Evolution of *Dendrocolaptes platyrostris* (Aves: Furnariidae) between the South American open vegetation corridor and the Atlantic forest

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The open vegetation corridor of South America is a region dominated by savanna biomes. It contains forests (i.e. riverine forests) that may act as corridors for rainforest specialists between the open vegetation corridor and its neighbouring biomes (i.e. the Amazonian and Atlantic forests). A prediction for this scenario is that populations of rainforest specialists in the open vegetation corridor and in the forested biomes show no significant genetic divergence. We addressed this hypothesis by studying plumage and genetic variation of the Planalto woodcreeper *Dendrocolaptes platyrostris* Spix (1824) (Aves: Furnariidae), a forest specialist that occurs in both open habitat and in the Atlantic forest. The study questions were: (1) is there any evidence of genetic continuity between populations of the open habitat and the Atlantic forest and (2) is plumage variation congruent with patterns of neutral genetic structure or with ecological factors related to habitat type? We used cytochrome *b* and mitochondrial DNA control region sequences to show that *D. platyrostris* is monophyletic and presents substantial intraspecific differentiation. We found two areas of plumage stability: one associated with Cerrado and the other associated with southern Atlantic Forest. Multiple Mantel tests showed that most of the plumage variation followed the transition of habitats but not phylogeographical gaps, suggesting that selection may be related to the evolution of the plumage of the species. The results were not compatible with the idea that forest specialists in the open vegetation corridor and in the Atlantic forest are linked at the population level because birds from each region were not part of the same genetic unit. Divergence in the presence of gene flow across the ecotone between both regions might explain our results. Also, our findings indicate that the southern Atlantic forest may have been significantly affected by Pleistocene climatic alteration, although such events did not cause local extinction of most taxa, as occurred in other regions of the globe where forests were significantly affected by global glaciations. Finally, our results neither support plumage stability areas, nor subspecies as full species. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 801–820.

ADDITIONAL KEYWORDS: Caatinga – Cerrado – mitochondrial DNA – plumage – population genetic structure – woodcreepers.

INTRODUCTION

The Neotropical Atlantic forest (AF) is separated from the forests of Amazonia and Andes by an open vegetation corridor formed by the biomes: Caatinga, Cerrado, and Chaco (Olson *et al.*, 2001) (Fig. 1). Although dominated by different forms of savanna, the open vegetation corridor contains forests as humid relicts (*brejos*), as a network of gallery rainforests following water streams, and as seasonally dry forests (Veloso, 1991; Prado, 2000; Pennington, Lavin & Oliveira-Filho, 2009). Most rainforests within this

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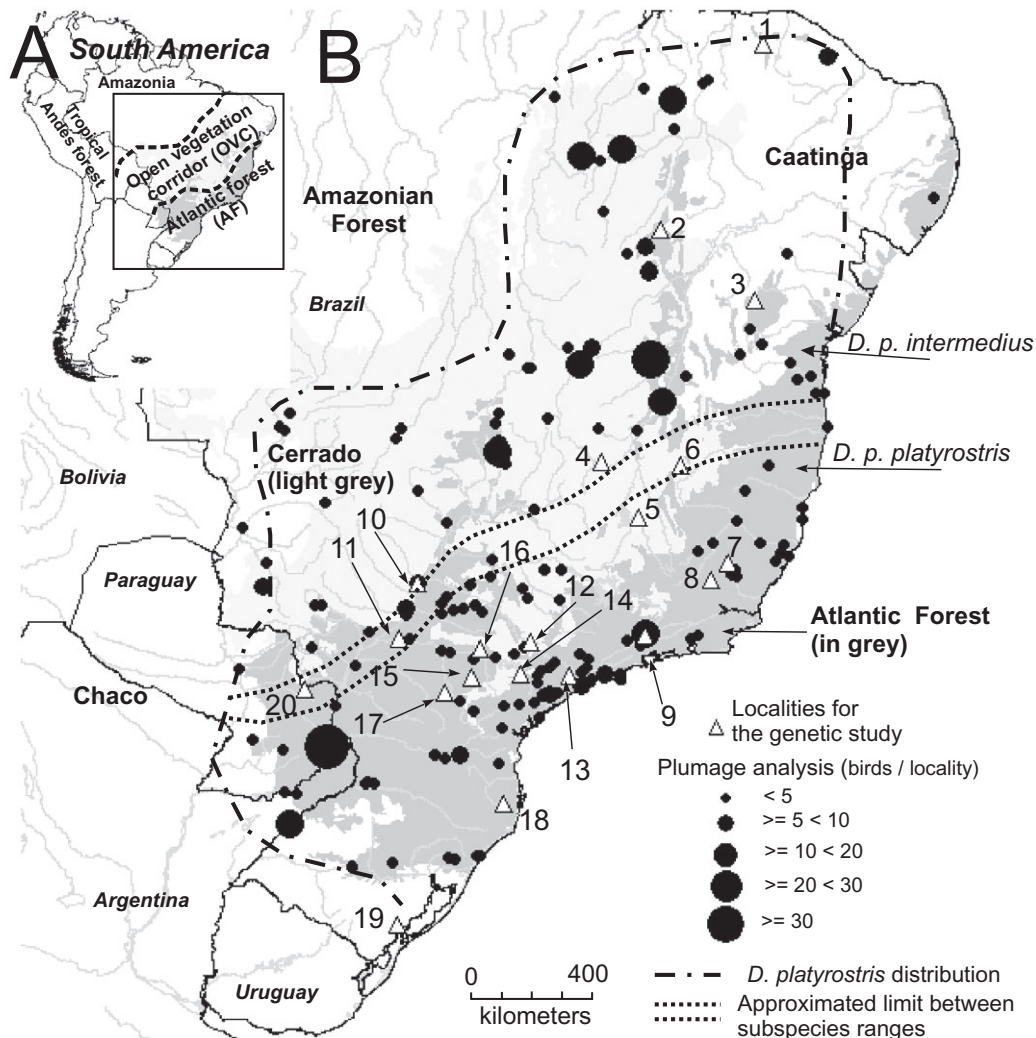
Figure 1. A, study area, distributions of the open vegetation corridor (Caatinga, Cerrado, and Chaco) and of the Atlantic forest. B, sampling localities for the plumage and genetic analysis of *Dendrocolaptes platyrostris*. For details of genetic sampling localities, see Appendix, Table A2. Distribution of biomes and of subspecies followed Olson *et al.* (2001) and Marantz (1997), respectively.

open habitat are physical extensions of the Atlantic and the Amazon rainforest (Cabrera & Willink, 1973; Rizzini, 1976), or were part of them during global glaciations, when larger tracts of rainforests existed in central South America (Ledru, 1992, 1993; Ledru *et al.*, 2006). This particular phytogeographical scenario could have affected the evolution of rainforest specialists inhabiting the open vegetation corridor (Costa, 2003). Particularly, the existence of a network of riverine forests and the historic expansion and retraction of forests may have allowed them to reach the core of the open habitat and to colonize other biomes. Thus, from the biogeographical standpoint of rainforest taxa, the open vegetation corridor might be viewed as a region that is not totally independent of forested biomes, notwithstanding the existence of

