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ORIGINAL ARTICLE

Hybridization in brushfinches (*Atlapetes*, Emberizidae) from the southeast Andes of Colombia: a consequence of habitat disturbance?

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Abstract

Hybridization between *Atlapetes* brushfinches has been scarcely documented across the 28 species of the genus. An unusual *Atlapetes* was observed and collected in the foothills of the southeast Andes of Colombia. We analysed plumage, morphometrics and mitochondrial and nuclear DNA sequences to test whether this specimen represented a hybrid or an aberrant individual of a local species. We found genetic and morphological evidence that the specimen is a hybrid between White-naped Brushfinch *Atlapetes albinucha* and Dusky-headed Brushfinch *Atlapetes fuscoolivaceus*. Phylogenetic analyses based on mitochondrial DNA suggest that its female parent was *A. fuscoolivaceus*, whereas nuclear DNA suggests that *A. albinucha* is likely the male parent. Moreover, the hybrid exhibits a combination of plumage characters of both parents, although morphometrically it is more similar to the male parent. We hypothesize that hybridization was likely facilitated by forest clearance enabling geographic contact between individuals of these species, which presumably were formerly isolated on different mountain slopes.

Keywords Geographic contact · Introgression · Oscines · Plumage differentiation · Phylogenetic analysis

Zusammenfassung

Hybridisierung bei Buschammern (*Atlapetes*, Emberizidae) im Südosten der kolumbianischen Anden: Eine Folge von Habitatbeeinträchtigung?

Die Hybridisierung bei Buschammern (*Atlapetes*) ist zwischen den 28 Arten dieser Gattung nur spärlich dokumentiert. Eine ungewöhnliche Buschammer wurde in den Ausläufern der südöstlichen Anden in Kolumbien beobachtet und zu Forschungszwecken entnommen. Wir analysierten neben Gefieder und Morphometrie auch mitochondriale und nukleare DNA Sequenzen dieses Individuums, um festzustellen, ob es sich um einen Hybrid oder um ein abnormales Tier der lokalen Art handelte. Wir fanden sowohl genetische als auch morphologische Belege, dass das untersuchte Individuum ein Hybrid zwischen Weißnacken-Buschammer *A. albinucha* und Rußkopf-Buschammer *A. fuscoolivaceus* ist. Phylogenetische Analysen auf Basis mitochondrialer DNA deuten auf *A. fuscoolivaceus* als weibliches Elterntier hin, wohingegen laut Analyse der Zellkern-DNA

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A. albinucha wahrscheinlich das männliche Elterntier ist. Darüber hinaus zeigte der Hybrid eine Kombination der Gefiedermerkmale beider Eltern, obwohl das Tier morphometrisch dem Vater ähnlicher war. Wir vermuten, dass die Hybridisierung wahrscheinlich durch Waldrodung und dem daraus resultierenden räumlichen Kontakt zwischen Individuen der beiden Arten begünstigt wurde, die bislang vermutlich durch das Bewohnen unterschiedlicher Berghänge isoliert voneinander waren.

Introduction

Mating between individuals of different species (i.e. interspecific hybridization) is a widespread phenomenon among birds. Approximately 9–16% of avian species are known to hybridize with others (Grant and Grant 1992; McCarthy 2006; Ottenburghs et al. 2015), yet these figures are likely underestimates of how widespread hybridization is given our scarce knowledge of the reproductive biology of many species, especially in the tropics. Although hybridization is a natural evolutionary process (Arnold 1992; Barton 2001), its frequency may be influenced by human impacts on the environment such as the introduction of exotic species, modification of habitat structure, or climate change (Allendorf et al. 2001; Taylor et al. 2015). In particular, habitat disturbance may allow formerly allopatric species to come into geographic contact in areas where they may hybridize (Grabenstein and Taylor 2018), especially if they occur at relatively low densities in such areas (Hubbs 1955; Randler 2002; Klein et al. 2017).

