub-Andean zones: implications for the development of the Amazon drainage basin. In: *Amazonia, Landscape and Species Evolution* (eds Hoorn C, Wesselingh FP), pp. 38–60. Wiley, Oxford.

Newton I (2003) *The Speciation and Biogeography of Birds*. Academic Press, Amsterdam.

Nyári AS (2007) Phylogeographic patterns, molecular and vocal differentiation, and species limits in *Schiffornis turdina* (Aves). *Molecular Phylogenetics and Evolution*, **44**, 154–164.

Nylander JAA (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Nylander JAA, Olsson U, Alström P, Sanmartín I (2008a) Accounting for phylogenetic uncertainty in biogeography: a Bayesian approach to dispersal-vicariance analysis of the thrushes (Aves: *Turdus*). *Systematic Biology*, **57**, 257–268.

Nylander JAA, Wilgenbusch JC, Warren DL, Swofford DL (2008b) AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics*, **24**, 581–583.

Palumbi SR (1996) Nucleic acids II: the polymerase chain reaction. In: *Molecular Systematics*, 2nd edn (eds Hillis DM, Moritz C, Mable BK), pp. 205–247. Sinauer Associates, Sunderland, Massachusetts.

Patane JSL, Weckstein JD, Aleixo A, Bates JM (2009) Evolutionary history of *Ramphastos* toucans: molecular phylogenetics, temporal diversification, and biogeography. *Molecular Phylogenetics and Evolution*, **53**, 923–934.

Pellegrino KCM, Rodrigues MT, Waite AN, Morando M, Yassuda YY, Sites JW Jr (2005) Phylogeography and species limits in the *Gymnodactylus darwinii* complex (Gekkonidae, Squamata): genetic structure coincides with river systems in the Brazilian Atlantic forest. *Biological Journal of the Linnean Society*, **85**, 13–26.

Raikow RJ (1994) A phylogeny of the woodcreepers (Dendrocolaptidae). *The Auk*, **111**, 104–114.

Rambaut A, Drummond AJ (2009) TRACER: MCMC trace analysis tool v1.5.0. Available at: http://beast.bio.ed.ac.uk/.

Ribas CC, Moyle RG, Miyaki CY, Cracraft J (2007) The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in *Pionus* parrots. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2399–2408.

Ricklefs RE (1987) Community diversity: the relative roles of regional and local processes. *Science*, **235**, 167–171.

Ridgely RS, Tudor G (1994) *The Birds of South America (Volume 2: The Suboscine Passerines)*, University of Texas Press, Austin.

Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Sedano RE, Burns KJ (2009) Are the Northern Andes a species pump for Neotropical birds? Phylogenetics and biogeography of a clade of Neotropical tanagers (Aves: Thraupini). *Journal of Biogeography*, **37**, 325–343.

Shimodaira H, Hasegawa M (1999) Multiple comparisons of loglikelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution*, **16**, 1114–1116.

Sick H (1967) Rios e enchentes na Amazonia como obstaculo para a avifauna. In:*Atlas do simposio sobre a biota Amazonica. vol. 5 (Zoologia)* (ed. Lent H), pp. 495–520. Conselho Nacional de Pesquisas, Rio de Janeiro.

Stephens M, Donnelly P (2003) A comparison of bayesian methods for haplotype reconstruction. *American Society of Human Genetics*, **73**, 1162–1169.

Stephens M, Smith NJ, Donnelly P (2001) A new statistical method for haplotype reconstruction from population data. *American Society of Human Genetics*, **68**, 978–989.

Swofford DL (2002) *PAUP* 4.0b10: Phylogenetic Analysis Using Parsimony (*And Other Methods)*. Sinauer Associates, Sunderland, Massachusetts.

Weir JT (2006) Divergent timing and patterns of species accumulation in lowland and highland Neotropical birds. *Evolution*, **60**, 842–855.

Weir JT (2009) Implications of genetic differentiation in Neotropical montane forest birds. *Annals of the Missouri Botanical Garden*, **96**, 410–433.

Weir JT, Schluter D (2007) The latitudinal gradient in recent speciation and extinction rates. *Science*, **315**, 1574–1576.

Weir JT, Schluter D (2008) Calibrating the avian molecular clock. *Molecular Ecology*, **17**, 2321–2328.

Weir JT, Bermingham E, Miller MJ, Klicka J, González MA (2008) Phylogeography of a morphologically diverse Neotropical montane species, the Common Bush-Tanager (*Chlorospingus ophthalmicus*). *Molecular Phylogenetics and Evolution*, **47**, 650–664.

Weir JT, Bermingham E, Schluter D (2009) The Great American biotic interchange in birds. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 21737–21742.

Willis EO (1972) The behaviour of plain-brown woodcreepers, *Dendrocincla fuliginosa*. *Wilson Bulletin*, **84**, 377–420.

Willis EO (1992) Zoogeographical origins of eastern Brazilian birds. *Ornitologia Neotropical*, **3**, 1–15.

Yu Y, Harris AJ, He X (2010) S-DIVA (Statistical Dispersal-Vicariance Analysis): a tool for inferring biogeographic histories. *Molecular Phylogenetics and Evolution*, **56**, 848–850.

Zimmer JT, Mayr E (1943) New species of birds described from 1983 to 1941. *The Auk*, **60**, 249–262.

J.W. is interested in the biogeographic, ecological and evolutionary factors that promote high Neotropical species diversity. M.P. is interested in the evolution of virulence in bacterial systems.

Data accessibility

DNA sequences: GenBank accessions are provided in Table 1.

Phylogenetic data: Phylogenetic trees in fasta format are in the supporting online dataset.

Supporting information

Additional supporting information may be found in the online version of this article.

Fig. S1 Bayesian majority-rule consensus phylogenies generated for individual nuclear genes and a concatenated dataset of nuclear genes.

Dataset S1 Phylogenetic trees from Figures 3 and 4 in fasta format.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.