substantial landscape differences (Redford & Fonseca, 1986; Silva, 1996; Costa, 2003). Specifically, Costa (2003) found that Cerrado populations of some small no-volant mammals (i.e. species of *Philander* and *Caluromys*) are phylogenetically closely linked to either Atlantic forest or Amazonian populations. If Cerrado populations were not linked to other biogeographical regions, divergent local populations should have been found. Also, Silva (1996) showed that several rainforest birds use riverine forests and dry forests within the Cerrado, reaching the nucleus of this savanna-like biome. Because most forests within the open vegetation corridor are physical extensions of the neighbouring forested biomes, a recent historical connection between populations of the two habitats might be expected. A prediction for this scenario
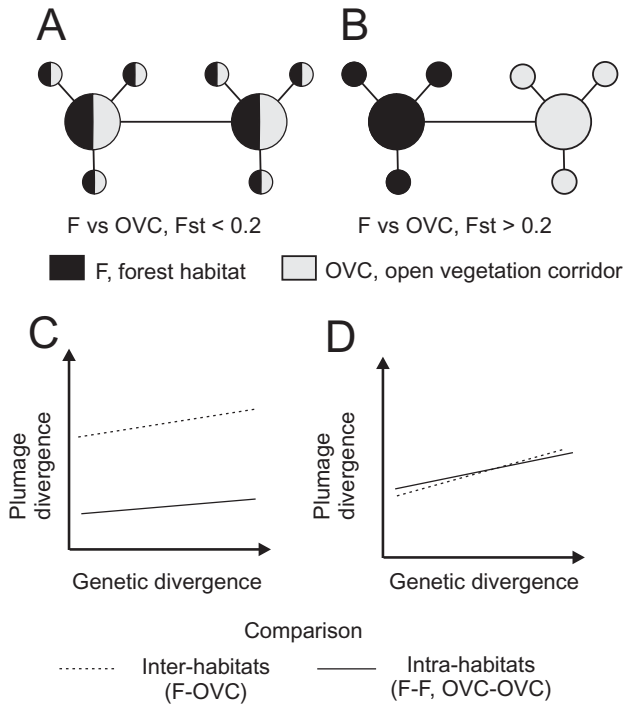
Figure 2. Working hypotheses and their predictions for rainforest taxa. A, predicted haplotype network if the open vegetation corridor (OVC) is not biogeographically independent from neighbouring rainforests (F). Specifically, it is expected that F and OVC contiguous populations belonged to the same evolutionary lineage, in terms of the network and at the population level (expected fixation index $F_{ST} < 0.2$) (Hedrick, 2005). Haplotypes are represented as circles at the nodes and tips of the network. The size of each circle is proportional to the frequency of the haplotype. B, alternative hypothesis, with both regions as being independent biogeographically. Corresponding populations are expected to be reciprocally monophyletic and substantial population isolation should be found ($F_{ST} > 0.2$). Depending on the age of isolation between populations, monophily might be partial. C, expected pattern of plumage versus neutral genetic divergences if selection is responsible for plumage variation (primary divergence). For a given level of genetic divergence in neutral markers, we expected to find greater plumage divergence in between-habitat comparisons than in within-habitat comparisons, Adapted from Moritz *et al.* (2000) and Smith *et al.* (2005b). D, expected pattern of plumage and genetic divergences if plumage variation accompanied population structure and not the type of biome of occurrence (isolation and secondary contact). Patterns should be similar in both habitats.

of biogeographical continuity is that populations of rainforest specialists in the open vegetation corridor and in the forested biomes show no significant genetic divergence, except for cases of divergence as a result of isolation by distance (Fig. 2A). Alternatively, if the open vegetation corridor were an independent biogeographical region, we would expect substantial genetic differentiation between populations of the open and the continuous forested habitats (Fig. 2B).

There are species that occur in both the continuous forests (Atlantic forest or Amazon) and in the open vegetation corridor and present different phenotypes associated with each region (i.e. bird plumage coloration and fur coloration in mammals) (Ridgely & Tudor, 1996; Emmons & Feer, 1997). This is a pattern that might not be in accordance with a biogeographical continuity between habitats. However, it is important to note that forests in the open vegetation corridor are differentiated from forests of the neighboring continuous forests in several aspects, such as climate, humidity, seasonality, and luminosity levels (Veloso, 1991), which may create different selective regimes on adaptive traits between habitats. This selection on adaptive traits may lead to morphologically differentiated populations, despite the presence of gene flow (Moritz *et al.*, 2000; Smith *et al.*, 2005a, b; Smith *et al.*, 2011). For example, higher luminosity levels and lower levels of humidity might favour lighter plumages in birds in the open habitat (Zink & Remsen, 1986; Willis, 1992). Therefore, different phenotypes associated with each habitat do not necessarily reject a biogeographical continuity between the open vegetation corridor and the forest biomes.

In the present study, we investigated plumage and genetic variation of the Planalto woodcreeper (*Dendrocolaptes platyrostris* Spix (1824) Aves, Furnariidae), a bird found throughout the Atlantic forest and also occuring in gallery and dry forests within the open vegetation corridor (Fig. 1). This bird has two subspecies, each one associated with each habitat (Marantz *et al.*, 2003). The nominal subspecies is associated with the Atlantic forest and has a strongly streaked and olive–brown overall plumage. Subspecies *intermedius* is associated with gallery and dry forests of the open vegetation corridor and presents a paler and more cinnamon overall plumage. According to Willis & Oniki (2001), the subspecies present vocal differences suggesting that they could be considered as species. Even though there are intermediates at the transition between the open habitat and the forest (Marantz, 1997; Willis & Oniki, 2001; Marantz *et al.*, 2003), the phenotypic discontinuity between the open habitat and the Atlantic forest deserves to be studied. This phenotypic discontinuity may have been originated by isolation with posterior secondary contact, or by primary divergence in the presence of gene flow. If primary divergence is responsible for the plumage variation in *D. platyrostris* (e.g. by differential selection between habitats), it is expected that phylogeographical gaps within each habitat do not match significant changes in plumage characters.

Thus, for a given level of genetic divergence in neutral markers, we expected to find greater plumage divergence in between-habitat comparisons than in within-habitat comparisons (Fig. 2C) (Moritz *et al.*, 2000; Smith *et al.*, 2005a, b; Norman *et al.*, 2007). Alternatively, if plumage transition accompanied population secondary contact instead of habitat transitions, the pattern shown in Figure 2D should be found.

The present study aimed to investigate plumage and genetic variation of *D. platyrostris* to determine: (1) is there any evidence of genetic continuity between *D. platyrostris* populations of the open vegetation corridor and of the Atlantic forest and (2) is plumage variation congruent with patterns of neutral genetic structure or with ecological factors related to habitat type? To address these questions, we studied five plumage characters and mitochondrial (mt)DNA to evaluate the predictions shown in Figure 2. Marantz (1997) performed a qualitative analysis of plumage variation in *D. platyrostris* to check the diagnosability of subspecies, although plumage variation at the intra-population level was not described. To further understand the geographical plumage variation and to make comparisons between genetic and plumage dissimilarity, we performed a semi-quantitative analysis of plumage variation. In addition, because some studies (Willis, 1992) consider subspecies of *D. platyrostris* as possible species, we also present the systematic implications of our results.

MATERIAL AND METHODS

PLUMAGE ANALYSIS

To describe geographical regions of plumage stability and to obtain plumage divergence estimations, we examined 510 adult specimens (180 females, 302 males, and 28 undetermined) from the museums: Museu Paraense Emílio Goeldi, Brazil; Museu de Zoologia da Universidade de São Paulo, Brazil; and American Museum of Natural History, USA. These specimens were collected in 172 localities that encompassed the entire range of the species (Fig. 1).

We recorded five plumage characters from each study skin. For each character, we defined a scoring system of states, subdividing the total range of variation of colour or pattern (see Appendix, Table A1). The number of states per character varied from three to four, depending of the magnitude of variation of each character. Specimens were scored by only one observer (F.M. d'Horta) by comparison with reference specimens. Colours were described according to the Munsell Soil Color Charts (Munsell Color Company, 2000).

Because previous studies did not show sexual dimorphism in plumage (F. M. d'Horta, unpubl. data)

(Marantz, 1997), males and females were analyzed together. *Sensu* Cracraft (1989), we first analyzed the variation of plumage characters to identify and delimit the smallest cluster of populations that are diagnosably distinct from other clusters. The unit of plumage analysis was the population sample ($N = 38$ population samples), each consisting of at least five specimens from the same or nearest localities. For each population sample, and for each character, we obtained a median 'character score', which was the numerical score that represented the middle measurement of the data set, according to a definition of the statistic median (Quinn & Keough, 2002). Then, we obtained a population total score, or 'total plumage score', which is equal to the sum of median scores of each of the five characters.