The genus *Atlapetes* (Emberizidae) comprises 28 species of songbirds distributed in montane forest from Mexico to northwestern Argentina (Chesser et al. 2017; Remsen et al. 2017). Some species of *Atlapetes* have patchy distributions, and complex elevational and latitudinal replacements result in few cases of local co-occurrence of species in the genus (Paynter 1972, 1978; Remsen and Graves 1995). Molecular phlylogenetic analyses suggest recent diversification of *Atlapetes* and shallow genetic differentiation among species (García-Moreno and Fjeldså 1999; Sánchez-González et al. 2015). Despite their recent origin and low genetic divergence, hybridization seems to be rare and restricted to at most five cases of hypothetical hybrids (Fjeldså and Krabbe 1990; García-Moreno and Fjeldså 1999; Donegan et al. 2014; Sánchez-González et al. 2015). All the alleged cases of hybridization in the genus have been based on plumage intermediacy, but conclusive hybrid diagnosis identifying parental species has not been provided for any of them using genetic data or quantitative morphological analyses.

Here, we document the finding of an unusual individual in the genus *Atlapetes* from the Andes of southeast Colombia and test the hypothesis that it is a hybrid. We analysed DNA sequences of one mitochondrial gene, which is inherited maternally, and one nuclear gene, which is inherited biparentally. If the specimen were a hybrid, then it should have a mitochondrial haplotype from the female parent species and nuclear alleles shared with male and female parent species. Alternatively, if the specimen were an aberrant individual of a known species, then its mitochondrial and nuclear haplotypes would be most similar and phylogenetically closest to haplotypes found in such species. Our genetic analyses, coupled with plumage and morphometric comparisons, confirmed that the specimen most likely represents a hybrid between White-naped Brushfinch *Atlapetes albinucha* and Dusky-headed Brushfinch *Atlapetes fuscoolivaceus*.

Methods

On 4 March 2014, D. C. A. and Katherine Certuche-Cubillos observed a distinctive *Atlapetes* brushfinch along a secondary forest edge in the Cristales sector of the Upper Mocoa River Watershed Forest Reserve (01°12′N, 76°43′W; 1420 m elevation). This reserve is located 10 km northwest of the municipality of Mocoa, department of Putumayo, on the east slope of the Andes of Colombia. The individual was photographed while moving and foraging in low vegetation, and after 2 days of fieldwork, it was mist-netted and collected on 7 March 2014 (Fig. 1). The specimen, prepared by D. C. A., is an adult male in fresh plumage and reproductive condition (left testis, 9 × 7 mm, skull 80% ossified, no bursa). The specimen and a tissue sample were deposited in the Ornithological Collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (catalogue number ICN 38899) and the Banco de Tejidos of Universidad de los Andes (ANDES-T 2649), respectively.

As far as is known, five species of *Atlapetes* potentially occur at mid-elevations on either slope of this sector of the Eastern Cordillera (Fig. 1): White-naped Brushfinch *Atlapetes albinucha*, Yellow-breasted Brushfinch *Atlapetes latinuchus*, Dusky-headed Brushfinch *Atlapetes fuscoolivaceus*, White-rimmed Brushfinch *Atlapetes leucopis,* and Slaty Brushfinch *Atlapetes schistaceus* (Hilty and Brown 1986). However, the Mocoa specimen differs from all these species in its blackish facial pattern, light crown stripe and yellowish underparts, which led us to hypothesize at first that it may be an aberrant individual of a local species or a hybrid. Based on head pattern and coloration we suspected that the Mocoa specimen could be an aberrant *A. albinucha*, a common species in the area (Figs. 1, 2), or, alternatively, a hybrid between *A. albinucha* and another species of *Atlapetes* with a yellow belly.

Fig. 1 Pictures of *Atlapetes* brushfinches occurring on the southeast slope of the Colombian Andes. **a** White-napped Brushfinch (*Atlapetes albinucha gutturalis*) and **b** the Mocoa *Atlapetes* specimen captured at the same locality in Putumayo, Colombia; **c** Dusky-headed Brushfinch (*Atlapetes fuscoolivaceus*), Pitalito, Huila, Colombia; **d** White-rimmed Brushfinch (*Atlapetes leucopis*), Vía Sibundoy-Mocoa, Putumayo, Colombia; **e** Slaty Brushfinch (*Atlapetes schistaceus schistaceus*), Jardín, Antioquia, Colombia; **f** Yellow-breasted Brushfinch (*Atlapetes latinuchus spodionotus*), Yanacocha Reserve, Pichincha Province, Ecuador

