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Molecular systematics, species limits, and diversification of the genus *Dendrocolaptes* (Aves: Furnariidae): Insights on biotic exchanges between dry and humid forest types in the Neotropics

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Abstract

The true diversity and interspecific limits in the Neotropical endemic avian genus *Dendrocolaptes* (Furnariidae) remain a highly controversial subject, with previous genus-wide assessments, based mostly on morphological characters, producing poorly resolved phylogenies. The lack of well-resolved, robust, and taxonomically densely sampled phylogenies for *Dendrocolaptes* prevents reliable inferences on the genus' actual species diversity and evolutionary history. Here, we analyzed 2,741 base pairs of mitochondrial and nuclear genes from 43 specimens belonging to all species and the majority of subspecies described for *Dendrocolaptes* to evaluate species limits and reconstruct its diversification through time. Our phylogenies recovered a monophyletic *Dendrocolaptes*, with two main highly supported internal clades corresponding to the *D. certhia* and *D. picumnus* species complexes. Also, our analyses supported the monophyly of most *Dendrocolaptes* species recognized today, except *D. picumnus*, which was consistently recovered as paraphyletic with respect to *D. hoffmannsi*. A coalescent-based test supported a total of 15 different lineages in *Dendrocolaptes* and indicated that the number of currently accepted species within the genus may be greatly underestimated. Particularly relevant, when combined with previous analyses based on plumage characters, comparative high levels of genetic differentiation and coalescent analyses support the recognition of *D. picumnus transfasciatus* as a full species that is already under threat. Ancestral area reconstructions suggest that diversification in *Dendrocolaptes* was centered in lowland Amazonia, with several independent dispersal events leading to differentiation into different adjacent dry and high elevation forest types throughout the Neotropics, mainly during the Middle and Late Pleistocene.

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Amazonia, multispecies coalescent model, plumage evolution, South American "dry diagonal", taxonomy

1 | INTRODUCTION

Both dry and humid forest vegetation types account for a significant portion of the Neotropical biomes, but it remains less clear in which way and to what extent diversification processes are coupled between these two distinct habitats (Capurucho, Ashley, Ribas, & Bates, 2018; Garcia-Moreno & Silva, 1997; Silva, 1996, but see Antonelli et al., 2018). For instance, drier climatic conditions typically associated with glacial maxima are thought to promote the expansion of dry biomes, while at the same time causing the fragmentation and reduction in humid forest cover (Hooghiemstra & van der Hammen, 1998; Werneck, 2011). Therefore, historical factors such as extreme variations in climate may have affected dry and humid Neotropical forests synchronously, albeit in very contrasting ways (Silva et al., 2019; Werneck, Nogueira, Colli, & Costa, 2012). Current evidence points toward the existence of many lineages that have long evolved separately in dry and humid forest types throughout the Neotropics, with only a small number of taxa known to occur indistinctly in both habitats (Capurucho et al., 2018; Fenker et al., 2020; Porzecanski & Cracraft, 2005; Sousa-Neto, Cianciaruso, & Collevatti, 2016). Lineages occurring in both dry and humid forest types are the best targets for evaluating any connections between these habitats because they can provide both spatial resolution and temporal clues on comparative diversification processes within both vegetation types. These investigations are of paramount importance because climate change may not only increase or reduce the area covered by each dry and humid forest types, but also shift their mutual ranges through time, hence providing multiple opportunities for close geographic contact and biotic exchange between them (Capurucho et al., 2018; Oliveras & Mahli, 2016; Sousa-Neto et al., 2016).

The Neotropical endemic genus *Dendrocolaptes* (Furnariidae) occurs in a wide variety of both humid (lowland and montane) and dry forest types from southern Mexico to northern Argentina (Marantz, Aleixo, Bevier, & Patten, 2020a). Currently, five species are usually recognized within the genus (Gill, Donsker, & Rasmussen, 2020; Marantz & Patten, 2010; Remsen et al., 2020), but interspecific limits remain uncertain in many cases (Marantz, Aleixo, Bevier, & Patten, 2020b), and highly controversial in others (Batista et al., 2013; del Hoyo, Collar, & Kirwan, 2020; Piacentini et al., 2015). To this day, genus-wide taxonomic assessments have been based primarily on morphological characters (Cory & Hellmayr, 1925; Marantz, 1997; Marantz & Patten, 2010; Peters, 1951; Zimmer, 1934), with one genetic analysis focused at the family level lacking adequate sampling for *Dendrocolaptes* at the subspecific level (Derryberry et al., 2011). In sum, a well-resolved, robust, and taxonomically densely sampled phylogeny is still lacking for the genus *Dendrocolaptes*, which precludes any reliable inferences on the actual species diversity in the genus and its evolutionary history.

Here, we provide the first phylogenies for *Dendrocolaptes* with dense taxonomic sampling and use them to evaluate species limits within the genus, as well as reconstruct its diversification through time. Specifically, we evaluated whether past changes in the extent and distribution of dry and humid forest types influenced the genus' evolutionary history. If biotic exchanges between Neotropical dry and humid forest types were important events through time, we anticipate that *Dendrocolaptes* sister lineages will often replace each other across these habitats. In contrast, if biotic exchange was limited, dry and humid forest *Dendrocolaptes* lineages would have evolved separately within each biome for the most part of their evolutionary history. Finally, we contrast our results with previous taxonomic work on *Dendrocolaptes* and make recommendations concerning the classification of its taxa as either species or subspecies.

2 | MATERIALS AND METHODS

2.1 | Sampling

We sequenced 19 specimens and used previously available sequences from 24 specimens (Batista et al., 2013; Silva et al., 2019) from all five species and 15 out of the 23 subspecies of *Dendrocolaptes* currently considered valid (Gill et al., 2020). Our sampling included the following taxa distributed in each of the currently recognized species of *Dendrocolaptes* (Gill et al., 2020; Marantz et al., 2020b; Marantz, Aleixo, Bevier, & Patten, 2020c, 2020e; Figure 1): (a) in the polytypic Amazonian Barred Woodcreeper *Dendrocolaptes certhia*: *D. c. certhia* (Boddaert, 1783) (distributed on the Guiana shield), *D. c. concolor* Pelzeln, 1868 (distributed in the Madeira–Tapajós interfluve), *D. c. juruanus* Ihering, 1905 (distributed west of the Madeira and south of the Amazon rivers in southwestern Amazonia), *D. c. medius* Todd, 1920 (distributed east of the Tocantins River to northwestern Maranhão), *D. c. radiolatus* Sclater & Salvin, 1868 (found west of the Negro and north of the Amazon rivers), *D. c. retentus* Batista et al., 2013 (distributed in the Xingu–Tocantins interfluve), and *D. c. ridgwayi* Hellmayr, 1905 (distributed between the Tapajós and Xingu rivers); (b) in the polytypic Black-banded Woodcreeper *Dendrocolaptes picumnus*: *D. p. costaricensis* Ridgway, 1909 (found in the highlands of Costa Rica and Panama), *D. p. pallescens* Pelzeln, 1868 (distributed mainly in the Chaco in Bolivia, Brazil, and Paraguay, and the eastern Andes foothills in northwestern Argentina), *D. p. picumnus* Lichtenstein, 1820 (from the Guiana shield), *D. p. transfasciatus* Todd, 1925 (distributed between the Tapajós and Tocantins rivers), and *D. p. validus* Tschudi,

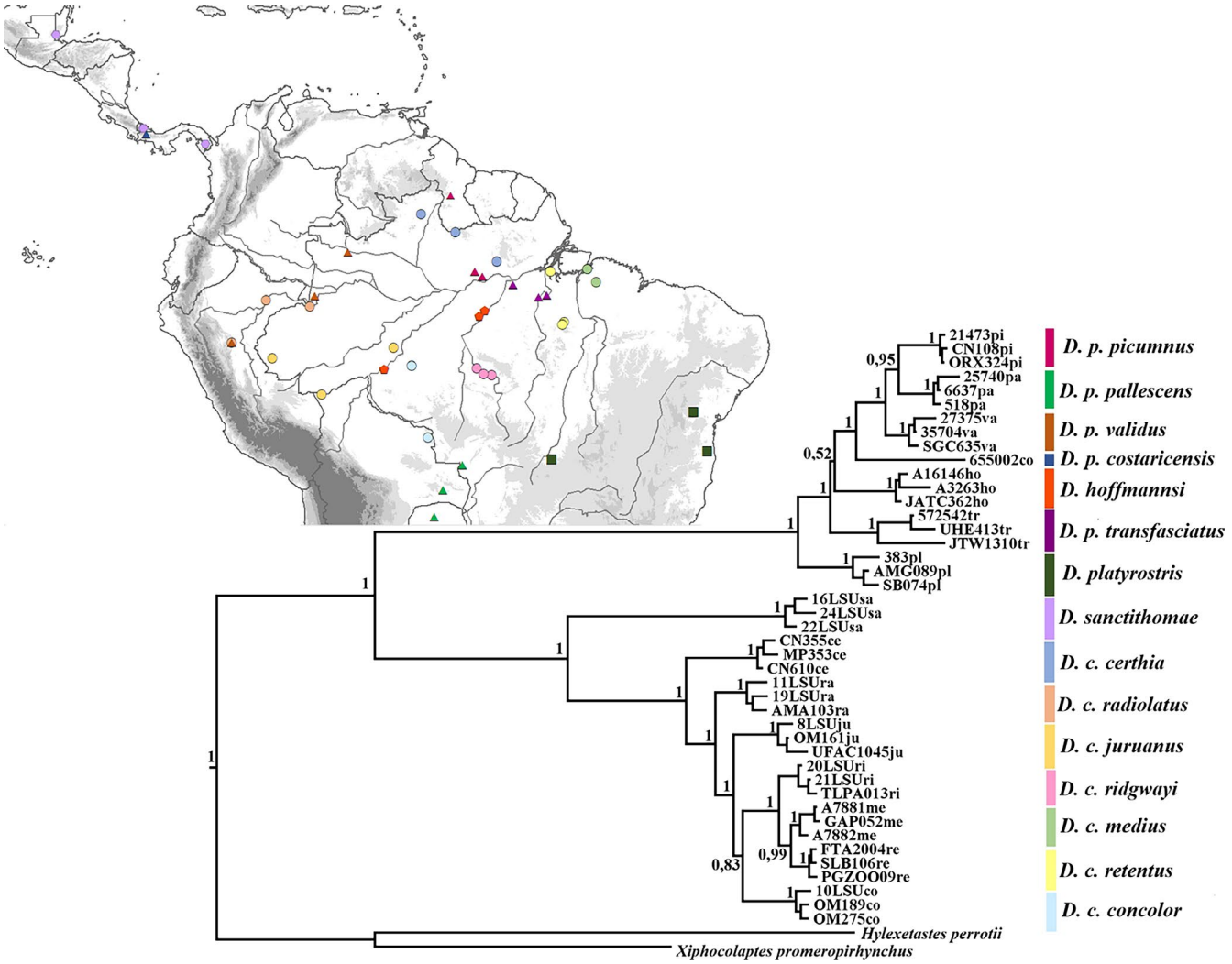

FIGURE 1 Above: map with locations of analyzed samples of *Dendrocolaptes* sequenced in this study (triangles—*D. picumnus*, circles—*D. certhia*, hexagons—*D. sanctithomae*, pentagons—*D. hoffmannsi*, and squares—*D. platyrostris*). Below: concatenated Bayesian phylogeny estimate for *Dendrocolaptes* based on all sequenced genes (*ND2*, *Cytb*, *FIB5*, and *G3PDH*). Node values correspond to posterior probabilities. See Table 1 for detailed sample information