The geographical variation in median scores of plumage characters was mapped without considering any a priori taxonomic arrangements (i.e. subspecies). This procedure allowed us to identify geographical areas with little or no change in states of a given character (zones of phenotypic stability) and areas with abrupt changes (transition zones). Individual character maps were then overlapped to identify populations that can be diagnosed by a unique combination of plumage character states (congruent zones of phenotypic stability). To avoid considering portions of clines as zones of phenotypic stability, we only considered regions of at least three population samples. For a similar analysis, see D'Horta, Silva & Ribas (2008).

GENETIC DATASETS

We used muscle and blood samples to obtain DNA. Sampling localities and vouchers are presented in the Appendix (Table A2). The subspecific status of samples was inferred from the distribution of subspecies, *sensu* Marantz (1997). To test the monophyly of *D. platyrostris* and its subspecies, we used 983 bp of the cytochrome *b* (cyt *b*) and 584 pb of the mtDNA control region (CR) from 33 *D. platyrostris* (one from GenBank and the others sequenced in the present study), four *D. picumnus*, one *D. certhia*, and one *D. sanctithomae*. We used *Xiphocolaptes promeropirhynchus* as the outgroup (Aleixo, 2002). For the population genetic study, we used CR of 43 samples from 19 localities. We selected CR for the population analyses because a preliminary study indicated that it is more variable than cyt *b*. Procedures for obtaining cyt *b* sequences and CR were carried out *sensu* Cabanne *et al.* (2008) and Cabanne *et al.* (2007), respectively. Because both cyt *b* and CR are physically linked in a single molecule (mitochondrial genome), the results obtained with both markers are totally compatible because they reflect a single

genealogy and history (Avise, 2000). For an example on this strategy, see McCormack, Bowen & Smith (2008). GenBank accession numbers are JF276349–JF276385 for cyt *b* and JF276306–JF276348 for CR.

GENETIC DATA EXPLORATION

We used cyt *b* and CR to perform Neighour-joining, maximum likelihood, and Bayesian analyses in MEGA, version 4.0 (Tamura *et al*., 2007), PHYML, version 2.4.4 (Guindon & Gascuel, 2003) and MrBayes, version 3.1 (Ronquist & Huelsenbeck, 2003), respectively, to obtain phylogenetic trees for testing the monophyly of the species and subspecies, and to identify intraspecific clades. Molecular evolution models were selected in MODELTEST, version 3.7 (Posada & Crandall, 1998). We only sequenced CR for *D. platyrostris*; for the other taxa, we coded this region as missing data. Bayesian analyses considered each gene as a different partition. Population analyses only used CR sequences. Relationships among CR sequences were studied by constructing a median-joining network in NETWORK, version 4.1.0.8 (http://www.fluxus-engineering.com). The neutrality tests of Tajima (1989), Ramos-Onsins & Rozas (2002) and McDonald & Kreitman (1991) (MK test) were performed in DNASP, version 4.0 (Rozas *et al*., 2003). *Dendrocolaptes picumnus* was used as outgroup in the MK test. Analyses of molecular variance (AMOVA) were performed using ARLEQUIN, version 3.1 (Excoffier, Laval & Schneider, 2006). For evaluation of whether sequence samples were representative of the genetic constitution of the species, we estimated $P = [(k - 1)/(k + 1)]$, which represents the probability that a sample of size k and the whole population share the most recent ancestor (Hein, Schierup & Wiuf, 2005). P can be interpreted as the probability of the sample of being representative of the genetic diversity of the population. The population diversity parameter Θ (theta) was estimated in LAMARC, version 2.1.2b (Kuhner, 2006) (see Supporting information).

GENETIC LANDSCAPE SHAPE

We used a visualization method to obtain a graphical representation of the pattern of genetic distances between individuals across the study area. The procedure was carried out *sensu* Miller *et al*. (2006) and using AIS, version 1.0 (Miller *et al*., 2006). We performed analyses using *p*-distances between individuals because no other distance model was available in AIS, and using residual genetic distances derived from a regression between genetic and geographical distances. Because the results of both analyses were the same, we only present those obtained with genetic distances. Conditions of the AIS analysis: # coordinates bins (X and Y) = 100; distance weight value = 5. The surface for the landscape shape interpolation was based on midpoint of edges derived from a Delaunay triangulation.

DIVERGENCE, GENE FLOW, AND HISTORICAL DEMOGRAPHY

We used CR sequences and the isolation–migration (IM) model (Nielsen & Wakeley, 2001; Hey & Nielsen, 2004), implemented in IM, version 21 April 2008 (Hey & Nielsen, 2004) to estimate gene flow and divergence times. We also used IM to evaluate whether a model without migration adjusted better to the observed data than a model with migration. According to Akaike (1985), the model that minimized AIC = $-2[\log(L) - d]$ is the best, where d is the number of parameters. We assumed the Hasegawa–Kishino–Yano model of evolution, similar population parameter theta values ($\Theta_1 = \Theta_2 = \Theta_a$), and $m_1 = m_2$. Analyses used a burn-in of 500 000 iterations and 30–100 million total iterations. We transformed time parameter t into time in years by $t = t/u$, where u is the mutation rate per marker, and migration parameter m into the effective number of migrant genes (= females) by $M = (\Theta m)/2$. We assumed a generation time of one year. To obtain u for CR sequences, we scaled the cyt *b*-rate of change (obtained from 2.1% divergence per Myr; Weir & Schluter, 2008) with the ratio between the population parameters of each marker $\Theta_{CR}/\Theta_{cytB}$, where Θ_{CR} is the Θ-value of the CR and Θ_{cytB} is the Θ-value of the cyt *b*. The calibration for CR obtained with this method was 14.2% of divergence per Myr (for details, see Results). A published application of this approach to obtain a calibration rate for CR sequences is provided in Toon *et al*. (2007).

We also evaluated historical demography by calculating the R_2 statistic (Ramos-Onsins & Rozas, 2002) in DNASP, version 4.0. Significant and low values of R_2 suggest demographic expansion if neutrality was not rejected.

MODEL-BASED PHYLOGEOGRAPHY

To further investigate the evolutionary history of populations, and particularly their relationships, we evaluated the goodness of fit of the CR sequences to simulated data under different demographic scenarios. Reviews on this approach are provided by Richards, Carstens & Knowles (2007) and Knowles (2009). Sequence simulations were performed in BAYESSC, a modification of software SERIAL SIMCOAL (Anderson *et al*., 2005; Chan, Anderson & Hadly, 2006). We tested models that differed in terms of number of populations, migration rates, and time of divergence (see Supporting information). Parameters

for the simulations were introduced as intervals instead of single values. The modelled historical events, or populations splits, occurred at climatic extremes of the Late Quaternay (6000 years ago, 21 000 years ago, and before) (Carnaval & Moritz, 2008). For each model, we performed 1000 simulations and estimated, using ARLEQUIN, two independent summary statistics suitable for this application (Hickerson, Dolman & Moritz, 2006), namely nucleotide diversity and F_{ST}. For evaluating the goodness of fit of the observed data to simulated data, we used the empirical likelihood of each summary statistic. First, we estimated the proportion P of simulated values equal and higher than the observed summary statistics, and then we obtained an overall P-value for each model by combining invididual P-values by the Fisher's method in the program METAP (Whitlock, 2005).

ANALYSIS OF GENETIC AND PLUMAGE DIVERGENCE

To study genetic divergence, we performed a multiple correlation analysis (multiple Mantel tests; Manly & Manly, 2001) using, as a dependent variable, average Tamura & Nei (1993) (TN 93) genetic distances between individuals from pairs of localities (variable DGEN) and two independent variables, DGEO and DHAB. DGEO was equal to the straight geographical distance between localities and variable DHAB was an indicator variable that indicated whether comparisons were made within the same habitat (within open vegetation corridor or within AF, DHAB = 0) or between habitats (open vegetation corridor versus AF, DHAB = 1). An explanation on indicator variables is provided in Quinn & Keough (2002). If genetic distances are only affected by geographical isolation, we expected DGEO to be the only predictor of DGEN. However, if habitat transition was also related to genetic divergence, we also expected a significant correlation between DGEN and DHAB. We used FSTAT (Goudet, 2002) to perform partial Mantel tests with 20 000 replicates to check significance.