Genetic analyses

We focused our genetic analyses on the second subunit of the mitochondrial NADH dehydrogenase gene (ND2 gene) and the fifth intron of the nuclear β-fibrinogen gene (β-fib5) because of the availability of published (Flórez-Rodríguez et al. 2011; Barker et al. 2013; Klicka et al. 2014; Sánchez-González et al. 2015) and unpublished (J. L. Pérez-Emán et al., in litt.) sequence data for comparison with other *Atlapetes*. We extracted DNA from pectoral tissue following a phenol-chloroform protocol (Sambrook and Russell 2001; Gutiérrez-Pinto et al. 2012). Then, we amplified a fragment of the ND2 (800 bp) and β-fib5 (569 bp) genes using primers L5215 and H6313 (Sorenson et al. 1999), and FIB5 and FIB6 (Marini and Hackett 2002), respectively. We followed standard protocols for PCR (Cadena et al. 2007; Klicka et al. 2014), and conducted DNA sequencing at the Universidad de los Andes, Bogotá. DNA sequences were edited manually and aligned in Geneious version 9.1.2 (Kearse et al. 2012). Ambiguous positions in β-fib5 were codified following IUPAC codes. We phased haplotypes for β-fib5 sequences using the PHASE algorithm in DNAsp version 5.10 (Librado and Rozas 2009), ran for 10,000 iterations, with a thinning interval of ten and a burn-in of 1000 iterations. Missing data in the β-fib5 dataset were changed to gaps before the run-in phase.

The combined ND2 data represents 22 of the 28 recognized species in the genus *Atlapetes* (Chesser et al. 2017; Remsen et al. 2017), including all the species that potentially occur at mid-elevations in the Upper Magdalena valley and on the east slope of the Eastern Cordillera (Hilty and Brown 1986). The β-fib5 data set was more reduced, with only 14 *Atlapetes* species, yet it included all but one of the species potentially co-occurring with the Mocoa specimen (*A. leucopis* was missing). Following Klicka et al. (2014), we conducted analyses including five species of the genera

Fig. 2 Ventral (*top*), dorsal (*middle*) and lateral (*bottom*) views of Colombian specimens of *A. albinucha gutturalis* (*left*; ICN 38086), *A. fuscoolivaceus* (*middle*; ICN 27333) and the Mocoa specimen hybrid (*right*; ICN 38899). Photos by J. E. A.

Pipilo, *Pezopetes*, *Melospiza* and *Aimophila* as outgroups, plus *Pselliophorus*, which is part of the *Atlapetes* clade (Table S1).

We reconstructed phylogenetic relationships for each gene using Bayesian Inference (BI). The best-fit models of molecular substitution were estimated in PartitionFinder version 1.1.1 according to the Akaike information criterion (Lanfear et al. 2012; Table S2). A three-codon partition scheme was selected for ND2 (1st codon, HKY + I + G; 2nd codon, GTR + I; 3rd codon, TIM + I + G), and a two-codon partition scheme was selected for β-fib5 (1st codon, HKY; 2nd and 3rd codons, HKY + G). The Bayesian tree was inferred using MrBayes 3.2.2 (Huelsenbeck and Ronquist 2001). This analysis consisted of four runs, each of one cold and three hot chains with a temperature of 0.175, and 30 million generations with a sampling frequency of 1000. We discarded the first 25% of sampled trees as burn-in and calculated a majority rule consensus tree among the trees retained. We assessed convergence among independent runs based on effective sample sizes of parameters (> 200) in Tracer version 1.6 (Rambaut et al. 2003). BI analyses were run in MrBayes on XSEDE version 3.2.6 in the CIPRES portal (Miller et al. 2010; http://www.phylo.org/). We also constructed a haplotype network for the nuclear sequences using a median-joining algorithm in the software PopART (Leigh and Bryant 2015). Finally, we calculated mean uncorrected *p*-distances on the ND2 data set using a partial deletion option between selected taxa in MEGA6 (Tamura et al. 2013).

Phenotypic analyses

Based on molecular data (see below) it was evident that the most likely hypothesis was that the Mocoa specimen is a hybrid, with its parental species being *A. albinucha* and *A. fuscoolivaceus*. Therefore, we described the plumage coloration of these species and of the Mocoa specimen following Smithe (1975-1981). We also took the following morphological measurements to the nearest 0.1 mm with a dial caliper: length of exposed and total culmen; commissure width (between each corner of the mouth); height of the bill at the midpoint of the nares; length of the chord of the folded wing; length of the tail from the insertion of the middle pair of rectrices; and tarsus length. Body mass was taken from specimen labels and measured with a 100-g Pesola professional digital scale to the nearest 0.1 g for the Mocoa specimen. We measured a total of 24 adult male *A. albinucha*, and six adult male *A. fuscoolivaceus*, plus the Mocoa male specimen. Specimens were inspected at the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia, Bogotá, and the Museo Jorge Ignacio Hernández-Camacho of the Instituto Alexander von Humboldt, Villa de Leyva, Colombia (Table S3).