1844 (widely distributed in western Amazonia, from the west bank of the Negro river to the west bank of the Madeira river in Brazil, also including Amazonian Bolivia, Peru, Ecuador, and Colombia); (c) the monotypic Hoffmann's Woodcreeper *Dendrocolaptes hoffmannsi* Hellmayr, 1909 (distributed in the Madeira–Tapajós interfluve); (d) in the polytypic Planalto Woodcreeper *Dendrocolaptes platyrostris*: *D. p. intermedius* Berlepsch, 1883 (distributed in central and northeastern Brazil, and northeastern Paraguay) and *D. p. platyrostris* Spix, 1824 (distributed in eastern, southeastern, and southern Brazil, northeastern Argentina, eastern Paraguay, and northeastern Uruguay); and (e) in the polytypic Northern Barred Woodcreeper *Dendrocolaptes sanctithomae*: *D. s. sanctithomae* (Lafresnaye, 1852) (distributed from southern Mexico to northwestern Colombia). Thus, five *D. picumnus* (*D. p. casaresi* Steullet & Deautier, 1950, *D. p. multistrigatus* Eyton, 1851, *D. p. olivaceus* Zimmer, 1934, *D. p. puncticollis* Sclater & Salvin, 1868, and *D. p. seilerni* Hartert & Goodson, 1917) and three *D. sanctithomae* (*D. s. hesperius* Bangs, 1907, *D. s. punctipectus* Phelps & Gilliard, 1940, and *D. s. sheffleri* Binford, 1965) subspecies could not be sampled due to either unavailability of tissues or unresponsiveness from tissue collections holding requested samples. Despite these gaps, our sampling does cover three out of the four main subspecies groups detected in each polytypic *D. picumnus* and *D. sanctithomae* species, based on previous extensive plumage and morphometric analyses (Marantz, 1997; Marantz & Patten, 2010). The number of tissues sequenced for each taxon sampled varied from one to three, with each recognized species-level taxon (Gill et al., 2020) represented by samples from at least three different localities (Table 1). We used the following species belonging to two closely related genera to *Dendrocolaptes* as out-groups (Derryberry, 2011): *Hylexetastes perrotii* (Lafresnaye, 1844)—Red-billed Woodcreeper and *Xiphocolaptes promeropirhynchus* (Lesson, 1840)—Strong-billed Woodcreeper (Table 1).

TABLE 1 Detailed voucher information associated with each *Dendrocolaptes* specimen whose sequences were used in this study. New sequences generated herein are highlighted in bold. Taxonomy follows Gill et al., (2020)

Taxon/voucher #	Sample ID code	Locality	GenBank accession numbers			
			ND2	*Cytb*	*BF5*	*G3PDH*
D. certhia certhia						
MPEG 65027[a]	CN355ce	Brazil, Pará, Óbidos Flota do Trombetas	KC815046.1	KC874915.1	MG651782	MG777027
MPEG 65836	CN610ce	Brazil, Pará, Oriximiná ESEC Grão Pará	KC815047.1	KC874916.1	MG651783	MG777028
MPEG 56524	MP353ce	Brazil, Roraima, Alto Alegre, Fazenda Paraense	KC815052.1	KC874921.1	MG651788	MG777033
D. certhia radiolatus						
MPEG 72661	AMA103ra	Brazil, Amazonas, Tabatinga, R. Solimões, Teresina	KC815058.1	KC874925.1	MG651792	MG777037
LSUMZ 27484	11LSUra	Peru, Loreto D. NE bank of R. Cushabatay 84km Contamana	KC815065.1	KC874932.1	MG651797	MG777044
LSUMZ 103585	19LSUra	Peru, Loreto D. S bank Maranon R., Samiria R. Est.Biol.Pithecia.	KC815070.1	KC874936.1	MG651802	MG777049
D. certhia juruanus						
MPEG 71170	OM161ju	Brazil, Amazonas, Humaitá I. bank R. Madeira, Ipixuna	KC815073.1	KC874938.1	MG651811	MG777059
MPEG 62044	UFAC1045ju	Brazil, Acre, Porto Walter Igarapé Cruzeiro do Vale, Colônia Dois Portos	KC815077.1	KC874942.1	MG651815	MG777062
LSUMZ 9446	8LSUju	Bolivia, Pando D. Nicolas Suarez, 12 km S of Cobija, 8 km W to Mucden	KC815077.1	KC874942.1	MG651815	MG777062
D. certhia concolor						
LSUMZ 12285	10LSUco	Bolivia, D. Santa Cruz, 32 km E. Parque Nacional Noel Kempff Mercado	KC815088.1	KC874952.1	MG651825	MG777072
MPEG 71168	OM189co	Brazil, Rondonia, Machadinho D'Oeste r. bank R. Jiparana	KC815089.1	KC874953.1	MG651826	MG777073
MPEG 71169	OM275co	Brazil, Rondonia, Machadinho D'Oeste r. bank R. Jiparana	KC815090.1	KC874954.1	MG651827	MG777074
D. certhia medius						
MPEG 70139	GAP052me	Brazil, Pará, Tome-açu	KC815095.1	KC874959.1	MG651832	MG777081
MPEG A07881	A7881me	Brazil, Pará, Barcarena Reserva do hotel Samaúma	KC815096.1	KC874960.1	—	MG777082
MPEG A07882	A7882me	Brazil, Pará, Barcarena Reserva do hotel Samaúma	KC815097.1	KC874961.1	MG651833	MG777083
D. certhia ridgwayi						
LSUMZ 35382	20LSUri	Brazil, Pará, Island R. Teles Pires 900m mouth of R. São Benedito	KC874962.1	KC874962.1	MG651836	MG777086

(Continues)

TABLE 1 (Continued)

Taxon/voucher #	Sample ID code	Locality	GenBank accession numbers			
			ND2	*Cytb*	*BF5*	*G3PDH*
LSUMZ 35460	21LSUri	Brazil, Mato Grosso, n. bank R. Cristalino 1.5km R. Teles Pires 34km	KC874963.1	KC874963.1	MG651837	MG777087
MPEG 67348	TLPA013ri	Brazil, Pará, Paranaita R. Teles Pires	KC815105.1	KC874968.1	MG651843	MG777093
D. certhia retentus						
MPEG 70097	FTA2004re	Brazil, Pará, Marabá, Flona Tapirape Aquiri	KC815110.1	KC874974.1	MG651850	MG777100
MPEG 71346	PGZOO09re	Brazil, Pará, Melgaço FLONA Caxiuanã	KC815111.1	KC874976.1	MG651852	MG777102
MPEG 70633	SLB106re	Brazil, Pará, Serra dos Carajás Área de Controle	KC815112.1	KC874977.1	MG651853	MG777103
D. sanctithomae sanctithomae						
LSUMZ 46547	16LSUsa	Panama, Province Rancho Frio ca 10km S El Real	KC815117.1	KC874984.1	MG651860	MG777111
LSUMZ 8768	22LSUsa	Belize, Toledo District	MG603731	KC874985.1	MG651861	MG777112
LSUMZ 41631	24LSUsa	Panama, Bocas del Toro, Valle de Risco - Chiriqui Grande Hwy	MG603732	KC874987.1	MG651863	MG777114
D. picumnus validus						
LSUMZ 27375	27375va	Peru, Loreto Department, NE bank upper Rio Cushabatay, 84 km WNW Contamana	**MT465866**	**MT502571**	**MT502590**	**MT502609**
LSUMZ 35704	35704va	Brazil, Amazonas, *N.* bank Rio Solimoes, Santa Rita de Weil,	**MT465867**	**MT502572**	**MT502591**	**MT502610**
MPEG 77695	SGC635va	Brazil, Amazonas, São Gabriel da Cachoeira, T.I. médio Rio Negro, Arabo	**MT465868**	**MT502573**	**MT502592**	**MT502611**
D. picumnus picumnus						
MPEG 64655	CN108pi	Brazil, Pará, FLOTA de Faro, ca 70 km NW de Faro	**MT465869**	**MT502574**	**MT502593**	**MT502612**
MPEG 71697	ORX324pi	Brazil, Pará, Faro, Vila Maracanã, Rio Xingu	**MT465870**	**MT502575**	**MT502594**	**MT502613**
ANSP 21473	21473pi	Guyana, Potaro-Siparuni, Iwokrama Reserve, Surama, Potaro-Siparuni Region	**MT465871**	**MT502576**	**MT502595**	**MT502614**
D. picumnus costaricensis						
USNM 655002	655002co	Panamá, Los Planes, 10 km N, Fortuna Field Station	**MT465872**	**MT502577**	**MT502596**	**MT502615**
D. picumnus pallescens						
LSUMZ 6637	6637pa	Bolivia, Santa Cruz Department,3K S & 3K W Santiago by road	**MT465873**	**MT502578**	**MT502597**	**MT502616**
DZUFMG 5774	518pa	Brazil, Mato Grosso, Fazenda Baía de Pedra, Cáceres,	**MT465874**	**MT502579**	**MT502598**	**MT502617**

(Continues)

TABLE 1 (Continued)

Taxon/voucher #	Sample ID code	Locality	GenBank accession numbers			
			ND2	*Cytb*	*BF5*	*G3PDH*
LSUMZ 25740	25740pa	Paraguay, Alto Paraguay Department, S side Cerro León	**MT465875**	**MT502580**	**MT502599**	**MT502618**
D. picumnus transfasciatus						
USNM 572542	572542tr	Brazil, Pará, Altamira, 52 km SSW, E Bank Rio Xingu	**MT465876**	**MT502581**	**MT502600**	**MT502619**
MPEG 55652	UHE413tr	Brazil, Pará, Rio Xingu, margem direita, Senador José Porfírio	**MT465877**	**MT502582**	**MT502601**	**MT502620**
MPEG 75342	JTW1310tr	Brazil, Mato Grosso, Guarantã do Norte, Fazenda São Jorge	**MT465878**	**MT502583**	**MT502602**	**MT502621**
D. hoffmannsi						
INPA A 3263	A3263ho	Brazil, Rondonia, Margem direita do Rio Jaci, 95 km SW de Porto Velho	**MT465879**	**MT502584**	**MT502603**	**MT502622**
INPA A 16146	A16146ho	Brazil, Pará, Margem esquerda do Rio Tapajós, ca 70 km SW Itaituba	**MT465880**	**MT502585**	**MT502604**	**MT502623**
MPEG 76680	JATC362ho	Brazil, Pará, Itaituba, margem esquerda Rio Tapajós, Jatobá	**MT465881**	**MT502586**	**MT502605**	**MT502624**
D. platyrostris platyrostris						
MPEG 71838	SB074pl	Brazil, Bahia, Camacã, RPPN Serra Bonita	**MT465882**	**MT502587**	**MT502606**	**MT502625**
D. platyrostris intermedius						
MPEG 79896	AMG089pl	Brazil, Bahia, Iberaba, Serra do Orobo, Fazenda Canabrava, Monte Verde	**MT465883**	**MT502588**	**MT502607**	**MT502626**
DZ 5401	383pl	Brazil, Goiás, Fazenda Saloba, Montes Claros de Goiás,	**MT465866**	**MT502589**	**MT502608**	**MT502627**
Out-groups						
H. perrotii			MH972323.1	AY443002.1	GQ140117.1	MH972422.1
X. promeropirhynchus			JF975342.1	AY442996.1	GQ140122.1	MH973806.1

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2.2 | Extraction, amplification, and sequencing of DNA

Genomic DNA from all samples was extracted using the DNeasy Blood & Tissue kit (Qiagen Inc.) according to the manufacturer's instructions. Purified DNA was quantified and assessed for quality with Qubit® (Thermo Fisher Scientific).