Population isolation was evaluated by mtDNA neutral genetic divergence. To evaluate whether plumage variation was related to population isolation and habitat transitions, we performed two analyses. First, we used a multiple Mantel test to address whether plumage variation between pairs of localities (variable DPLUM) was related to two independent variables, namely genetic distances (DGEN) and DBIOM. DPLUM consisted of a Manhattan distance (Quinn & Keough, 2002) equal to the sum (across characters) of absolute differences in the median character scores between pair of localities with associated genetic data (Fig. 1; see also Appendix, Table A2). To obtain DPLUM plumage, character states were considered as ordered. We also performed

analyses considering plumage states as unordered but, because the results were similar to those obtained with ordered states, we only present the results with ordered states. Some localities with genetic data did not have available associated museum specimens for plumage scoring. For those localities, we assumed plumage states from the nearest locality within a radius of 50 km (see Appendix, Table A2). We used FSTAT to perform partial Mantel tests (20 000 replicates). A second plumage analysis qualitatively evaluated the relationship between DPLUM and DGEN to test the predictions of Figure 2C, D. Analyses of this section excluded localities Felixlândia and Bocaiuva, which were located in an area of transition between Cerrado and AF, and have neither museum specimens for the plumage analysis available, nor close localities to extrapolate plumage data.

RESULTS

PLUMAGE VARIATION

Two areas of plumage stability were found: populations I and II (Fig. 3). The core of population I was located at Cerrado and the diagnosis was: HEAD very dark greyish–brown with streaks pale yellow (state 2); TAIL dark reddish–brown (state 3); UPPERTAIL-coverts yellowish–red (state 2); BACK dark yellow–brown without streaks (state 0); and VENT light yellowish–brown with thin bars and very dark greyish brown (state 2). Population II was located at southern Atlantic forest and was diagnosed by: HEAD black with white streaks (state 6); TAIL dark reddish–brown (state 6); UPPERTAIL-coverts dark brown with a black patch at the subterminal portion of feathers (state 6); BACK dark brown streaked white (state 6); and VENT light olive–brown with bold bars dark greyish brown (state 6).

GENETIC ANALYSIS

We obtained a cyt *b*-CR alignment of 33 *D. platyrostris* and seven other dendrocolaptids [1567 bp, 214 variable positions, 125 (58.4%) informative for parsimony]. Neutrality of the cyt *b* from *D. platyrostris* was not rejected by the MK test (*G*-test $P > 0.05$), the test of Tajima ($D = -0.092$, $P > 0.1$) and by the R_2 test of Ramos–Onsins and Rozas ($R_2 = 0.1189$, $P > 0.05$). The CR alignment had 43 *D. platyrostris* (584 bp, 41 variable positions, 33 (80.5%) informative for parsimony]. The test of Tajima for the CR data set was not significant ($D = -0.03438$, $P > 0.1$) and the R_2 test of Ramos-Onsins and Rozas ($R_2 = 0.1101$, $P > 0.05$). The cyt *b*-CR and the CR set of sequences have a 94% and 95.5% probability of having correctly sampled the size
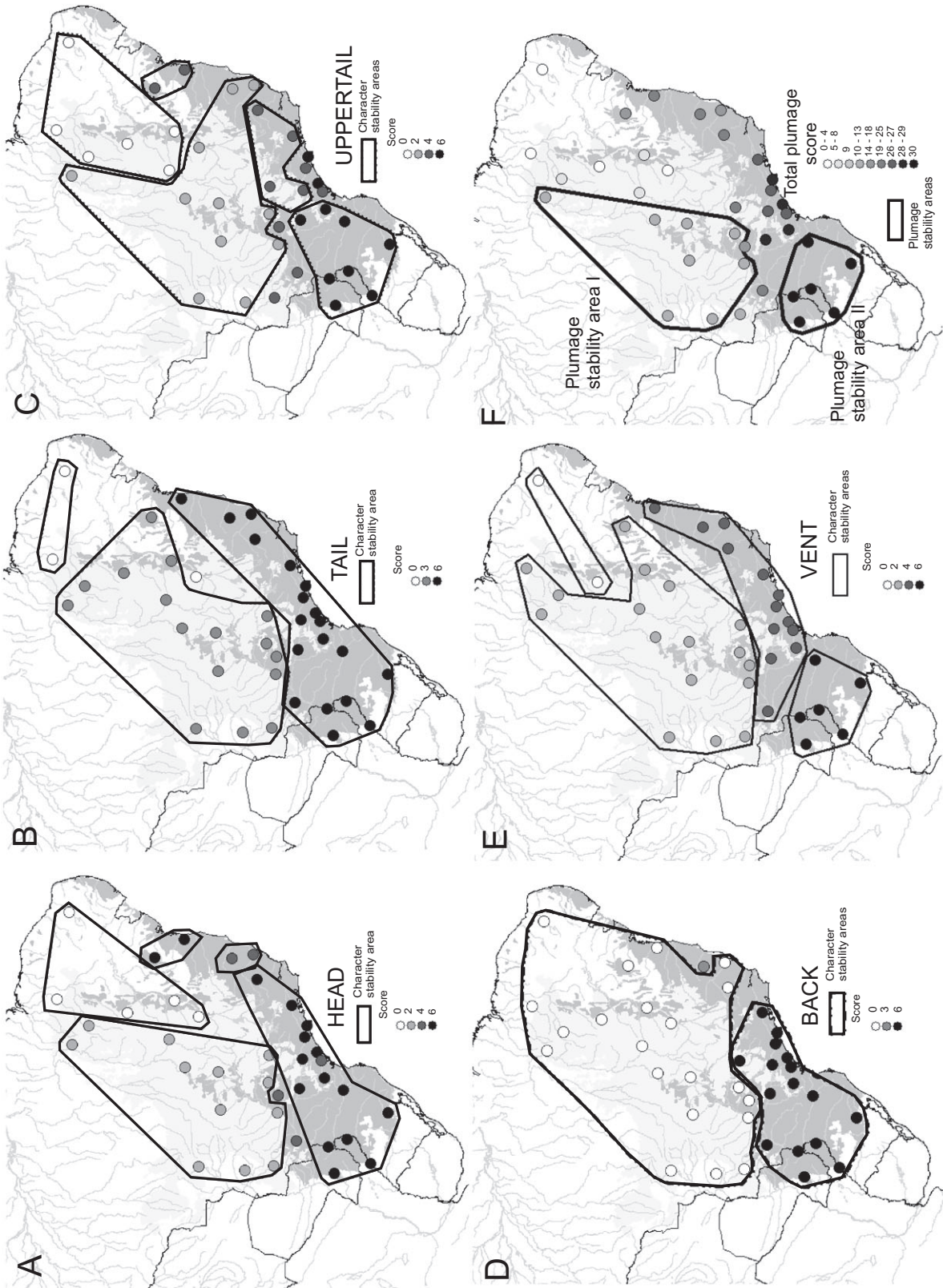
Figure 3. Geographical distribution of plumage variation in *Dendrocolaptes platyrostris*. Circles represent plumage units of analysis (population samples) and different levels of grey represent character states. A, B, C, D, E, single plumage characters. For a detailed description of character states, see Appendix (Table A1). F, areas of plumage stability obtained by overlapping A to E.