We conducted a discriminant function analyses of all morphometric measurements except body mass, to determine whether parental species were distinguishable in a multivariate space and whether the Mocoa specimen was morphologically intermediate, as one may expect given the hypothesis that it is a hybrid. We classified specimens in three groups discriminating by taxon (*A. albinucha*, *A. fuscoolivaceus* and the putative hybrid), and focused on canonical discriminant functions with eigenvalues greater than 1.0. This analysis was run using the function lda of the package MASS (Ripley et al. 2017) implemented in R (R Development Core Team 2016).

Results

Genetic analyses

The Bayesian tree based on ND2 sequences recovered similar phylogenetic relationships among *Atlapetes* species to those found by previous studies in the group (Fig. 3). The Mocoa specimen was not genetically distinct from other species of *Atlapetes*. Instead, it formed a clade with two specimens of *A. fuscoolivaceus* (posterior probability = 1.0; Fig. 3) from which it differed in only three base pairs (0.4% uncorrected *p*-distance). Genetic distances to other species of *Atlapetes* potentially occurring in the study area were much greater (Table 1).

Phase analysis of β-fib5 sequences only recovered one haplotype for the Mocoa specimen. Therefore, our nuclear analysis included only one sequence per individual. Phylogenetic relationships among 13 *Atlapetes* species based on β-fib5 were mostly unresolved (results not shown) likely due to the scarcity of informative sites. However, the haplotype network suggested that the haplotype observed in the Mocoa specimen is identical to a haplotype shared by individuals of *A. albinucha albinucha* and *A. albinucha gutturalis* (Fig. 4), and slightly more divergent (i.e. separated by one mutational step) from a common haplotype shared between *A. fuscoolivaceus* and nine other species.

Taken together, the molecular evidence points strongly to the hypothesis that the Mocoa specimen is a hybrid. The close similarity in mitochondrial DNA sequence to that of *A. fuscoolivaceus* suggests this species was the female parent, and nuclear DNA suggests *A. albinucha* is the most likely male parent. These species also share several plumage traits with the Mocoa specimen that other *Atlapetes* species in the region lack (Figs. 1, 2). Therefore, we next describe the plumage of parental species and the hybrid.

External morphology

Description of the Mocoa specimen (ICN 38899)

Dorsum dark dull olive (nearest 49, greenish olive) becoming lighter to rump. Remiges and rectrices brown (nearest 221, Van Dyke brown) edged with olive (49, greenish olive). Face and front black (119, sepia); auricular area sepia darker; crown to nape pale yellow (between 56, straw yellow and 157, sulphur yellow), more yellowish near to the front (55, spectrum yellow with 157, sulfur yellow) with black bases of feathers (119, sepia) giving mottled appearance. Sides of nape and neck becoming darker with poorly defined edges broader with sepia colour (119, sepia). Malar region, chin, and throat rich yellow (55, spectrum yellow). Breast, lower breast and belly pale yellow (157, sulfur yellow tending 55, spectrum yellow), these feathers with base and centre whitish. Thighs olive (49, greenish olive) and under tail coverts yellow (157, sulfur yellow). Soft part colours: iris reddish brown, bill entirely black, legs and feet brownish-grey.

Description of Colombian specimens of *A. albinucha* gutturalis (males ICN 18850, 27375, 29713)

Dorsum dark grey (mixed 82, blackish natural grey and 30, olive). Crown with median stripe white intense overhead. Sides of head, facial area, sides of neck and nape black (119, sepia). Throat, malar region and chin intense yellow (55, spectrum yellow). Breast, lower breast pale grey dusty (86, pale neutral grey), and belly centre more whitish. Feathers of the flanks broadly grey along shafts thinly bordered olive (nearest 30, olive). Under tail coverts grey with the lateral borders olive (30, olive), becoming more intense on thighs producing dirty appearance. Wings and tail pale brown (near 119A hair brown) edged with paler grey tinged olive (varying 86, pale neutral grey). Soft part colours: iris reddish brown, bill black, legs and feet light brown.