We sequenced the following mitochondrial and nuclear markers (see Table S1 for information on primers used): NADH dehydrogenase subunit 2 (*ND2*), *cytochrome b* (*Cytb*), beta-fibrinogen intron 5 (*FIB5*), and glyceraldehyde-3-phospho-dehydrogenase intron 11 (*G3PDH*). Polymerase chain reactions (PCRs) were optimized as follows: initial denaturation at 94°C for 4 min, 35 cycles of 1 min at 94°C, 1 min at 49°C/52°C/69°C (*G3PDH*, *Cytb*, and *FIB5* + *ND2*, respectively), 1 min at 72°C, and a final extension at 72°C for 5 min. The success of each amplification was confirmed through electrophoresis in 1% agarose gel. Positive PCR amplicons (Table S1) were purified with polyethylene glycol (PEG8000-2.5M; Hawkins, O'Connor-Morin, Roy, & Santillan, 1994). Forward and reverse sequence strands for each gene fragment were obtained with the

ABI PRISM BigDye Terminator Cycle sequencing protocol (Applied Biosystems®). Sequencing products were run in an ABI PRISM 3130 Genetic Analyzer (Applied Biosystems®).

Sequence chromatograms were edited using the software Geneious 9.1.2 (http://www.geneious.com; Kearse et al., 2012) and aligned in BioEdit 7.2.6.1, using the ClustalW algorithm (Hall, 1999; Thompson, Higgins, & Gibson, 1994). Heterozygous sites for the nuclear genes were confirmed by the presence of double peaks in both complementary strands of DNA and coded according to IUPAC codes. All DNA sequences generated were deposited on GenBank (Table 1; see also Alignments S1–S6).

2.3 | Phylogenetic analyses and divergence time estimates

Two distinct phylogenies were estimated using Bayesian inference (BI) in the software MrBayes (Ronquist et al., 2012), using the CIPRES Science Gateway Portal 3.1 in the San Diego Supercomputer Center (Miller, Pfeiffer, & Schwartz, 2010; www.phylo.org/portal/): one concatenated inference using all four amplified genes (*ND2*, *Cytb*, *FIB5*, and *G3PDH*) and another including only mitochondrial markers (*ND2* and *Cytb*). Sequences were concatenated in Sequence Matrix 1.7.8 (Vaidya, Lohman, & Meier, 2011), and the best partition scheme and substitution models were selected with PartitionFinder 2.1.1 using the Bayesian information criterion (BIC) (Lanfear, Calcott, Ho, & Guidon, 2012; results in Table S2). Three independent runs were made for a total of 10^7 generations with parameters sampled every 1,000 generations and a 25% burn-in. The multilocus concatenated phylogeny was used as a guide tree to test species boundaries based on coalescent methods (see below). To this end, statistically well-supported (PP ≥ 0.95) reciprocally monophyletic groups recovered in this analysis that were also geographically structured and morphologically diagnosable according to previous analyses (Marantz, 1997; Marantz & Patten, 2010) were assumed as hypothesized species.

We used the algorithm *BEAST implemented in BEAST 1.8.0 (Drummond, Suchard, Xie, & Rambautt, 2012) to generate a species tree (ST) and estimate divergence times between the clades supported by previous analyses. This algorithm was also run in CIPRES (Miller et al., 2010; www.phylo.org/portal/). We assumed an uncorrelated lognormal molecular clock model for each locus and applied a calibration derived from the *Cytb* mutation rate estimated as 0.0105 substitutions/ million years (*SD* = 0.0034) (Weir & Schluter, 2008). Mutation rates for the other genes were estimated by *BEAST under a Yule model of speciation chosen as tree prior. Three independent *BEAST runs of $2x10^8$ generations were performed and later combined in LogCombiner considering a 10% burn-in (Drummond et al., 2012), with topologies summarized in TreeAnnotator (Drummond et al., 2012). For all Bayesian analyses, data convergence was verified in Tracer 1.6 (Rambaut, Suchard, Xie, & Drummond, 2014), with a threshold of effective sample size (ESS) of 200 for each sampled parameter. Trees were visualized in FigTree (Rambaut, 2009).

2.4 | Species delimitation

To investigate interspecific boundaries among lineages of the genus *Dendrocolaptes*, we used the Bayesian Phylogenetics and Phylogeography (BP&P) software 3.3 (Yang, 2015). BP&P uses a multilocus coalescence-based Bayesian modeling approach, inferring phylogenetic relationships and describing the likelihood of independence between lineages (Yang, 2015). We used the ST topology as our guide tree in BP&P, which included 15 reciprocally monophyletic lineages in total. After an initial test evaluating different parameters, we implemented Yang's (2015) approach, performing analyses using three parameter combinations representing different population sizes and divergence times: 1) small ancestral population sizes and ancient divergence times [θ and τ gamma priors G (2, 2000) and G (1,10)]; 2) large ancestral population sizes and ancient divergence times [θ and τ gamma priors G (1, 10) and G (1,10)]; and 3) small ancestral population sizes and recent divergence times [θ and τ gamma priors G (2, 2000) and G (2, 2000)]. We chose the reversible-jump Markov chain Monte Carlo method (Yang, 2015), with algorithm 0 and $\varepsilon = 2$, for 500,000 generations (sampling interval of five) and a burn-in of 50,000.

Pairwise uncorrected genetic distances (*p*-distances) between lineages were calculated for each mitochondrial marker in MEGA 7.0 (Kumar, Stecher, & Tamura, Stecher & Tamura, 2016).

2.5 | Historical biogeography reconstruction

To reconstruct the geographical ancestral history of the genus *Dendrocolaptes*, we used BioGeoBEARS (Biogeography with Bayesian [and likelihood] Evolutionary Analysis) in R 3.5.3 (Matzke, 2014; R Core Team, 2019), using the ST chronogram and topology as input. We defined four areas based on the distribution of the sampled *Dendrocolaptes* lineages: (a) Amazonian lowlands; (b) Trans-Andean South America and Central America; (c) Southern-Central South America (corresponding to the Chaco area and neighboring Andean foothills); and (d) Central and Eastern South America (corresponding to the Caatinga, Cerrado, and Atlantic Forest biomes). Six different models were tested: dispersal–extinction–cladogenesis model (DEC), a maximum likelihood version of DIVA (DIVALIKE), a BI from discrete area ancestry (BAYAREALIKE), and their respective versions including a founding effect (+J; Matzke, 2014).

3 | RESULTS

3.1 | Sequence statistics and phylogenetic relationships

After trimming primer sequences, we obtained a total of 2,741 base pairs (bp) for all 19 specimens of *D. hoffmannsi*, *D. picumnus*, and *D. platyrostris* sequenced in this study, distributed as follows: *ND2* (964 bp), *Cytb* (856 bp), *FIB5* (544 bp), and *G3PDH* (377 bp). These

sequences were combined with homologous ones available for *D. certhia* and *D. sanctithomae* (Batista et al., 2013; Silva et al., 2019), and out-groups, from GenBank (see Table 1 and Alignments S1–S6). Mean uncorrected mtDNA (*ND2* + *Cytb*) *p*-distances within *Dendrocolaptes* species and subspecies ranged from 0.01% to 0.08% for *ND2* and 0.01% to 1.5% for *Cytb* (Table S3), whereas between taxa varied from 0.7% to 11.6% for *ND2* and 0.4% to 8.5% for *Cytb* (Table S3).

The multilocus Bayesian phylogeny recovered *Dendrocolaptes* as monophyletic with high statistical support (PP = 1; Figure 1). Within the genus, two main highly supported clades were present: one grouping all taxa formerly attributed to the polytypic *D. certhia* (hereafter referred to as the "certhia complex"; PP = 1), including *D. c. certhia*, *D. c. concolor*, *D. c. juruanus*, *D. c. medius*, *D. c. radiolatus*, *D. c. retentus*, *D. c. ridgwayi*, and *D. sanctithomae*; and a second group (hereafter called as "picumnus complex"; PP = 1), including *D. p. costaricensis*, *D. p. pallescens*, *D. p. picumnus*, *D. p. transfasciatus*, *D. p. validus*, *D. hoffmannsi*, and *D. platyrostris* (Figure 1).

Relationships within the certhia complex were well-resolved and generally statistically well supported, except for the position of *D. c. concolor* as the sister taxon to either *D. c. juruanus* or (more likely) a clade grouping *D. c. medius*, *D. c. retentus*, and *D. c. ridgwayi* (Figure 1). Also, *D. sanctithomae* was recovered as the sister taxon to all the other taxa in the certhia complex (Figure 1). Within this latter group, the Guiana shield endemic *D. c. certhia* was recovered as the sister taxon to all remaining *D. certhia* taxa, followed by subsequent divergences leading to *D. c radiolatus* (from northwestern Amazonia), *D. c. juruanus* (distributed south of the Amazon and west of the Madeira River), *D. c. concolor* (distributed roughly between the Madeira and Tapajós rivers), *D. c. ridgwayi* (distributed between the Tapajós and Xingu rivers), and a clade grouping the southeastern-most *D. c. medius* and *D. c. retentus* (Figure 1).

Similarly, relationships within the picumnus complex were also generally well-resolved and statistically well-supported, except for the poorly supported sister relationship between a major clade grouping the majority of *D. picumnus* subspecies (with the exception of *D. p. transfasciatus*) and *D. hoffmannsi*. This renders the polytypic *D. picumnus* paraphyletic as currently delimited (Figure 1). Within the picumnus complex, *D. platyrostris* was recovered as the sister group to all remaining taxa, followed by subsequent splits originating *D. picumnus transfasciatus*, *D. hoffmannsi*, *D. p. costaricensis*, *D. p. validus*, and a clade joining the reciprocally monophyletic *D. p. pallescens* and *D. p. picumnus* (Figure 1).

The mitochondrial tree recovered a similar topology to that of the concatenated multilocus tree, except for the basal relationships within the picumnus complex, which involved nodes with little statistical support (PP ≤ 0.7; Figure S1).