Table 1. Summary statistics of *Dendrocolaptes platyrostris* lineages based on the mitochondrial DNA control region

| | All samples | Populations | | |
		OVC	CAF	SAF
Sample size	43	19	13	11
Population diversity parameter, Θ (95% CI)	0.0395 (0.025–0.063)	0.0278 (0.015–0.051)	0.0072 (0.003–0.017)	0.0131 (0.006–0.030)
Nucleotide diversity, π (SE)	0.0168 (0.0031)	0.014 (0.003)	0.0042 (0.0015)	0.00116 (0.0024)
Tajima's D	–0.03438	–0.02490	–0.94334	–0.25745
R^2	0.1101	0.1266	0.1206	0.1382*

*$P < 0.05$. Significance determined based on 1000 coalescent simulations under a model of population stability using empirical sample sizes and estimates of Θ.

95% confidence intervals (CI) are shown within parentheses. For configuration of populations, see Fig. 3.

OVC, open vegetation corridor; CAF, central Atlantic forest; SAF, southern Atlantic forest.

of the gene genealogy of the whole population, respectively. Therefore, our gene samples are suitable for the subsequent studies.

We evaluated the relative diversity of cyt *b* and of CR in a subsample of 31 individuals. Θ for CR was 0.0395 [95% confidence interval (CI) = 0.025–0.063] and for cyt *b* was 0.005843 (95% CI – 0.003–0.0105). The ratio was $\Theta_{RC}/\Theta_{cyt\,b} = 6.76$. Because we used the same individuals for this analysis, the ratio $\Theta_{RC}/\Theta_{cyt\,b}$ indicated that the mutation rate at the CR of *D. platyrostris* was approximately 6.7-fold higher than the rate for cyt *b*, in accordance with rates of change described for mtDNA control region of other birds (Ruokonen & Kvist, 2002). Therefore, we selected CR for the phylogeographical analyses because it was more variable than cyt *b*.

Even though we studied four species of a total of five (Marantz *et al.*, 2003), *D. hoffmannsi* was not sampled, our analysis supported *D. platyrostris* as being monophyletic. The phylogeny grouped *D. platyrostris* and *D. picumnus* as sister taxa (Fig. 4A), in agreement with plumage and morphology (Raikow, 1994; Marantz & Patten, 2010). Subspecies were not supported as monophyletic. The concatenated Bayesian phylogeny did not resolve well the basal node of *D. platyrostris*. This may have occurred because CR sequences were only available for *D. platyrostris*. We repeated the Bayesian phylogeny only using cyt *b* and confirmed the results obtained with the other two methods. *Dendrocolaptes platyrostris* appears to be a young species, as inferred by the moderate intraspecific differentiation (cyt *b* TN 93 + G distance of 0.47% at the basal node; approximately 0.22 Mya) and to the proximity to *D. picumnus* (TN 93 + G cyt *b* distance of 3.35%; approximately 1.6 Mya), in contrast to results obtained with other endemic passerines that are older species (Pessoa *et al.*, 2006; Cabanne *et al.*, 2008; d'Horta *et al.*, 2011). The low sequence variation within this species relative to the congeners that we

studied suggests that we sampled the existing variation in *D. platyrostris*. Some intraspecific nodes of the phylogeny are weakly supported. This result was expected because the phylogenetic hypothesis was obtained with approaches developed to reconstruct interspecies relationships and many of the assumptions of these methods are violated by intraspecific datasets, which may result in low phylogenetic resolution (Crandall & Templeton, 1996; Posada & Crandall, 2001). Networks are more suitable for intraspecific datasets because they cope with population-level phenomena (i.e. ancestral and derived sequences present in the sample) that traditional species tree methods do not (Posada & Crandall, 2001).

The CR network, which presented 26 haplotypes, in conjunction with the phylogeny, indicated the existence of three main mtDNA lineages in *D. platyrostris* (Fig. 4A, B). The AIS analysis denoted two main genetic barriers: one between the open habitat and the AF and the other one within the AF (Fig. 4C). The genealogical analysis in conjunct with the AIS study indicated the existence of three regions with genetic identity, or lineages: the open vegetation corridor, the central AF, and the southern AF. Most sequences of central AF have an interior localization and multiple connections in the network, which are both conditions that, according to predictions of the coalescent theory, suggest that this lineage is ancestral (Posada & Crandall, 2001). Summary statistics for those lineages are presented in Table 1. The existence of the three lineages was further corroborated by the analysis AMOVA (Table 2); AMOVA I showed substantial structure among the three regions. In addition, AMOVA II showed structure between habitats, in accordance of the predictions of Figure 2B. AMOVA analyses III and IV showed that structure within the AF is higher than in the open habitat.

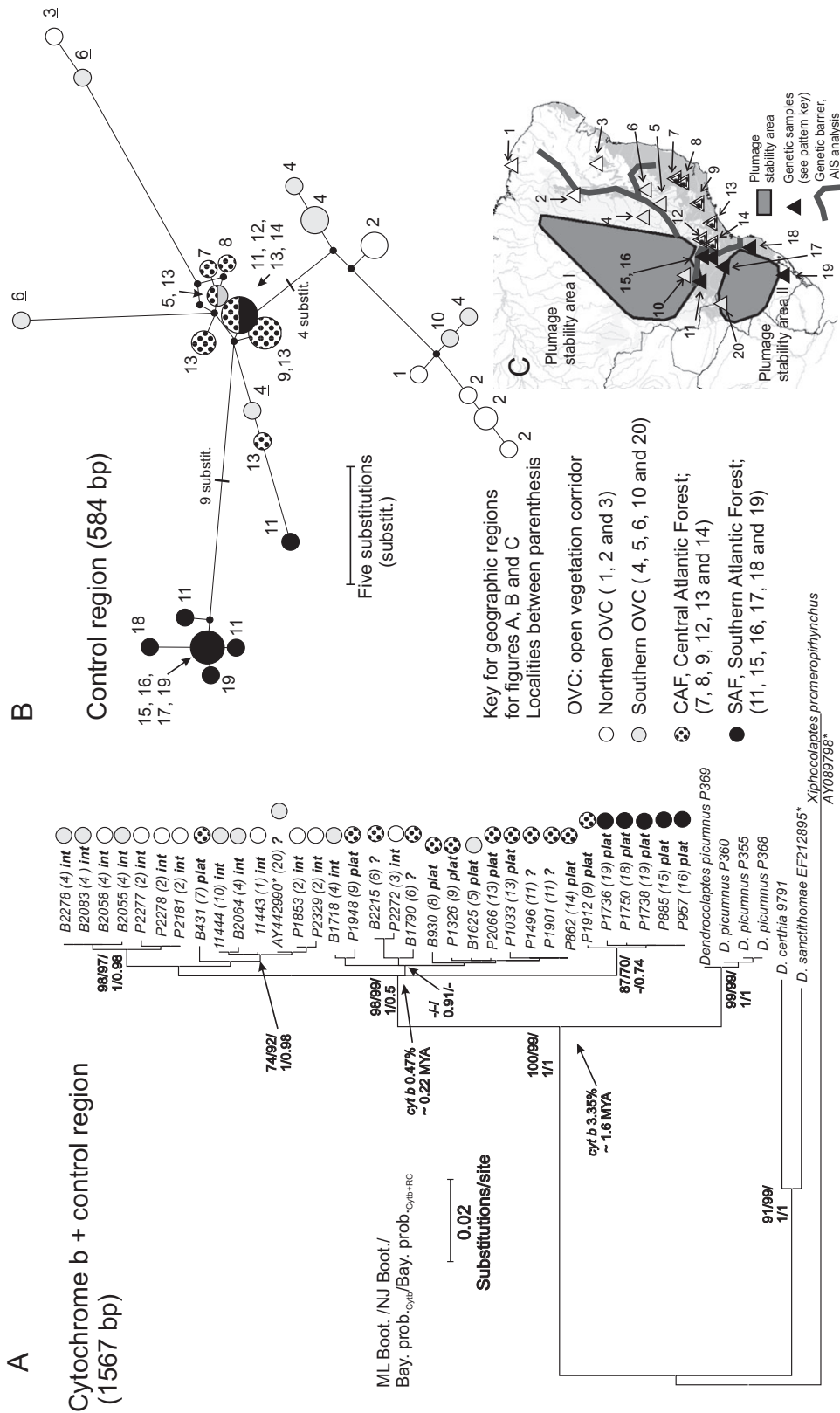The lineage of the open vegetation corridor was associated with the plumage stability area I and