Description of specimens of *A. fuscoolivaceus* (males ICN 27370, 27333; female ICN 27336)

Dorsum, rump and nape rich olive yellow [between 48, olive green (auxiliary) and 51, citrine)], becoming darker towards the head. Remiges and rectrices brown-olive (near 129, dark-brownish-olive) edged with light olive (48, olive green) to dull yellow (51, citrine). Crown dirty yellow, feathers broadly yellow (near 51, citrine) with external borders brown (near 129, dark-brownish-olive). Side of head, auricular and facial pattern like crown with more brownish tone. Forehead and loreal feathers more yellow-olive with bright yellow bases (combination of 157, sulfur yellow and 51, citrine). Malar region, chin and throat dull yellow with strongest tones (between 55, spectrum yellow and 157, sulfur

Fig. 3 Bayesian tree based on mitochondrial NADH dehydrogenase (ND2) gene showing the phylogenetic relationships among *Atlapetes* Brushfinches and the Mocoa specimen. *Asterisks* at *nodes* represent posterior probabilities higher than 0.95

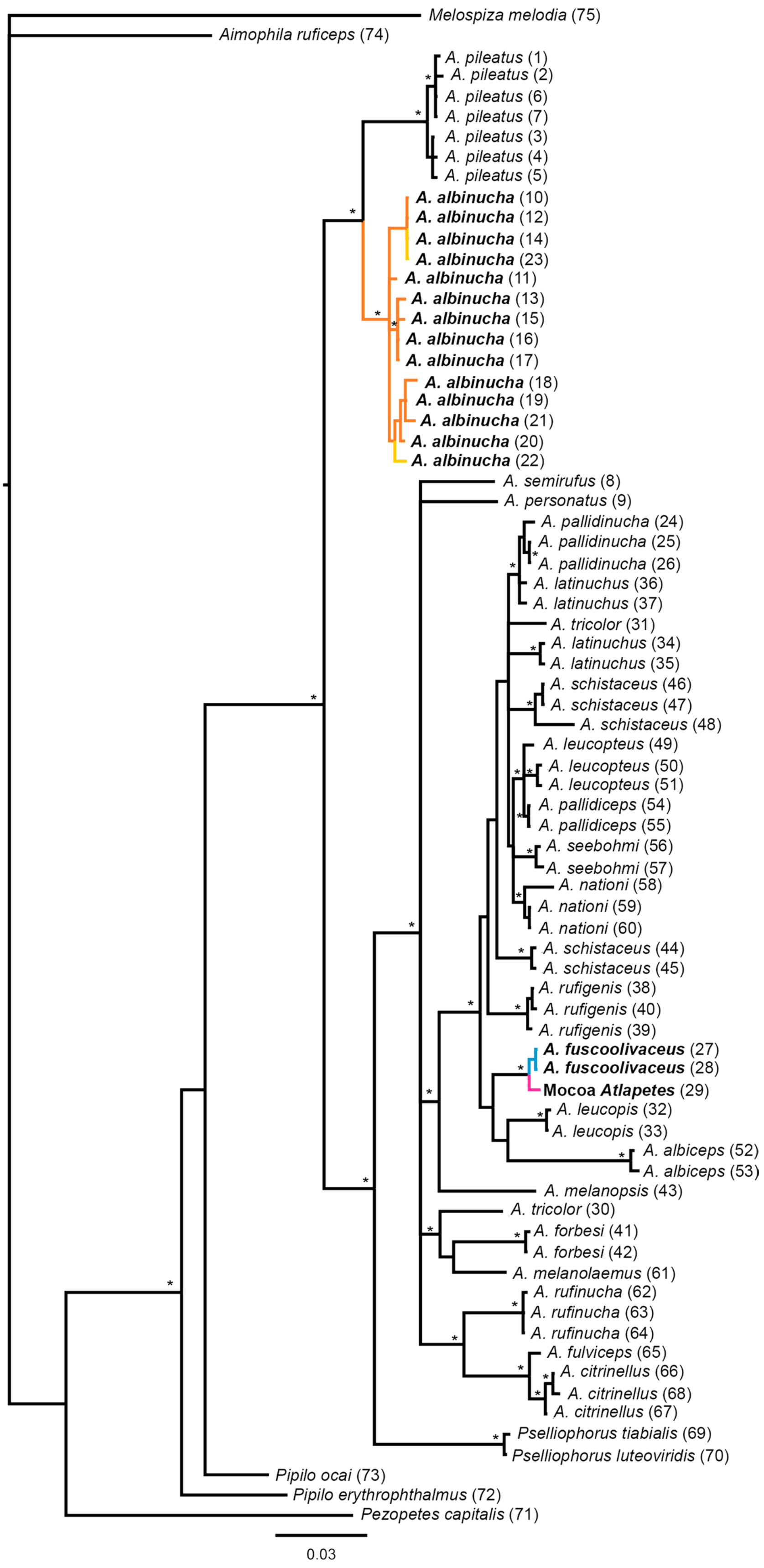

Table 1 Pairwise genetic distances (uncorrected *p*) based on mitochondrial NADH dehydrogenase (ND2) gene sequences, between the Mocoa specimen and closely related or geographically sympatric *Atlapetes* species

Taxa pair	Genetic distance (%)
Mocoa specimen—*Atlapetes fuscoolivaceus* (2)	0.4
Mocoa specimen—*Atlapetes albinucha* (14)	6.5
Mocoa specimen—*Atlapetes albinucha gutturalis* (Colombia; 2)	7.2
Mocoa specimen—*Atlapetes latinuchus* (north Ecuador; 2)	2.4
Mocoa specimen—*Atlapetes schistaceus* (Colombia-Ecuador; 2)	2.2
Mocoa specimen—*Atlapetes leucopis* (Ecuador; 2)	2.4
A. fuscoolivaceus—*A. albinucha gutturalis*	6.7

Numbers in parentheses correspond to the number of individuals compared per taxon

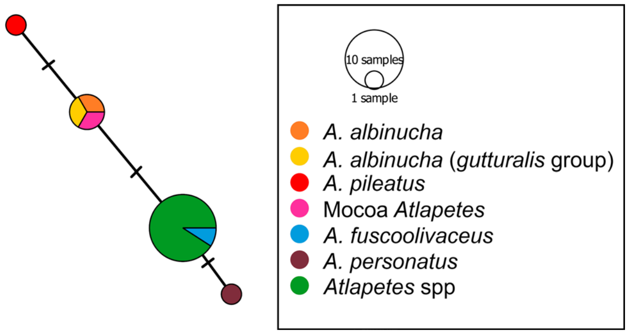