3.2 | Divergence time estimates and species limits

The divergence chronogram reconstructed in *BEAST was consistent for the most part with the concatenated phylogeny obtained with Bayesian methods, with minor discrepancies in the tree topology, but significant differences in the statistical support for most nodes (Figures 1 and 2). The only difference in topology pertained to the relationships within the *D. c. medius/ retentus/ ridgwayi* clade, which was consistently recovered as a highly supported clade by both analyses, but whereby the position of the sister group to the entire clade alternated between *D. c. ridgwayi* (according to the concatenated estimate; Figure 1) and *D. c. retentus* (according to the multilocus *BEAST estimate; Figure 2). With respect to nodal support values, while most basal nodes recovered by the coalescent tree were well-supported statistically, just like in the concatenated tree, nodes closer or associated with the tips received generally lower values than those in the concatenated tree (Figures 1 and 2).

According to the time estimates obtained, the earliest divergence event in *Dendrocolaptes* split the certhia and picumnus complexes during the mid-Pliocene at ca. 4.6 (5.6–3.5) million years ago (mya; Figure 2). The second oldest splitting event separated the trans-Andean lineage of the certhia complex (*D. sanctithomae*) from the remaining Cis-Andean lineages during the Plio-Pleistocene boundary at ca. 2.3 (3.1–1.5) mya. Subsequent splitting events within both certhia and picumnus complexes took place in the Pleistocene, mainly in the last 1 million years. For instance, the onset of diversification of the picumnus complex occurred at *ca*. 1.06 (1.33–0.81) mya, which overlaps broadly with the beginning of diversification in the Cis-Andean (mostly Amazonian) lineages of the certhia complex at ca. 0.95 (1.2–0.66) mya (Figure 2). The latest diversification events in the picumnus complex took place at ca. 0.33 (0.5–0.06) mya with the separation of *D. p. pallescens* and *D. p. picumnus*, whereas in the certhia complex it involved the splits between *D. c. ridgwayi*, *D. c. retentus*, and *D. c. medius* around 0.2 (0.38–0.04) mya.

All species delimitation and ST tests run by BP&P, irrespective of the demographic and divergence time model considered, confirmed with strong statistical support (PP ≥ 0.98) the existence of 15 lineages in *Dendrocolaptes* that have significantly coalesced with respect to each other for the molecular markers sequenced, as follows: *D. c. certhia*, *D. c. concolor*, *D. c. juruanus*, *D. c. medius*, *D. c. radiolatus*, *D. c. retentus*, *D. c. ridgwayi*, *D. p. costaricensis*, *D. p. pallescens*, *D. p. picumnus*, *D. p. transfasciatus*, *D. p. validus*, *D. hoffmannsi*, *D. platyrostris*, and *D. sanctithomae* (Figure 2 and Table 2).

3.3 | Biogeographic reconstruction

Of the six models evaluated, the best fit to our dataset was DIVALIKE + J (LnL = −13.98), followed by DEC + J (LnL = −14.09), BAYAREALIKE + J (LnL = −15.02), and DIVALIKE (LnL = −17.47) (Table 3). Given the conceptual problems with the DEC model and the "jump speciation" +J parameter implemented in BioGeoBEARS as described by Ree and Sanmartin (2018), we chose the DIVALIKE as the best estimate of the ancestral area relationships in *Dendrocolaptes*.

According to DIVALIKE, lowland Amazonia was estimated as the most likely ancestral area for the genus *Dendrocolaptes* (Figure 3).

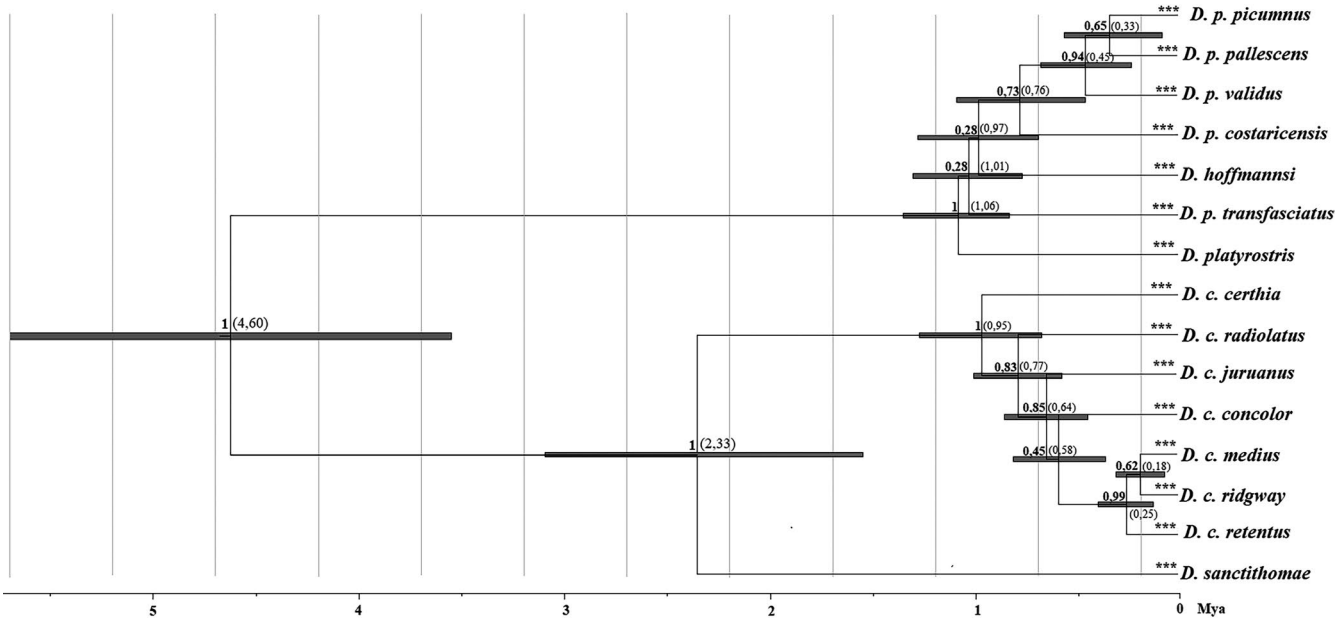

FIGURE 2 Multilocus coalescent species tree estimated for *Dendrocolaptes* using *BEAST. Bars indicate confidence intervals for time divergences scaled in millions of years. Average dates are shown in parentheses and the posterior probability of each node is in bold. Numbers of asterisks at the tips (*) correspond to the number of times the respective taxon was recovered as an independent lineage (probability ≥ 0.98) out of a total of three demographic models combining different priors on ancestral population sizes and divergence times (see text and Table 2 for details)

TABLE 2 Results of different divergence scenarios tested for reciprocally monophyletic lineages in *Dendrocolaptes* revealed by a Bayesian concatenated analysis using BPP. θ and τ are priors for population size parameters and divergences time at the root of the species tree, respectively. Results at $p > .95$ indicate that the taxon in question has coalesced significantly with respect to all other lineages for the scenario tested

Scenarios	1		2		3	
Priors	$\theta = 2\ 2{,}000$	$\tau = 1\ 10$	$\theta = 1\ 10$	$\tau = 1\ 10$	$\theta = 2\ 2{,}000$	$\tau = 2\ 2{,}000$
D. certhia certhia	1	1	1	1	1	1
D. certhia radiolatus	1	1	1	1	0.99	1
D. certhia juruanus	0.99	1	1	1	0.99	1
D. certhia concolor	0.99	1	1	1	0.99	1
D. certhia medius	0.99	0.99	0.99	0.99	0.99	0.99
D. certhia ridgwayi	0.99	0.99	0.99	0.99	0.99	0.99
D. certhia retentus	0.99	0.99	0.99	0.99	0.99	0.99
D. sanctithomae sanctithomae	1	1	1	1	1	1
D. picumnus validus	1	1	0.98	1	1	1
D. picumnus picumnus	0.99	0.99	0.98	0.99	0.99	0.99
D. picumnus costaricensis	0.99	0.99	0.98	0.99	0.99	0.99
D. picumnus pallescens	1	1	0.98	1	1	1
D. picumnus transfasciatus	1	1	0.98	1	0.99	1
D. hoffmannsi	1	1	0.98	1	0.99	1
D. platyrostris	1	1	1	1	1	1

The genus dispersed outside of the Amazon for the first time during the Plio-Pleistocene (3.1–1.5 mya), when it colonized the trans-Andean lowland forests, resulting in the split of *D. sanctithomae* (Figure 3). The initial diversification of the picumnus complex started during the Middle Pleistocene (1.33–0.81 mya), also as the result of a second dispersal out of the Amazon into Central-Eastern South America (Figure 3). Also around that time, the Cis-Andean diversification of the certhia complex began to intensify within the Amazonian lowlands, lasting until the Late Pleistocene. In contrast, while also centered in Amazonia, the diversification in the picumnus

complex continued to involve dispersal of ancestral lineages outside of this region, with a trans-Andean colonization event taking place around 0.76 mya and leading to the establishment of the complex in Central America (Figure 3). The last dispersal outside of Amazonia took place between 0.06 and 0.5 mya and involved the establishment of *D. p. pallescens* in the dry forests of Central South America (Figure 3).

4 | DISCUSSION

4.1 | Phylogenetic relationships and plumage evolution

Our estimated phylogenies provide an unprecedented resolution into the diversification of the genus *Dendrocolaptes* in the Neotropics, even considering the sampling limitations of our study (see below). First, we have confirmed with the largest number of specimens and taxa sequenced so far, previous anatomical and molecular results pointing to the monophyly of *Dendrocolaptes* (Derryberry et al., 2011; Raikow, 1994). In contrast, a study based exclusively on plumage characters failed to recover the genus monophyly, mainly because the "streaked" *Dendrocolaptes* group shares this particular plumage character with other woodcreeper genera such as *Xiphocolaptes* and *Hylexetastes*, which has been interpreted as a source of homoplasy (Marantz, 1997). Second, our study provides the most robust evidence to date supporting two reciprocally monophyletic groups in *Dendrocolaptes*, herein named the certhia and picumnus complexes, confirming a previous family-wide molecular phylogeny (Derryberry et al., 2011). From a phenotypic perspective, previous taxonomists had already recognized the certhia and picumnus complexes, respectively, as the "barred" and "streaked" *Dendrocolaptes* groups, although membership of *D. hoffmannsi* to each of them remained controversial due to its intermediate anatomical and plumage characteristics (Raikow, 1994; Willis, 1982). Herein, our data confirm with high support that *D. hoffmannsi* belongs to the "streaked" picumnus complex, as also supported by a previous molecular study (Derryberry et al., 2011), as well as vocal characters and behavior (Marantz, 1997; Marantz & Patten, 2010; Willis, 1982).