Figure 4. A, maximum likelihood phylogenetic tree based on concatenated cytochrome *b* (cyt *b*) and mitochondrial (mt)DNA control region of *Dendrocolaptes platyrostris* and closely-related species. *int*, *Dendrocolaptes platyrostris intermedius*; *plat*, *Dendrocolaptes platyrostris platyrostris*. Model: HKY + I (I = 0.65) + G (α = 0.8421), Tr/Tv ratio = 11.066. Estimated base frequencies: A = 0.296., C = 0.303, G = 0.130, T = 0.269. Support values at nodes: maximum likelihood ×500 bootstrap/Neighbour-joining ×500 bootstrap/Bayesian probability analysis with cyt *b* + CR. Bootstrap > 70 and Bayesian probabilities > 0.5. Divergence time obtained using cyt *b* corrected distances and 2.1% of divergence/MYr. Numbers within parenthesis indicate sampling locality (Fig. 1; see also Appendix, Table A2). Distribution of samples by region is also shown. B, median-joining network based on the mtDNA control region of *D. platyrostris*. Numbers indicate the sampling localities of Fig. 1 and the Appendix (Table A2). Numbers that are underlined represent localities at the open habitat-forest ecotone. C, location of plumage stability areas and the main genetic barriers inferred by analysis of mtDNA control region sequences in AIS, version 1.0 (Miller *et al.*, 2006).

Table 2. Analyses of molecular variance of *Dendrocolaptes platyrostris* based on 584 bp of the control region of the mitochondrial DNA

Analysis	Tested population structure	Φ_{ST} (95% confidence interval)
I, All study region	[OVC][CAF][SAF]	0.332 (0.23–0.41)*
II, AF versus OVC	[AF][OVC]	0.483 (0.38–0.58)*
III, within AF	[CAF][SAF]	0.752 (0.58–0.857)*
IV, within OVC	[Northen OVC] [southern OVC)]	0.329 (0.297–0.357)*

*Significant with Bonferroni correction, $P < 0.01$.
See configuration of populations in Fig. 3.
OVC, open vegetation corridor; CAF, central Atlantic forest; SAF, southern Atlantic forest.

subspecies *intermedius*. The other lineages were associated with the nominal subspecies and the AF. The CR network also denoted derived haplotypes that occur in the ecotone between the open habitat and the forest (e.g. localities 3 and 6; Fig. 4B). Those derived haplotypes may indicate a past range expansion of forest birds toward the open habitat, followed by a restriction of gene flow and divergence (Omland, Baker & Peters, 2006).

COALESCENCE ANALYSIS

Studies with IM and the Akaike (1985) criterion indicated that a model of isolation with migration was the best explanation for all the studied divergences (Table 3). Migration rates were moderate to high. Point divergence estimations were in the range 80 000–148 000 years, although their posterior distributions were flat at ends and did not reach likelihood zero (data not shown). This pattern may be consequence of lack of information about a specific divergence time because gene flow rates are high and therefore divergences are very shallow.

We simulated CR sequences under 12 different demographic scenarios to explore whether populations fitted the following four situations: (1) a single panmictic population; (2) three populations connected by gene flow without a specific data of divergence; (3) three populations that diverged together from an ancestral population (politomy); and (4) three particular hierarchical relationships among the three lineages. Seven models were rejected (for details on each model, see the Supporting information, Table S1). Specifically, simulations rejected the model of a single

panmictic population, the models of politomy, one model considering central AF and the open vegetation corridor as sisters, and all models where the open habitat and southern AF were sister populations. The two simplest models not rejected suggested that the open habitat, and the central and southern AF, are connected with low to moderate gene flow (migration rate interval 0–0.0001) without a specific divergence time period (see Supporting information, Table S1, models 2a and 2b).

Simulations supported *D. platyrostris* populations as being neither panmictic, nor indicating a specific divergence date. Even though IM analyses estimated point divergence times, their posterior distributions denoted a reduced amount of information regarding divergence dates (Table 3). Thus, we consider the results of both approaches to be in complete agreement. They have indicated a lack of information about a specific divergence time, possibly because gene flow rates might have been high for a long time. Relationships among the open habitat, and the central and southern AF, suggested in Figure 4 are not very strong because populations are closely related and because the study used a single marker. However, the simulation of sequences, an approach that considers stochastic variation in genealogies (Richards, Carstens & Knowles, 2007; Knowles, 2009), did reject a sister condition between the open habitat and the southern SAF, and supported models that considered the open habitat sister of central AF and southern AF sister of central AF (see Supporting information, Table S1). Even though simulations did not support a single relationship among populations, they corroborated what was suggested by the network (i.e. that central AF sequences were not derived) (Fig. 4B).

GENETIC VERSUS PLUMAGE VARIATION

Multiple Mantel tests indicated that genetic distances are moderately correlated with geographical distances and only marginally related to habitats transition (Table 4, analysis I). Other analysis indicated that plumage divergence was not correlated with genetic divergence but was substantially related to habitat transitions (Table 4, analysis II). The historical demographics analysis indicated that only the SAF clade presented evidence of past population expansion (Table 1). Specifically, the R_2 statistic is significant and the region SAF presented a low level of genetic diversity.

The relationship between plumage and genetic divergence within and between habitats indicated that, for a specific genetic distance, comparisons between habitats in most of the cases resulted in larger plumage divergences than comparisons within habitats (Fig. 5).

Table 3. Divergence time and migration between pairs of populations of *Dendrocolaptes platyrostris* based on the mitochondrial DNA control region and in a model of isolation with migration (Hey & Nielsen, 2004)

Analysis	Model	Migration (females/generation)	Φ (absolute substitutions)	Divergence time (years)	AIC
OVC × CAF	With migration	2.41 (0.52–10.42)	26.43 (17.01–42.57)	83 590 (29 900–240 000[aproximately])	2047.364
	No migration	Forced to be zero	44.3852 (31.00–62.00)	11 940 (3 980–22 800)	2048.606
OVC × SAF	With migration	1.87 (0.12–8.11)	36.30 (22.77–57.24)	84 318 (22 000–280 000[aproximately])	2156.752
	No migration	Forced to be zero	48.60 (32.87–72.15)	35 800 (16 000–61 000)	2159.05
CAF × SAF	With migration	1.97 (0.08–18.79)	22.34 (13.37–38.36)	148 000 (> 47 000)·	2152.53
	No migration	Forced to be zero	36.94 (22.65–54.88)	19 900 (7 600–36 500)	2153.718

Models with and without migration were contrasted by the Akaike information criterion (AIC). The model that minimized AIC was the best. Confidence intervals are HPD90. Maximum values of HPD90 tagged (approximately), or absent, indicate that the end of the posterior distribution was flat and did not reach likelihood zero. For properties of samples, see Fig. 3 and Table 1. OVC, open vegetation corridor; CAF, central Atlantic Forest; SAF, southern Atlantic Forest.

Table 4. Multiple Mantel tests in *Dendrocolaptes platyrostris* to analyze the correlation of genetic distances (DGEN) and plumage divergence (DPLUM) with geographical distances (DGEO) and habitat transitions (DHAB)

	Partial correlation coefficient (r)	P	R^2
Analysis I: DGEN in function of (DGEO, DHAB)			0.20
DGEN × (DGEO)	0.421	0.0003	
DGEN × (DHAB)	0.171	0.026	
Analysis II: DPLUM in function of (DGEN, DHAB)			0.56
DPLUM × (DGEN)	0.35	0.815	
DLUM × (DHAB)	0.662	0.0000	

Predictor variables are shown within parenthesis. DGEN is based on 584 pb of the mitochondrial DNA control region.