Fig. 4 Median-joining haplotype network showing the relationships among β-fib5 haplotypes of 14 *Atlapetes* Brushfinch species. Each *circle* represents a different haplotype; circle *sizes* are proportional to the number of individuals carrying that haplotype; *colours* distinguish different taxa, but the *green* haplotype groups nine *Atlapetes* species (see Supplementary material). Note that the Mocoa specimen shares a haplotype with members of the *A. albinucha* group, whereas *A. fuscoolivaceus* shares a haplotype with several other *Atlapetes* species (colour figure online)

yellow) contrasting with defined brownish-olive auricular and face region. Thin olive malar streaks like dorsum [mixed 48, olive green (auxiliary) and 51, citrine] extending 10 mm from the mandible base. Lower throat, breast and belly pale yellow (between 157, sulfur yellow and 51, citrine) becoming duller olive on the flanks and under tail coverts; thighs olive-brown (mixed 48, olive green and 55, spectrum yellow). Soft parts: iris reddish brown, bill black, legs and feet brownish.

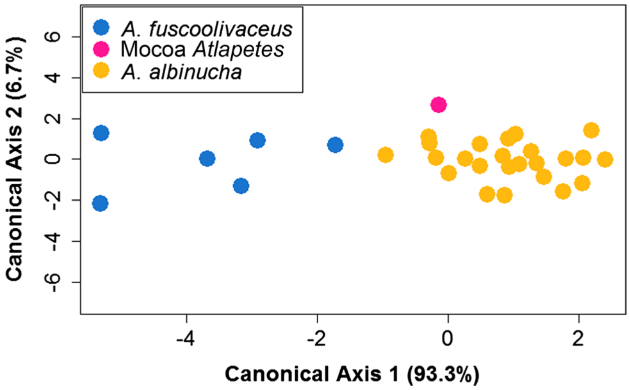

Fig. 5 Discriminant function analysis showing the first two canonical functions that explain 100% of the variance of the seven morphometric variables measured in male specimens of *A. albinucha*, *A. fuscoolivaceus* and the male Mocoa specimen. Note the closer morphological resemblance between the Mocoa specimen and *A. albinucha*

In summary, the Mocoa specimen resembles *A. albinucha* in its dark face and head with a light median crown, and in its yellow throat without a malar stripe. It also resembles *A. fuscoolivaceus* in its bright yellow underparts, with flanks and thighs slightly shaded olive (Fig. 2). The dark dull olive dorsum and brown olive remiges and rectrices seem intermediate between *A. albinucha* and *A. fuscoolivaceus*.