Phylogenetic relationships within each the certhia and picumnus complexes were also generally well resolved in our phylogenies, contrasting strongly with a previous study based on plumage characters that did not recover well-resolved phylogenetic relationships within these groups (Marantz, 1997). Supposedly, convergence in plumage features among taxa living in sympatry or in areas with similar climatic conditions could be behind this pattern (Marantz, 1997; Miller, Leighton, Freeman, Lees, & Ligon, 2019). Our results confirm that plumage differentiation is not tightly linked with the phylogeny in *Dendrocolaptes*, as shown by the grouping of the most uniform colored and least marked taxa such as *D. c. retentus*, *D. hoffmannsi*, and *D. p. pallescens* as sister lineages to the richly colored and heavily marked *D. c. medius*, *D. picumnus spp.*, and *D. p. picumnus*, respectively (Batista et al., 2013, Figure 1). Indeed, the more uniform plumage characteristics shared between the largely sympatric *D. c. concolor* and *D. hoffmannsi* could be due to either convergence or parallel evolution, given their distant phylogenetic affinities (Marantz, 1997; Figure 1). One possibility is that *D. c. concolor* lost the intense marking that characterizes the more basal taxa in the certhia complex (e.g., *D. c. certhia*, *D. c. radiolatus*, and *D. c. juruanus*: Figure 1) in response to a strong selective pressure to mimic the weakly marked plumage of the more aggressive and syntopic *D. hoffmannsi*, which normally dominates at most woodcreepers (including *D. c. concolor*) over army-ant swarms (Willis, 1982). Members of the picumnus complex are larger and heavier than those in the certhia complex (Marantz et al., 2020a), and given their wide ecological overlap and sympatry throughout most of the Amazon (Marantz, 1997; Willis, 1982), plumage mimicry and convergence are possible outcomes between these groups, as documented extensively for another trunk-climbing bird lineage worldwide (Miller et al., 2019). Outside of the Amazon, the certhia and picumnus complexes tend to exclude each other altitudinally, hence reducing the possibility of mimicry-driven plumage convergence between them. Another striking example of dissociation between plumage and phylogenetic proximity in *Dendrocolaptes* pertains to the highly disparate color and marking patterns between the allopatrically distributed *D. p. picumnus* and *D. p. pallescens*, which were recovered as sister taxa with high statistical support (Figure 1). While the darker and boldly patterned plumage of *D. p. picumnus* is typically associated with more humid areas such as the wet Amazonian Guiana shield, the less marked and paler yellowish-brown plumage of the open Chaco forest endemic *D. p. pallescens* is in accordance with Gloger's rule, which predicts that birds inhabiting drier and more seasonal areas will have lighter plumage types (see Miller et al., 2019). In summary, our

TABLE 3 Statistics of models of ancestral area estimates obtained with BioGeoBEARS. Values of log-likelihood (LnL), number of parameters, as well as dispersal (*d*), extinction (*e*), founder (*j*), and Akaike's information criterion (AIC) scores are given for each model implemented. The best-fitting model without a + J parameter chosen (DIVALIKE) is shown in bold (see text for details)

Model	LnL	Parameters	*d*	*e*	*j*	AIC
DEC	−21.00	2	0.079	0.034	0	46.01
DEC + J	−14.09	3	10^{-12}	10^{-12}	0.069	34.18
DIVALIKE	**−17.47**	**2**	**0.083**	**10^{-12}**	**0**	**38.95**
DIVALIKE + J	−13.98	3	10^{-12}	10^{-12}	0.075	33.95
BAYAREALIKE	−25.91	2	0.11	0.28	0	55.83
BAYAREALIKE + J	−15.02	3	10^{-7}	10^{-7}	0.074	36.04

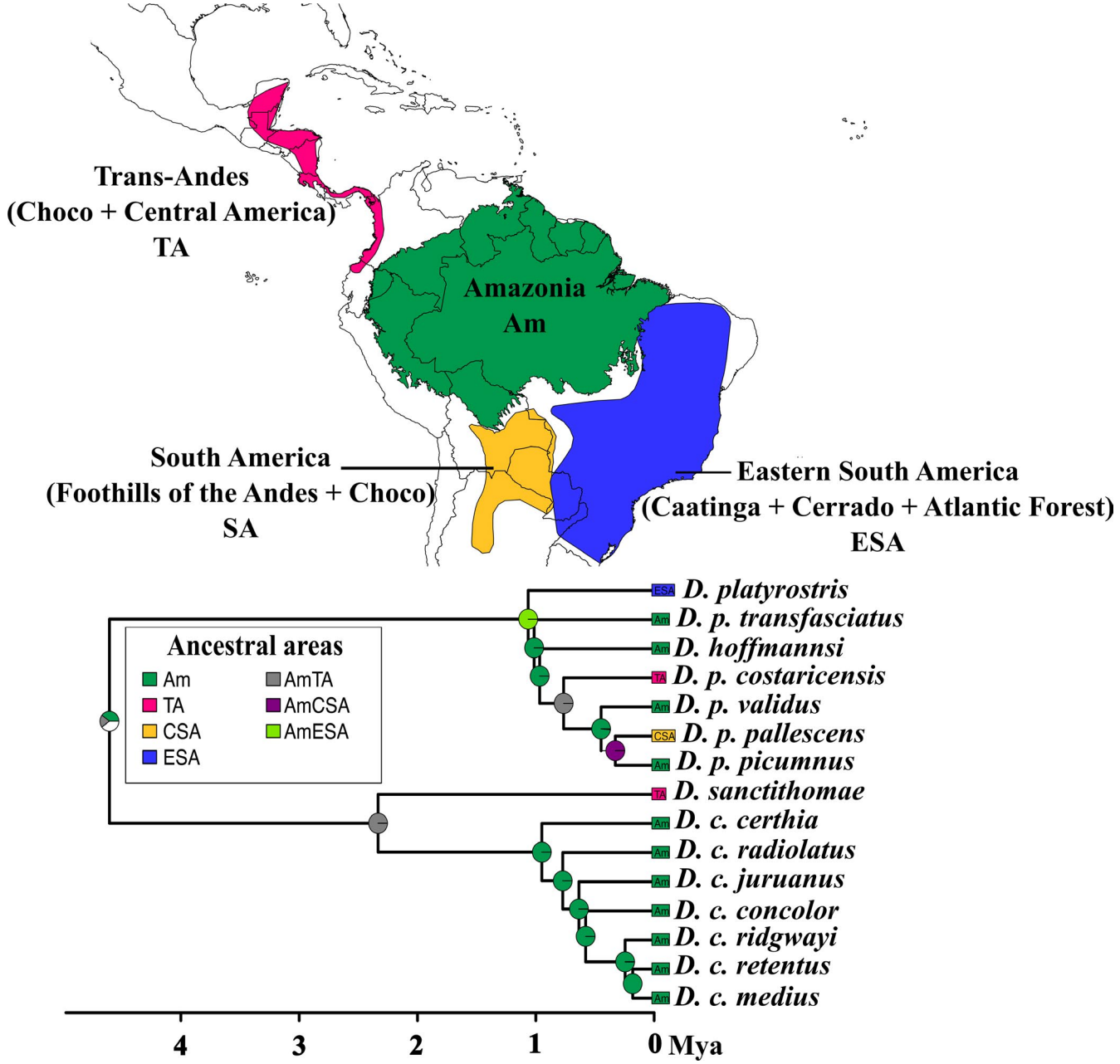

FIGURE 3 Ancestral area estimates for *Dendrocolaptes* obtained with BioGeoBEARS and using the multilocus coalescent phylogeny as a tree prior. Node pie charts show the likelihoods of ancestral areas according the selected DIVALIKE model. Colors in the map represent the selected areas for the analysis. Colors different from those inserted in the map are combinations of areas (see Ancestral Areas' legend)

well-resolved phylogeny corroborates previous claims that patterns of plumage variation in *Dendrocolaptes* are highly influenced by environmental and ecological factors, rendering them of little use for phylogenetic reconstruction (Batista et al., 2013; Marantz, 1997).

4.2 | Species limits in *Dendrocolaptes*

A previous phylogenetic study that sampled all *Dendrocolaptes* taxa known at the time produced plumage-based trees that failed to recover well-resolved relationships among taxa grouped in both the certhia and picumnus complexes (Marantz, 1997). While those trees did recover the certhia complex as monophyletic (with overall little internal resolution), the picumnus group was recovered as polyphyletic, with only a few taxa in it grouped as each other closest relatives depending on the tree building criterion chosen (Marantz, 1997). A subsequent study that sampled the same taxa through morphometric characters also obtained relatively little resolution with respect to classifying different groups according to accepted species and subspecies boundaries (Marantz & Patten, 2010). This overall lack of resolution provided by morphological characters caused species limits in both the certhia and picumnus complexes to be loosely defined historically and vary significantly depending on the taxonomic source considered (Batista et al., 2013; Cory & Hellmayr, 1925; del Hoyo

et al., 2020; Marantz, Aleixo, Bevier, & Patten, 2020c; Peters, 1951; Piacentini et al., 2015; Pinto, 1938, 1978; Willis, 1982). This is perhaps best exemplified by Marantz et al. (2020b) statement concerning the most frequent treatment of the picumnus complex as including three distinct species (*D. hoffmannsi*, *D. picumnus*, and *D. platyrostris*), that "…work [is] needed to justify their continued separation."

In contrast, molecular studies sampling multiple *Dendrocolaptes* taxa have recovered well-resolved and for the most part statistically well-supported phylogenies (Batista et al., 2013; Derryberry et al., 2011; Silva et al., 2019), which allow for a more explicit evaluation of interspecific limits under an evolutionary perspective. Confirming these previous molecular studies, our phylogenies estimated for a combined sample of 16 *Dendrocolaptes* taxa were also well-resolved and overall statistically well-supported (Figures 1 and 2). However, unlike in these previous studies, here we formally tested for the first time interspecific limits in *Dendrocolaptes* through a robust coalescent-based method (i.e., BP&P; see Leaché, Zhu, Rannala, & Yang, 2019 and references therein). BP&P supported the existence of a total of 15 different lineages in the genus that have coalesced significantly with respect to each other for the molecular markers analyzed under widely different demographic and divergence scenarios (Figure 2), a precondition for their ranking as separate species-level taxa (see Gill, 2014). While eight of those lineages were grouped in the certhia complex (*D. c. certhia*, *D. c. concolor*, *D. c. juruanus*, *D. c. medius*, *D. c. radiolatus*, *D. c. retentus*, *D. c. ridgwayi*, and *D. sanctithomae*), the remaining seven clustered together in the picumnus complex (*D. p. costaricensis*, *D. p. pallescens*, *D. p. picumnus*, *D. p. transfasciatus*, *D. p. validus*, *D. hoffmannsi*, and *D. platyrostris*). In all but one case (*D. c. ridgwayi*), our 15 significantly coalesced lineages revealed by BP&P are also consistently diagnosed by morphological (mostly plumage) characters (Marantz & Patten, 2010), including some such as *D. c. concolor*, *D. p. pallescens*, and *D. p. transfasciatus* that have previously been treated as full species (Cory & Hellmayr, 1925; Peters, 1951), supporting their ranking as separate species-level taxa. This contrasts markedly with the current number of only five to six species recognized in the genus according to most modern taxonomic sources (Gill et al., 2020; del Hoyo et al., 2020; Remsen et al., 2020), but see Piacentini et al., (2015). With respect to *D. c. ridgwayi*, Batista et al., (2013) did not support claims of Marantz (1997) and Marantz and Patten (2010) that it consists of an introgressed population (based on overall plumage intermediacy) between *D. c. concolor* and *D. c. medius*. Our BP&P analyses agree with Batista et al., (2013) and Silva et al., (2019) in supporting *D. c. ridgwayi* as a phylogenetically distinct lineage that is morphologically closer to the weakly barred *D. c. concolor*, although it belongs in a clade that includes both weekly barred (*D. c. retentus*: not described before Marantz, 1997 and Marantz & Patten, 2010) and barred (*D. c. medius*) taxa. As discussed above, the boldness of barring on plumage is not correlated with the phylogeny in *Dendrocolaptes* and other woodcreeper genera, and this was the only criterion used by Marantz (1997) to regard *D. c. ridgwayi* as a hybrid swarm.