Figure 5. Relationships of plumage divergence versus mitochondrial DNA control region genetic distances of *Dendrocolaptes platyrostris* within and between habitats. TN 93: Tamura & Nei (1993). OVC, open vegetation corridor; AF, Atlantic Forest.

DISCUSSION

PLUMAGE COLOUR IN *D. PLATYROSTRIS*

The analysis identified two areas of phenotypic stability (Fig. 3). Birds from population I were lighter, less streaked, and associated with subspecies *intermedius*. Birds from population II were the darkest and were associated with the nominal subspecies. Both populations are associated with subspecies, although their geographical ranges are smaller than the subspecies ones (Fig. 1). Birds outside the phenotypic stability regions showed different combinations of characters, grading from population I to population II (Fig. 3). As suggested by the subspecific taxonomy, our results on plumage variation of *D. platyrostris* do not support the idea of continuity between the open vegetation corridor
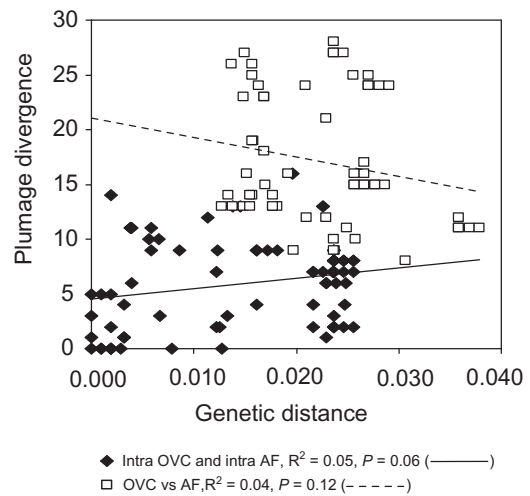
and the AF because each plumage type (populations I and II) is associated with each habitat. Plumage of *D. platyrostris* followed the rule of Gloger, which states that plumages in humid regions are darker and plumages in dryer regions are lighter (Zink & Remsen, 1986). The pattern is not only evident in the comparison Cerrado-Atlantic forest, but also the birds from the Catinga (an even dryer region) appear to be even lighter than in the Cerrado, thus making the pattern even stronger (Fig. 3F).

GENETIC PATTERN AND POSSIBLE ORIGIN

According to some studies, gallery forests in the open vegetation corridor act as corridors between the Amazonian and Atlantic forests (Costa, 2003). Under this

model, we expected to find no genetic divergence between contiguous populations in the forest habitat and in the open habitat (Fig. 2A), a prediction that was not supported for *D. platyrostris*. Even though the genetic divergence between habitats is shallow (Fig. 4), the phylogeographical gap is substantial ($\Phi_{ST} = 0.48$) (Table 2). This result was further confirmed by multiple Mantel tests, which indicated that habitat transitions, as well as geographical distances, are correlated with genetic differentiation (Table 4). Under the evaluated model of biogeographical continuity between the open habitat and the forest habitat, we expected to find no significant correlation between genetic distances and habitat transition. Also, the existence of population structure was supported by simulations that rejected models of panmixia.

Potential explanations for our findings are: (1) isolation and secondary contact along habitats transition or (2) divergence with gene flow (primary contact). We consider secondary contact unlikely because current and historical transitions between the open habitat and the forest habitat are gradual and occur over a latitudinal axis of thousand of kilometers (Fig. 1), and also because geographical landmarks (i.e. valleys, rivers or mountain ranges) that could have isolated both habitats do not exist. One scenario that would make vicariance and secondary contact plausible suggests that a small population could have been isolated in a forest relict, diverged in isolation, and then expanded to all the open habitat gallery forests. This model is known as the 'vanishing refuge' (Vanzolini & Williams, 1981; Moritz *et al.*, 2000). However, this hypothesis predicts signals of population expansion to be found in the open habitat, which were not found in the present study. Specifically, the R_2 test was not significant (Table 1) and no star-like genealogy was observed (Fig. 4B).

On the other hand, primary contact appears to be more likely not only because secondary contact was not very plausible, but also because the model was supported by the IM analysis. Under a scenario of divergence with gene flow, the habitat transition might be a partial barrier if populations acquired adaptations for their corresponding habitats. Characters favoured at the open habitat could have been negatively selected at the forests, and vice versa, which could have caused a partial barrier along the transition of habitats that, over the long term, was reflected by neutral markers such as the mtDNA (Norman *et al.*, 2007). A future study for further discrimination between vicariance and divergence with gene flow across the open and forest habitat transition may incorporate multiple independent markers aiming to analyze the distribution of migration events over time using the isolation migration model in IM. Currently, populations of the open habitat and of the central AF meet at the transition of habitats (Fig. 4). If this pattern was generated by vicariance followed by secondary contact, intense recent gene flow should be observed (Won & Hey, 2005; Niemiller, Fitzpatrick & Miller, 2008; Nosil, 2008). Otherwise, if the pattern evolved in parapatry, migration should be distributed homogeneously during the divergence period.

The results obtained in the present study are congruent with the few studies available on population genetic of birds from the open vegetation corridor (Bates, Tello & Silva, 2003; D'Horta *et al.*, 2008; Nodari, 2008). These studies suggest that those birds have a lower genetic differentiation among populations than do birds from continuous forests (Aleixo, 2004; Cheviron, Hackett & Capparella, 2005; Pessoa *et al.*, 2006; Nyari, 2007; Cabanne *et al.*, 2008). The population genetic structure of *D. platyrostris* in the open habitat was smaller than in the AF (Table 2), which would indicate different demographical processes in each habitat. Additional studies are needed in an attempt to explain this apparent difference.

EVOLUTION OF PLUMAGE: POPULATION HISTORY VERSUS HABITAT TRANSITIONS

We investigated whether plumage variation in *D. platyrostris* accompanied population histories, as evaluated by genetic divergences, or whether it could have been affected by other factors, such as differential selection associated with each habitat. Multiple Mantel tests indicated that genetic divergence did not affect plumage and that habitat transition was correlated with plumage variation (Table 4, analysis II). Furthermore, the relationship between plumage and genetic divergence always resulted in larger plumage divergences between habitats than within habitats (Fig. 5), supporting the predictions of Figure 2C. All these results are in accordance with what is expected for primary divergence of plumage.

Dendrocolaptes platyrostris at the open vegetation corridor was lighter and less streaked than at the forest habitat, representing a morph that is suggested to be an adaptation of woodcreepers for habitats with high luminosity levels, as are forests at the open vegetation corridor (Willis, 1992; Marantz, 1997). On the other hand, in continuous rainforest, individuals are darker and more streaked, and this is considered to be an adaptation for living in low luminosity and very humid conditions (Zink & Remsen, 1986; Willis, 1992; Marantz, 1997). For example, more melanic plumages are more resistant to feather degradation by bacteria that are abundant in humid habitats. Therefore, the results of the present study support the idea that the two regions of stable plumage of *D. platyrostris* may have evolved by divergent selection regimes between habitats.

The open vegetation corridor and its network of gallery forests and dry forests are contiguous with the Atlantic and Amazon forests. Our results support the idea that the two plumages types of *D. platyrostris* may have evolved by divergent selection regimes between habitats. There are several other species that occur in both habitats and might present a similar evolutionary story. For example, the pair of sister species *Thamnophilus ruficapillus* Vieillot (1816) and *Thamnophilus torquatus* Swainson (1825) (Brumfield & Edwards, 2007), which are mainly differentiated by plumage, may have diverged by selection in different habitats. *Thamnophilus ruficapillus* is the darkest and occurs in lower growth, borders, and secondary growth at AF and tropical Andes forests, whereas *T. torquatus* occurs in scrubs and lower growth at Cerrado and Caatinga. Females of both species are very similar. Another example might be the pair *Basileuterus culicivorus* Deppe (1830) and *Basileuterus hypoleucus* Bonaparte (1850). The former is the darkest and occurs in most of forested regions of the Neotropics, whereas the later occurs in forest borders and scrubs of the Cerrado. Both species are not reciprocally monophyletic (Vilaça & Santos, 2010); they hybridize (Robbins, Faucett & Rice, 1999) and plumage differentiation is subtle.