Morphometrics

Discriminant function analysis reduced the seven morphometric variables to two canonical functions (CF), where CF1 explained most of the variance (93.3%) and was positively correlated with length of exposed and total culmen, commissure width and height of the bill (Wilks's $\lambda = 0.171$, $\chi^2 = 44.127$, $p < 0.001$). CF2 explained 6.7% and was positively correlated with wing chord, tarsus and tail length; however, its discrimination power was not significative (Wilks's $\lambda = 0.794$, $\chi^2 = 5.779$, $p > 0.05$). This analysis showed that both *A. albinucha* and *A. fuscoolivaceus* males are distinguishable in morphometric multivariate space (Fig. 5), with 96.8% individuals classified correctly to their respective groups. The exception was one *A. albinucha* that was grouped with the Mocoa specimen. Cross-validation reduced the number of cases correctly classified (87.1%), grouping one *A. fuscoolivaceus* and two *A. albinucha*, whereas the Mocoa specimen was classified with *A. albinucha*. As shown by univariate data (Table 2), the Mocoa specimen exhibits a large bill typical of *A. albinucha* males.

Table 2 Morphological measurements (mm) of the Mocoa specimen, and of specimens of *Atlapetes fuscoolivaceus* and *Atlapetes albinucha*

Measurement	Mocoa specimen	*A. fuscoolivaceus* (♂)	*A. albinucha* (♂)
Wing	78	77 (± 2.28) (73–79) *n* = 6	76.7 (± 1.5) (74–79) *n* = 24
Total culmen	17.4	14.9 (± 1.15) (13.5–16.4) *n* = 6	17.5 (± 0.5) (16.5–18.5) *n* = 24
Exposed culmen	14	12.5 (± 1.3) (10.5–14.2) *n* = 6	14.1 (± 0.6) (13.2–15.6) *n* = 24
Bill height	8.1	7.5 (± 0.17) (7.3–7.8) *n* = 6	8.4 (± 0.32) (7.8–9.1) (*n* = 24)
Commissure width	10.2	9.9 (± 0.28) (9.7–10.5) *n* = 6	10.2 (± 0.5) (8.7–11.4) *n* = 24
Tarsus length	28	26.7 (± 0.65) (26–27.9) *n* = 6	27.5 (± 0.7) (26.1–28.7) *n* = 24
Tail length	90.9	86.1 (± 2.4) (82.3–87.9) *n* = 6	86.2 (± 1.79) (81.7 -88.5) *n* = 24
Weight	33.6	31.3 (± 2.5) (29–34) *n* = 3	34.7 (± 3.01) (30.5–40) *n* = 7

Data for *A. fuscoolivaceus* and *A. albinucha* are means and SDs, with the range for each measurement shown *in parentheses*

Discussion

Based on morphological, phenotypic, and mitochondrial and nuclear DNA sequence data, we conclude that the Mocoa *Atlapetes* specimen we discovered is a hybrid between *A. albinucha* and *A. fuscoolivaceus*, and not an aberrant individual of the former or any other species. Genetic data suggest that the hybrid's female parent was *A. fuscoolivaceus*, which it resembles in the coloration of the underparts. In turn, the hybrid shares with the likely male parent *A. albinucha* several morphological and plumage characters including the facial and head pattern, as well as the large bill. Although several putative *Atlapetes* hybrids have been reported in the literature based on plumage intermediacy, ours represents the most completely documented and conclusive instance of hybridization in the genus.