In conclusion, the lineage delimitation scheme provided by BP&P herein objectively recognizes genetically and morphologically diagnosable *Dendrocolaptes* taxa that can be regarded as consistent basal evolutionary units for classification purposes (Figure 2). The use of BP&P, and the multispecies coalescent model upon which it is based (MSC), has been criticized on the grounds that it captures mainly population-level structure rather than species divergences (Jackson, Carstens, Morales, & O'Meara, 2017; Sukumaran & Knowles, 2017). On a more recent study, Leaché et al., (2019) performed simulations to address these criticisms and showed that the Bayesian model selection implemented in BP&P may indeed over-split and recognize too many species, particularly in subdivided populations with ongoing gene flow. However, this trend is particularly true when hundreds or thousands of loci are analyzed, which contrasts strongly with the total of three independent loci sampled in our study (Leaché et al., 2019). These authors also pointed out that the MSC model (and any other species delimitation model currently available) is not intended to split lineages based on "speciation genes" or those genes accounting for reproductive isolation, and conclude that "Even if the genomic data or the BP&P program cannot distinguish populations and species, the genetic distinctness of the populations signifies the presence of reproductive barriers or isolation mechanisms." The 15 significantly coalesced lineages identified by BP&P in *Dendrocolaptes* fell within a range of population divergence parameters consistent with at least advanced degrees of reproductive isolation (Figure 2), which were also matched in most cases by existing (albeit subtle) phenotypic diagnoses (Marantz, 1997; Marantz & Patten, 2010). These patterns are totally consistent with a novel perspective of species delimitation whereby the burden of proof is placed on splitting rather than lumping taxa, as long as empirical evidence suggests the existence of distinct and reciprocally monophyletic sister populations, which are then interpreted as exhibiting some level of reproductive isolation in opposition to free interbreeding if occurring in sympatry (Gill, 2014). Although some sampling limitations of our study preclude the immediate translation of all significantly coalesced lineages revealed by BP&P into independent species-level taxa (see below), our results nevertheless represent a major step forward with respect to the historical taxonomic practice in *Dendrocolaptes*, which has essentially consisted in assessing species limits based on qualitative interpretations of comparative levels of plumage and vocal differentiation across taxa (Cory & Hellmayr, 1925; Marantz, 1997; Peters, 1951; Pinto, 1938, 1978; but see Batista et al., 2013).

4.3 | Historical diversification in dry and humid forests of the Neotropics

Our ancestral area estimates favored lowland Amazonia as the center of diversification for the genus *Dendrocolaptes* (Figure 3). While the earliest splits in the genus continued to take place in Cis-Andean South America, an early dispersal event across the Andes occurred during the Plio-Pleistocene (3.1–1.5 mya), leading to the establishment of *D. sanctithomae* in Central America, where it eventually expanded into a wide range of distinct forest types up to ca. 1,800 m (i.e., cloud forest, gallery, mangrove, pine-oak, and semi-deciduous),

albeit still favoring mature humid forest in the lowlands (Marantz, Aleixo, Bevier, Patten, & Kirwan, 2020d). Our analysis indicates that the remaining lineages of the certhia complex diversified almost entirely in the Amazonian lowland humid forests (Figure 3), although *D. c. medius* has reached the northern part of the also humid Atlantic Forest in northeastern Brazil (Marantz et al., 2020c). We did not successfully amplify DNA out of *D. c. medius* specimens from the Atlantic Forest since only relatively old skins were available of this now rare and highly endangered population (Aleixo et al., 2018). However, no apparent morphological differentiation has been detected between Amazonian and Atlantic Forest populations of *D. c. medius* (Marantz, 1997; Marantz & Patten, 2010), which could also indicate a lack of complete genetic isolation between them, analogous to what has been reported for at least two other suboscine lineages sharing similar disjunct distributions between these forest biomes (Rocha et al., 2015; Thom & Aleixo, 2015).

Albeit also centered in Amazonia, the diversification of the picumnus complex included three independent dispersal events outside of that region that also led to differentiation into different vegetation types. First, the differentiation of *D. platyrostris* in Central and Eastern South America (Caatinga, Cerrado, and Atlantic Forest biomes) took place through in situ vicariance after a recent dispersal from Amazonia during the Middle Pleistocene (1.33–0.81 mya). A second instance involved a new dispersal event into Central America (at ca. 0.76), with the establishment of *D. picumnus* mainly in humid forest montane habitats (Marantz et al., 2020b). The third and last episode occurred at ca. 0.3 mya, with *D. p. pallescens* differentiating in the southern "dry diagonal" Chaco biome and neighboring foothills of the Andes (Figure 3). Therefore, unlike inferred for other groups (Porzecanski & Cracraft, 2005; Werneck, 2011), *Dendrocolaptes* lineages replacing each other across the "dry diagonal" biomes of South America do not support a sister relationship linking the Chaco and Cerrado to the expense of the Caatinga biome, or a closer Chaco–Caatinga historical connection (Hayes, 2001; Lopes, Chaves, de Aquino, Silveira, & dos Santos, 2018). Instead, our results indicate that *Dendrocolaptes* lineages distributed in the "dry diagonal" are not monophyletic, but derived from two temporally independent Amazonian invasions. The diversification of the picumnus complex in particular supports that the Middle and Late Pleistocene were periods of intense biotic exchange both between lowland and montane biotas and between humid (particularly Amazonia) and drier forest types, such as those distributed along the South American dry diagonal. These results also support a keystone role for Amazonia as a major source of diversification in the Neotropics, mirroring previous findings (Antonelli et al., 2018).

4.4 | Taxonomic implications

Our analyses recovered with strong support the monophyly of most *Dendrocolaptes* species recognized by current taxonomy (Gill et al., 2020; Marantz & Patten, 2010; Remsen et al., 2020), except for the polytypic *D. picumnus*, which appeared consistently as a paraphyletic species with respect to *D. hoffmannsi* in both phylogeny estimates we obtained (Figures 1 and 2). However, statistical support for this relationship was weak in both trees, and a monophyletic *D. picumnus* cannot be ruled out given that the basal-most relationships in the picumnus complex are characterized by the presence of one (Figure 1) or two (Figure 2) short nodes with low statistical support (Figures 1 and 2). Interestingly, the apparent closer relationship of *D. hoffmannsi* to most taxa in the polytypic *D. picumnus* to the exclusion of *D. p. transfasciatus* (Figures 1 and 2) mirrors previous results pointing to a greater morphological similarity between the latter taxon and *D. platyrostris*, mainly due to the distinct blackish crown shared by these largely parapatric taxa (Marantz, 1997; Willis, 1982). Furthermore, the average pairwise mitochondrial sequence divergence level between *D. p. transfasciatus* and the remaining taxa of *D. picumnus* sampled herein is higher (2.65%) than that between *D. hoffmannsi* and the latter taxa (1.95%: Table S3), which are currently regarded as separate species (Gill et al., 2020; Marantz & Patten, 2010; Remsen et al., 2020). In sum, both significant levels of morphological and genetic differentiation, coupled with a significant degree of coalescence with respect to other closely related *Dendrocolaptes* lineages (Figure 2), support the recognition of *D. p. transfasciatus* as a species-level taxon distinct enough from the remaining taxa sampled in this study and grouped under *D. picumnus*. These findings confirm a previous taxonomic treatment that regarded *D. p. transfasciatus* as a separate species-level taxon in *Dendrocolaptes* (Cory & Hellmayr, 1925). Recently, *D. p. transfasciatus* (which is endemic to Brazil) has been regarded as "vulnerable" at the national level (Leal, Silva, & Marques, 2018).

The lack of four trans-Andean (*D. p. costaricensis*, *D. p. multistrigatus*, *D. p. puncticollis*, and *D. p. seilerni*) and two cis-Andean (*D. p. casaresi and D. p. olivaceus*) taxa from our sample precludes a more in depth assessment of the interspecific limits within the remaining taxa of the polytypic *D. picumnus*. While Marantz and Patten (2010) have found little support for the distinction of *D. p. casaresi* with respect to *D. p. pallescens* (which we did sample), the remaining missing taxa have been classified based on plumage characteristics into two distinct "montane" groups (sensu Marantz & Patten, 2010), only one of which was sampled by us (i.e., "montane group A," which includes *D. p. costaricensis*, for which we obtained just one sample). Nevertheless, our analyses did recover a reciprocally monophyletic and deeply coalesced *D. p. pallescens*, supporting a previous species-level treatment for this phenotypically distinct taxon (Cory & Hellmayr, 1925). However, recognizing *D. p. pallescens* as a separate species would render the resulting polytypic *D. picumnus* paraphyletic, a situation that could be circumvented by also elevating the other deeply coalesced *D. p. picumnus*, *D. p. validus*, and *D. p. costaricensis* to full species-level status. Even in this case though, it would be difficult to determine exactly under which deeply coalesced lineage (if any) the missing taxa from our sample would group, making it impossible to rule out the risk of delimiting paraphyletic species. Finally, our analyses confirmed previous findings concerning the lack of reciprocal monophyly between both recognized *D. platyrostris* subspecies

(*D. p. platyrostris* and *D. p. intermedius*; Cabanne, D'Horta, Meyer, Silva, & Miyaki, 2011), therefore not supporting the suggestion to treat them as separate species (Willis & Oniki, 2001). In conclusion, at this point, we recommend the recognition of only four species (*D. hoffmannsi*, *D. picumnus*, *D. platyrostris*, and *D. transfasciatus*) within the picumnus complex, with additional studies necessary to determine particularly the phylogenetic affinities of all "montane" *D. picumnus* subspecies (sensu Marantz & Patten, 2010).

Within the certhia complex, our MSC multilocus analysis confirmed a previous treatment based on a larger dataset supporting the recognition of eight species in this group: *D. certhia*, *D. concolor*, *D. juruanus*, *D. medius*, *D. radiolatus*, *D. retentus*, *D. ridgwayi*, and *D. sanctithomae* (Batista et al., 2013; Silva et al., 2019). Unfortunately, we lacked three *D. sanctithomae* subspecies from our sample (*D. s. hesperius*, *D. s. punctipectus*, and *D. s. sheffleri*), which precludes us from evaluating the suggestion to regard *D. s. punctipectus* as a full species based primarily on vocal differences with respect to Central American and Chocoan populations (Boesman, 2016; del Hoyo et al., 2020), although plumage characteristics (i.e., breast spotting) also clearly diagnose *D. s. punctipectus* (Marantz, 1997). However, it has been proposed that *D. s. punctipectus* intergrades with trans-Andean *D. sanctithomae* taxa in northern Colombia (Marantz, 1997), which could also not be addressed by us due to sampling limitations. Similarly, *D. s. sheffleri* from the northernmost part of *D. sanctithomae* range is also distinct in terms of plumage patterns and coloration (Marantz, 1997), and could well represent a distinct lineage. The remaining *D. sanctithomae* subspecies not sampled by us (*D. s. hesperius*) is the closest morphologically to the nominate subspecies, which argues in principle against a distant phylogenetic relationship. Considering the degree of uncertainty and the sampling limitations across *D. sanctithomae* taxa that affected not only our study, but also those analyzing their morphological (Marantz, 1997) and vocal (Boesman, 2016) differentiation, we recommend not treating *D. s. punctipectus* as a full species (thus, following Marantz, 1997; Marantz & Patten, 2010; Gill et al., 2020, and Remsen et al., 2020) until evidence becomes available concerning its phylogenetic position and degree of evolutionary independence with respect to other *D. sanctithomae* lineages.

In contrast, ample evidence is available by now that treating all Cis-Andean taxa of the certhia complex as one species (Gill et al., 2020; Remsen et al., 2020) implies in tremendously underestimating the true species diversity in this group (Batista et al., 2013; Silva et al., 2019; this study). The main reason for this continuing treatment as a single species has been the lack of vocal diagnoses among the different taxa currently grouped under a polytypic *D. certhia*, coupled with comparatively little genetic and morphological differentiation (Remsen et al., 2020; see http://www.museum.lsu.edu/~Remsen/SACCprop621.htm). Indeed, although no formal vocal analyses are available involving the Cis-Andean taxa of the certhia complex, existing qualitative assessments support very little variation in song and calls throughout its range (Marantz, 1997; Willis, 1992; AA pers. obs.), which mirrors the apparent lack of vocal variation among members of the picumnus complex, particularly between *D. hoffmannsi* and the polytypic *D. picumnus* (Marantz, 1997; Willis, 1982; AA, pers. obs.). Other woodcreeper genera in which little vocal variation is present, despite pronounced genetic differentiation and significant degree of coalescence consistent with the existence of cryptic species, are *Dendrexetastes* (Ferreira, Aleixo, & Silva, 2016) and *Hylexetastes* (Azuaje-Rodriguez et al., 2020). These significantly coalesced lineages are totally inconsistent with the hypothesis of free interbreeding among them, indicating that conservatism in vocal characters is not synonymous with lack of strong genetic isolation and speciation. Indeed, as shown recently for other Furnariidae, not even the mere existence of gene flow can be equated with lack of speciation, as suboscine lineages may evolve full reproductive isolation in a much longer time period than many Northern Hemisphere bird lineages (Pulido-Santacruz, Aleixo, & Weir, 2018, Pulido-Santacruz, Aleixo, & Weir, 2020; Weir & Price, 2019). In fact, the recognition of *D. certhia* as a single species is inconsistent even when considering comparative levels of genetic differentiation within the genus *Dendrocolaptes*. For instance, as discussed above, *D. picumnus* and *D. hoffmannsi*, which differ by 1.95% in their mitochondrial DNA (Table S3), are regarded as independent "biological" species by the same sources that lump *D. c. certhia* and the remaining taxa members of the same purported polytypic species, and which differ in their mitochondrial DNA by an average of 2.4% (Table S3; Gill et al., 2020; Remsen et al., 2020). Comparative levels of mitochondrial sequence divergence alone cannot be safely used as yardsticks for establishing species limits, but in this particular case they illustrate the subjectivity and lack of consistency in the application of a particular implementation of the "Biological Species Concept" (Johnson, Remsen Jr, & Cicero, 1999). For all these reasons, we recommend the treatment of the following significantly coalesced taxa according to our multilocus analyses (Figures 1 and 2) and currently regarded as subspecies of *D. certhia* by some sources (Gill et al., 2020; Marantz et al., 2020c; Remsen et al., 2020), as full species, mirroring the treatment by Piacentini et al. (2015): *D. certhia*, *D. concolor*, *D. juruanus*, *D. medius*, *D. radiolatus*, *D. retentus*, and *D. ridgwayi*.

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REFERENCES

Aleixo, A., Batista, R. S. S., Moura, N. G., Lees, A. C., Martínez, C., & Dantas, S. M. (2018). Dendrocolaptes medius Todd, 1920. In Instituto Chico Mendes de Conservação da Biodiversidade. (Org.), *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume III - Aves* (pp. 435–438). Brasília: ICMBio.

Antonelli, A., Zizka, A., Carvalho, F. A., Scharn, R., Bacon, C. D., Silvestro, D., & Condamine, F. L. (2018). Amazonia is the primary source of Neotropical biodiversity. *Proceedings of the National Academy of Sciences*, *115*(23), 6034–6039. https://doi.org/10.1073/pnas.0811421106

Azuaje, R., Weckstein, J., Dispoto, J., Patel, S., Cacioppo, J., Bates, J., … Aleixo, A. (2020). Molecular systematics of the Amazonian endemic genus *Hylexetastes* (Aves: Dendrocolaptidae): Taxonomic and conservation implications. *Ibis*, *162*(1), 119–136. https://doi.org/10.1111/ibi.12693

Batista, R., Aleixo, A., Vallinoto, M., Azevedo, L., Sena do Rego, P., Silveira, L. F., … Schneider, H.(2013). Molecular systematics and taxonomic revision of the Amazonian Barred Woodcreeper complex (*Dendrocolaptes certhia*: Dendrocolaptidae), with description of a new species from the Xingu-Tocantins interfluve. In Del Hoyo, J., Elliott, A., Sargatal, J., & Christie, D. (Eds), *Handbook of the birds of the world. Special volume: New species and global index* (pp. 245–247). Barcelona, Spain: Lynx Edicions.

Boesman, P. (2016). Notes on the vocalizations of Northern Barred Woodcreeper (*Dendrocolaptes sanctithomae*). HBW Alive Ornithological Note 81. In *Handbook of the Birds of the World Alive. Lynx Edicions*, Barcelona. Retrieved from http://www.hbw.com/node/931975 on 16 July 2016.

Cabanne, G. S., D'Horta, F. M., Meyer, D., Silva, J. M. C., & Miyaki, C. Y. (2011). Evolution of *Dendrocolaptes platyrostris* (Aves: Furnariidae) between the South American open vegetation corridor and the Atlantic forest. *Biological Journal of the Linnean Society*, *103*, 801–820. https://doi.org/10.1111/j.1095-8312.2011.01678.x

Capurucho, J. M. G., Ashley, M. V., Ribas, C. C., & Bates, J. M. (2018). Connecting Amazonian, Cerrado, and Atlantic forest histories: Paraphyly, old divergences, and modern population dynamics in tyrant-manakins (*Neopelma/Tyranneutes*, Aves: Pipridae). *Molecular Phylogenetics and Evolution*, *127*, 696–705. https://doi.org/10.1016/j.ympev.2018.06.015

Cory, C. B., & Hellmayr, C. E. (1925). Catalogue of birds of the Americas. *Field Museum of Natural History, Zoological Series*, *13*, 1–390.

del Hoyo, J., Collar, N., & Kirwan, G. M. (2020). Eastern barred Woodcreeper (Dendrocolaptes punctipectus). In J. del hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de juana (Eds.), *Handbook of the birds of the World Alive*. Barcelona, Spain: Lynx Edicions. Retrieved from https://www.hbw.com/node/1343628 on 20 February 2020).

Derryberry, E. P., Claramunt, S., Derryberry, G., Chesser, R. T., Cracraft, J., Aleixo, A., … Brumfield, R. T. (2011). Large-scale continental radiation: The Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution*, *65*(10), 2973–2986. https://doi.org/10.1111/j.1558-5646.2011.01374.x

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973. https://doi.org/10.1093/molbev/mss075

Fenker, J., Domingos, F. M. C. B., Tedeschi, L. G., Rosauer, D. F., Werneck, F. P., Colli, G. R., … Moritz, C. (2020). Evolutionary history of Neotropical savannas geographically concentrates species, phylogenetic and functional diversity of lizards. *Journal of Biogeography*, *47*(5), 1130–1142. https://doi.org/10.1111/jbi.13800.

Ferreira, G. G., Aleixo, A., & Silva, S. M. (2016). Systematic review of the Cinnamon-throated Woodcreeper *Dendrexetastes rufigula* (Aves: Dendrocolaptidae) based on a multilocus phylogeography. *Ornithology Research*, *24*(4), 358–369.

García-Moreno, J., & Silva, J. M. C. (1997). An interplay between forest and non-forest South American avifaunas suggested by a phylogeny of *Lepidocolaptes* woodcreepers (dendrocolaptinae). *Studies on Neotropical Fauna and Environment*, *32*(3), 164–173. https://doi.org/10.1080/01650521.1997.9709617

Gill, F. B. (2014). Species taxonomy of birds: Which null hypothesis? *The Auk*, *131*(2), 150–161.

Gill, F., Donsker, D., & Rasmussen, P. (Eds) (2020) *IOC World Bird List (v10.1)*. https://doi.org/10.14344/IOC.ML.10.1

Hall, T. A. (1999). BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, *41*, 95–98. https://doi.org/10.14601/Phytopathol_Mediterr-14998u1.29

Hawkins, T. L., O'Connor-Morin, T., Roy, A., & Santillan, C. (1994). DNA purification and isolation using a solid-phase. *Nucleic Acids Research*, *22*, 4543–4544. https://doi.org/10.1093/nar/22.21.4543

Hayes, F. E. (2001). Geographical variation, hybridization, and the leapfrog pattern of evolution in the Suiriri Flycatcher (*Suiriri suiriri*) complex. *The Auk*, *118*, 457–471. https://doi.org/10.1642/0004-8038(2001)

Hooghiemstra, H., & van der Hammen, T. (1998). Neogene and quaternary development of the Neotropical forest: The forest refugia hypothesis, and a literature overview. *Earth Science Reviews*, *44*, 147–183. https://doi.org/10.1016/S0012-8252(98)00027-0

Jackson, N. D., Carstens, B. C., Morales, A. E., & O'Meara, B. C. (2017). Species delimitation with gene flow. *Systematic Biology*, *66*, 799–812. https://doi.org/10.1093/sysbio/syw117

Johnson, N. K., Remsen, J. V. Jr, & Cicero, C. (1999). Resolution of the debate over species concepts in ornithology: a new comprehensive biologic species concept. In N. J. Adams, & R. H. Slotow (Eds.), *Proc. 22 Int. Ornithol. Congr., Durban* (pp. 1470–1482). Johannesburg: BirdLife South Africa.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., … Drummond, A. (2012). Geneious basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, *28*(12), 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger. *Molecular Biology and Evolution*, *33*, 1870–1874. https://doi.org/10.1093/molbev/msw054

Lanfear, R., Calcott, B., Ho, S. Y. W., & Guidon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, *29*, 1695–1701. https://doi.org/10.1093/molbev/mss020

Leaché, A. D., Zhu, T., Rannala, B., & Yang, Z. (2019). The Spectre of Too Many Species. *Systematic Biology*, *68*(1), 168–181. https://doi.org/10.1093/sysbio/syy051

Leal, D. C., Silva, S. B. L., & Marques, F. P. (2018). Dendrocolaptes picumnus transfasciatus Todd, 1925. In Instituto Chico Mendes de Conservação da Biodiversidade. (Org.), *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume III – Aves* (pp. 438–439). Brasília: ICMBio.