All putative cases of hybridization previously reported in *Atlapetes* involve closely related taxa with similarly coloured underparts (grey, yellow or dark olive): *Atlapetes leucopterus* × *Atlapetes nationi* (Fjeldså and Krabbe 1990); *Atlapetes seebohmi* × *Atlapetes rufigenis*, *Atlapetes rufinucha* × *Atlapetes melanolaemus* (García-Moreno and Fjeldså 1999); *Atlapetes latinuchus latinuchus* × *Atlapetes latinuchus comptus* (Sánchez-González et al. 2015); and *Atlapetes latinuchus nigrifrons* × *Atlapetes albofrenatus albofrenatus* [the "Perijá bird" in Donegan et al. (2014); Pérez-Emán et al. (in litt.)]. The case of hybridization between *A. albinucha* and *A. fuscoolivaceus* that we document thus appears to be exceptional in two respects. First, it involves taxa from distinct clades because *A. albinucha gutturalis* forms a clade with the Central American *Atlapetes albinucha albinucha* and *Atlapetes pileatus*, whereas *Atlapetes fuscoolivaceus* is part of a large clade formed by *Pselliophorus* and all other species of South American *Atlapetes* (García-Moreno and Fjeldså 1999; Klicka et al. 2014; Sánchez-González et al. 2015). These clades are 7.0% divergent (uncorrected *p*-distance), which, assuming a rate of 2.1% divergence per million years (Weir and Schluter 2008), suggests that hybridization is possible among *Atlapetes* taxa isolated for more than 3 million years. Second, the hybridizing species differ markedly in plumage coloration of the underparts: the breast and abdomen are grey in *A. albinucha,* and yellow in *A. fuscoolivaceus*.

The expression of yellow underparts inherited from *A. fuscoolivaceus* in the Mocoa specimen mirrors patterns of introgression of yellow plumage patches observed in some avian hybrid zones, where yellow plumage patches seem to be genetically dominant over white patches [*Manacus* (Brumfield et al. 2001); *Vermivora* (Toews et al. 2016)]. The coloration of the underparts is highly variable among *Atlapetes* brushfinches, and evolutionary changes from grey to yellow ventral plumage (and vice versa) have occurred repeatedly in the group (Remsen and Graves 1995; García-Moreno and Fjeldså 1999; Sánchez-González et al. 2015). Although such a pattern may well be explained by a simple genetic/biochemical basis underlying differences between grey and yellow pigmentation (Remsen and Graves 1995), our findings suggest it is possible that introgressive hybridization may have also contributed to the complicated patterns of geographic variation in plumage coloration existing in the genus (Paynter 1972; Remsen and Graves 1995; García-Moreno and Fjeldså 1999; Sánchez-González et al. 2015).

Hybridization between *A. albinucha* and *A. fuscoolivaceus* may have been facilitated due to the scarcity of conspecific mates of one or both parental species (Hubbs 1955; McCarthy 2006). Whereas *A. albinucha* was commonly observed and captured in the area, we did not detect *A. fuscoolivaceus*, suggesting low local abundance. Indeed, *A. fuscoolivaceus* is generally thought to be restricted to premontane slopes of the Upper Magdalena Valley (López-Lanús and Renjifo 2002; Renjifo et al. 2014), with its presence on the east slope of the Eastern Cordillera only suggested by recent records at the crest of the Serranía de los Churumbelos (Salaman et al. 2002) and at San Juan de Villalobos and Santa Rosa, Cauca (Sullivan et al. 2009; J. P. López-O. personal communication), in the divide between the Amazon the Magdalena watersheds. Our data confirm the presence of *A. fuscoolivaceus* on the east slope of the Andes; that the species is by no means abundant on this slope (i.e. in the periphery of its geographic range), may partly explain why it hybridized with the locally common *A. albinucha.*

Considering that *A. fuscoolivaceus* favours disturbed and secondary habitats over dense forest (Hilty and Brown 1986;

Gallo-Cajiao et al. 2014), its presence on the east slope of the Andes may represent a recent range extension facilitated by forest clearance, particularly driven by the opening of the Pitalito-Mocoa highway, which is one of the most active colonization fronts in the region (Salaman and Donegan 2007) and may account for other cross-Andes expansions of birds (Salaman et al. 2002). Thus, we hypothesize that habitat disturbance may have promoted the expansion of *A. fuscoolivaceus* from the Upper Magdalena Valley to the east slope of the Andes. Presumably, such an expansion involved populations at low densities, thereby resulting in the case of hybridization we observed as a consequence of scarcity of conspecific mates. A similar scenario was proposed by Sibley (1958) to account for hybridization between *Ramphocelus* tanagers that favour secondary growth and shrubby vegetation and may have come into contact following forest clearance resulting from road construction on the Pacific slope of the Andes (but see Morales-Rozo et al. 2017). Likewise, reductions in population sizes associated with forest fragmentation may have increased the likelihood of hybridization between bird species from forest habitats (Cadena et al. 2007). Thus, by altering the distribution and population sizes of species leading to hybridization, habitat destruction may be altering evolutionary processes in Andean bird assemblages.

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