Lopes, L. E., Chaves, A. V., de Aquino, M. M., Silveira, L. F., & dos Santos, F. R. (2018). The striking polyphyly of *Suiriri*: Convergent evolution and social mimicry in two cryptic Neotropical birds. *Journal of Zoological Systematics and Evolutionary Research*, *56*, 270–279. https://doi.org/10.1111/jzs.12200

Marantz, C. (1997). Geographic variation of plumage patterns in the woodcreeper genus *Dendrocolaptes* (Dendrocolaptidae). *Ornithological Monographs*, *48*, 399–429. https://doi.org/10.2307/40157545

Marantz, C. A., Aleixo, A., Bevier, L. R., & Patten, M. A. (2020a). Woodcreepers (Dendrocolaptidae). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Handbook of the Birds of the World Alive*. Barcelona: Lynx Edicions. Retrieved from https://www.hbw.com/node/52290 on 19 February 2020.

Marantz, C. A., Aleixo, A., Bevier, L. R., & Patten, M. A. (2020b). Black-banded Woodcreeper (*Dendrocolaptes picumnus*). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Handbook of the birds of the world alive*. Barcelona, Spain: Lynx Edicions. Retrieved from https://www.hbw.com/node/56616 on 19 February 2020.

Marantz, C. A., Aleixo, A., Bevier, L. R., & Patten, M. A. (2020c). Amazonian Barred Woodcreeper (*Dendrocolaptes certhia*). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Handbook of the birds of the world alive*. Barcelona, Spain: Lynx Edicions. Retrieved from https://www.hbw.com/node/56614 on 19 February 2020.

Marantz, C. A., Aleixo, A., Bevier, L. R., & Patten, M. A. (2020e). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Handbook of the birds of the world alive*. Barcelona, Spain: Lynx Edicions. Retrieved from https://www.hbw.com/node/56617 on 26 April 2020

Marantz, C. A., Aleixo, A., Bevier, L. R., Patten, M. A., & Kirwan, G. M. (2020d). Western Barred Woodcreeper (*Dendrocolaptes sanctithomae*). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Handbook of the birds of the world alive*. Barcelona, Spain: Lynx Edicions. Retrieved from https://www.hbw.com/node/56613 on 19 February 2020.

Marantz, C., & Patten, M. A. (2010). Quantifying subspecies analyzes: A case study of morphometric variation and subspecies in the woodcreeper genus *Dendrocolaptes*. *Ornithological Monographs*, *67*, 123–140.

Matzke, N. J. (2014). Model selection in historical biogeography reveals that founder event speciation is a crucial process in island clades. *Systematic Biology*, *63*(6), 951–970. https://doi.org/10.1093/sysbio/syu056

Miller, E. T., Leighton, G. M., Freeman, B. G., Lees, A. C., & Ligon, R. A. (2019). Ecological and geographical overlap drive plumage evolution and mimicry in woodpeckers. *Nature Communications*, *10*(1), 1602. https://doi.org/10.1038/s41467-019-09721-w

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)* (pp. 45–52). New Orleans, LA: IEEE.

Oliveras, I., & Malhi, Y. (2016). Many shades of green: The dynamic tropical forest–savannah transition zones. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1703), 20150308. https://doi.org/10.1098/rstb.2015.0308

Peters, J. L. (1951). *Check-list of birds of the world* (Vol. *VII*). Cambridge, MA: Harvard University Press.

Piacentini, V. Q., Aleixo, A., Agne, C. E., Maurício, G. N., Pacheco, J. F., Bravo, G. A., … Cesari, E. (2015). Annotated checklist of the birds of Brazil by the Brazilian Ornithological Records Committee. *Revista Brasileira de Ornitologia*, *23*, 91–298.

Pinto, O. M. O. (1938). Catálogo das aves do Brasil. Parte 1. *Revista Museu Paulista*, *22*, 1–566.

Pinto, O. M. O. (1978). Novo Catálogo das Aves do Brasil. Primeira Parte: Aves não Passeriformes e Passeriformes não Oscines, com exclusão da familia Tyrannidae. Empresa Gráfica da Revista dos Tribunais, São Paulo, SP, Brazil, 446 pp.

Porzecanski, A. L., & Cracraft, J. (2005). Cladistic analysis of distributions and endemism (CADE): Using raw distributions of birds to unravel the biogeography of the South American aridlands. *Journal of Biogeography*, *32*, 261–275. https://doi.org/10.1111/j.1365-2699.2004.01138.x

Pulido-Santacruz, P., Aleixo, A., & Weir, J. (2018). Morphologically cryptic Amazonian bird species pairs exhibit strong postzygotic reproductive isolation. *Proceedings of the Royal Society B*, *28520172081*, https://doi.org/10.1098/rspb.2017.2081

Pulido-Santacruz, P., Aleixo, A., & Weir, J. T. (2020). Genomic data reveal a protracted window of introgression during the diversification of a neotropical woodcreeper radiation. *Evolution*, *74*(5), 842–858. https://doi.org/10.1111/evo.13902.

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.r-project.org/index.html

Raikow, R. J. (1994). A Phylogeny of the Woodcreepers (Dendrocolaptinae). *The Auk*, *111*(1), 104–114. https://doi.org/10.2307/4088509

Rambaut, A. (2009) FigTree 1.3.1, a graphical viewer of phylogenetic trees. Retrieved from http://tree.bio.ed.ac.uk/software/figtree/

Rambaut, A., Suchard, M. A., Xie, D., & Drummond, A. J. (2014). Tracer v1.6. Retrieved from http://beast.bio.ed.ac.uk/Tracer

Ree, R. H., & Sanmartin, I. (2018). Conceptual and statistical problems with the DEC+ J model of founder-event speciation and its comparison with DEC via model selection. *Journal of Biogeography*, *45*(4), 741–749. https://doi.org/10.1111/jbi.13173

Remsen, J. V. Jr, Areta, J. I., Bonaccorso, E., Claramunt, S., Jaramillo, A., Pacheco, J. F., … Zimmer, K. J. (2020, *February 17*). A classification of the bird species of South America: American Ornithological Society. Retrieved from http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm

Rocha, T. C., Sequeira, F., Aleixo, A., Rego, P. S., Sampaio, I., Schneider, H., & Vallinoto, M. (2015). Molecular phylogeny and diversification of a widespread Neotropical rainforest bird group: The Buff-throated Woodcreeper complex, *Xiphorhynchus guttatus/susurrans* (Aves: Dendrocolaptidae). *Molecular Phylogenetics and Evolution*, *85*, 131–140. https://doi.org/10.1016/j.ympev.2015.02.004

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Hohna, S., … Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, *61*, 539–542. https://doi.org/10.1093/sysbio/sys029

Silva, J. M. C. (1996). Distribution of Amazonian and Atlantic birds in gallery forests of the cerrado region, South America. *Ornitologia Neotropical*, *7*, 1–18.

Silva, S. M., Peterson, A. T., Carneiro, L., Burlamaqui, T. C. T., Ribas, C. C., Sousa-Neves, T., … Aleixo, A. (2019). A dynamic continental moisture gradient drove Amazonian bird diversification. *Science. Advances*, *5*(7), eaat5752. https://doi.org/10.1126/sciadv.aat5752

Souza-Neto, A. C., Cianciaruso, M. V., & Collevatti, R. G. (2016). Habitat shifts shaping the diversity of a biodiversity hotspot through time: Insights from the phylogenetic structure of Caesalpinioideae in the Brazilian Cerrado. *Journal of Biogeography*, *43*, 340–350. https://doi.org/10.1111/jbi.12634

Sukumaran, J., & Knowles, L. L. (2017). Multispecies coalescent delimits structure, not species. *Proceedings of the National Academy of Sciences*, *114*(7), 1607–1612. https://doi.org/10.1073/pnas.1607921114

Thom, G., & Aleixo, A. (2015). Cryptic speciation in the white-shouldered antshrike (*Thamnophilus aethiops* – Aves, Thamnophilidae): The tale of a transcontinental radiation across rivers in lowland Amazonia and the northeastern Atlantic Forest. *Molecular Phylogenetics and Evolution*, *82*, 95–110. https://doi.org/10.1016/j.ympev.2014.09.023

Thompson, J. D., Higgins, D. G., & Gibson, T. J. (1994). CLUSTAL-W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. *Nucleic Acids Research*, *22*, 4673–4680. https://doi.org/10.1093/nar/22.22.4673

Vaidya, G., Lohman, D. J., & Meier, R. (2011). SequenceMatrix: Software de concatenação para a montagem rápida de conjuntos de dados de vários genes com informações sobre conjunto de caracteres e codões. *Cladistics*, *27*, 171–180. https://doi.org/10.1111/j.1096-0031.2010.00329.x

Weir, J. T., & Price, T. D. (2019). Song playbacks demonstrate slower evolution of song discrimination in Amazonia than in birds from temperate North America. *PLOS Biology*, *17*(10), e3000478. https://doi.org/10.1371/journal.pbio.3000478

Weir, J., & Schluter, D. (2008). Calibrating the avian molecular clock. *Molecular Ecololy*, *17*, 2321–2328. https://doi.org/10.1111/j.1365-294X.2008.03742.x

Werneck, F. P. (2011). The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. *Quaternary Science Reviews*, *30*, 1630–1648. https://doi.org/10.1016/j.quascirev.2011.03.009

Werneck, F. P., Nogueira, C., Colli, G. R., Sites, J. W. Jr, & Costa, G. C. (2012). Climatic stability in the Brazilian Cerrado: Implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot. *Journal of Biogeography*, *39*, 1695–1706. https://doi.org/10.1111/j.1365-2699.2012.02715.x

Willis, E. O. (1982). The behavior of Black-banded Woodcreepers (*Dendrocolaptes picumnus*). *Condor*, *84*, 272–285. https://doi.org/10.2307/1367369

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

Willis, E. O., & Oniki, Y. (2001). On a nest of the Planalto woodcreeper, *Dendrocolaptes platyrostris*, with taxonomic and conservation notes. *Wilson Bulletin*, *113*, 231–233. https://doi.org/10.1676/0043-5643(2001)113[0231:OANOTP]2.0.CO;2

Yang, Z. (2015). The BPP program for species tree estimation and species delimitation. *Current Zoology*, *61*, 854–865. https://doi.org/10.1093/czoolo/61.5.854.

Zimmer, J. T. (1934). Studies on Peruvian Birds XIV. The genera *Dendrocolaptes*, *Hylexetastes*, *Xiphocolaptes*, *Dendroplex*, and *Lepidocolaptes*. *American Museum Novitates*, *753*, 1–26.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Bayesian phylogeny estimated for *Dendrocolaptes* based on both mitochondrial genes sequenced (*ND2* and *Cytb*).

Table S1. Primer sequences used in this study.

Table S2. Best fit models and partitions selected by PartitionFinder.

Table S3. Uncorrected average pairwise *p*-distances for *Dendrocolaptes* lineages.

Alignment S1. Concatenated multilocus alignment used in the Bayesian Inference (BI).

Alignment S2. Concatenated mitochondrial alignment used in the Bayesian Inference (BI).

Alignment S3. *ND2* sequence alignment used in the species tree (ST).

Alignment S4. *Cytb* sequence alignment used in the species tree (ST).

Alignment S5. *FIB5* sequence alignment used in the species tree (ST).

Alignment S6. *G3PDH* sequence alignment used in the species tree (ST).

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