Intra-Atlantic forest biogeographical implications

The results of the present study are compatible with what is known about Atlantic forest evolution during the late Pleistocene (Cabanne *et al*., 2008; Carnaval & Moritz, 2008; Carnaval *et al*., 2009; d'Horta *et al*., 2011). Rainforests in the central region of the biome (i.e. Bahia, Espirito Santo, eastern Minas Gerais, and Rio de Janeiro) are proposed to be one of the most persistent during the climatic oscillations of the late Pleistocene, and apparently have acted as a refuge for forest organisms during the maximum of glaciations. Therefore, it is expected that populations of several forest specialist from that region were ancestral in relation to populations located in the periphery of the biome, such as the southern AF and the open vegetation corridor. This particular prediction is supported by the network and the simulations that positioned sequences associated with population central AF as the oldest population, and sequences from the open habitat and southern AF as the newest.

Dendrocolaptes platyrostris presented a mtDNA phylogeographical structure within the AF that resembles patterns described for other endemic taxa (Cabanne *et al*., 2008; Batalha-Filho *et al*., 2010; but see Mustrangi & Patton, 1997; Grazziotin *et al*., 2006; Pessoa *et al*., 2006; Carnaval *et al*., 2009; Fitzpatrick *et al*., 2009; Thomé *et al*., 2010; d'Horta *et al*., 2011).

The common pattern consists of the existence of two main mtDNA clades south of the Doce river that come into contact along no evident gene flow barrier in central-southern São Paulo (Fig. 4C). Some species present a third lineage, north of the Doce river. Another feature of the common pattern is that the corresponding southern populations present evidence of population expansion. In *D. platyrostris*, the southern AF population is the only one presenting evidence of past population expansion (Table 1). The existence of shared phylogeographical patterns suggests that common evolutionary events have affected an important proportion of the Atlantic forest taxa.

Several studies have proposed that the southern Atlantic forest region was dominated by grasslands during peaks of global glaciations. Palinology studies suggest that the forest southern limit shifted almost 750 km northward (Behling, 2002; but see also Prado & Gibbs, 1993). However, phylogeographical studies on AF organisms indicate the existence of endemic lineages to the southern portion of the biome (i.e. lineage southern AF of *D. platyrostris*; Mustrangi & Patton, 1997; Grazziotin *et al*., 2006; Pessoa, 2007; Cabanne *et al*., 2008; Carnaval *et al*., 2009; Batalha-Filho *et al*., 2010; Thomé *et al*., 2010; d'Horta *et al*., 2011), a pattern that suggest that this region maintained enough forest during the glacial maxima to avoid extinction of several forest organisms. Interestingly, many of these taxa are forest specialists, such as the passerines *Xiphorhynchus fuscus* Vieillot (1818) and *Sclerurus scansor* Ménétries (1835) (Cabanne *et al*., 2008; d'Horta *et al*., 2011). Thus, the results obtained in the present study, together with those of previous studies, indicate that the southern Atlantic forest may have been significantly affected by Pleistocene climatic alteration, although such events did not cause local extinction of most taxa, as occurred in other regions of the globe where forests were significantly affected by global glaciations (i.e. Europe; Hewitt, 2000).

Systematic implications

Do plumage stability areas I and II (Fig. 3), or the associated subspecies, deserve the status of species? Even though both plumage stability areas are diagnosable, a condition for considering a population as a full species according to the general lineage concept of species (de Queiroz, 1998; Aleixo, 2007), the genetic analysis sampled those areas only marginally and therefore did not demonstrate that they are reciprocally monophyletic (Fig. 4C). Reciprocal monophyly is another condition for considering populations as full species. Besides, both populations are connected by a large area of plumage transition across the open vegetation corridor–AF ecotone and along a large

track of AF (Fig. 3), indicating that they are evolutionary closely related. This close relationship is further demonstrated by the high gene flow rates that existed between regions (Table 3). The former considerations can also be made for both subspecies of *D. platyrostris*. They are neither reciprocally monophyletic, nor have stability of plumage. Thus, our results neither support plumage stability areas, nor subspecies as full species because they do not represent independent evolutionary lineages.

CONCLUSIONS

Despite the fact that the South American open vegetation corridor and the Atlantic forest are today physically contiguous and connected by gallery and dry forests, our results for *D. platyrostris* are not compatible with the idea that forest specialists in each region are linked at the population level. Different ecological conditions and selection in each biome might explain this result. Most of the plumage variation of *D. platyrostris* followed changes of habitat instead of population historical divergence, suggesting that selection might be directly related to the evolution of the plumage of this species. The results obtained in the present study do not support plumage stability areas, nor subspecies as full species because they do not represent independent evolutionary lineages. Further research with additional genetic samples and independent markers is needed to complement our findings.

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APPENDIX

Table A1. Studied plumage characters of *Dendrocolaptes platyrostris*

Characters (number of states)	Description of characters and states
HEAD (4)	Characteristics of contour feathers of the crown and nape. *State 0*, external (ext.) portion of the vane dark yellowish brown (10YR 3/3) and internal (int.) portion of the vane pale yellow (2,5Y 8/4) –ref. MZUSP 41640-. *State 2*, ext. vane very dark greyish brown (10YR 3/2) and int. vane pale yellow (10YR 8/2) –ref. MZUSP 72052-. *State 4*, ext. vane very dark grey (10YR 3/1) and int. vane white (2,5Y 8/8) –ref. MZUSP 72374-. *State 6*, ext. vane black (2,5Y 8/1) and int. vane as state 4 –ref. MZUSP 35465-. Heads with state 0 did not present strong streaks, whereas state 6 represented the most streaked heads.
TAIL (3)	Vane colour. *State 0*, yellowish–red (5YR 4/6) –ref. MZUSP 41640-. *State 3*, dark reddish–brown (5YR 3/4) -MZUSP 72374-. *State 6*, dark reddish–brown (5YR 3/2) –ref. MZUSP 35469-.
UPPERTAIL (4)	Uppertail-coverts. *State 0*, yellowish–red (5YR 5/8) –ref. MZUSP 41.640). *State 2*, yellowish–red (5YR 4/6) –ref. MZUSP 72.374-. *State 4*, background dark yellowish–brown (10YR 3/6) with three to four bars black (2,5Y 8/1) –ref. MZUSP 73767-. *State 6*, unbarred with background dark brown (7,5YR 3/4) and a black patch at the subterminal portion of feathers –ref. MZUSP 70204-.
BACK (3)	Mantle and back contours. *State 0*, no streaks, dark yellow–brown (10YR 4/4) –ref. MZUSP 41640-. *State 3*, no streaks evident, olive–brown (2,5Y 4/4) –ref. MZUSP 51859-. *State 6*, streaked, ext. vane dark brown (2,5Y 3/3) and int. vane white (2,5Y 8/8). Also, black mark at distal portion of internal vane –ref. MZUSP 35469-.
VENT (4)	Belly and flank contours. Varied from slightly barred to strongly barred. *State 0*, background olive–yellow (2,5Y 6/6) and fine bars dark olive–brown (2,5Y 3/3) –ref. MZUSP 41064-. *State 2*, background light yellowish–brown (2,5Y 6/4) and bars very dark greyish brown (2,5Y 3/2) –ref. MZUSP 72374-. *State 4*, background light olive–brown (2,5Y 5/3) and bars very dark greyish brown (2,5Y 3/2) –ref. MZUSP 35469-. *State 6*, colour as state 4 but bolder bars (thicker than 2 mm) –ref. AMNH 794072-.

Colours follow the Munsell Soil Color Charts (Munsell Color Company, 2000). Within parenthesis after each colour name are hue, value/chroma. ref., museum specimen taken as reference; MZUSP, Museu de Zoologia da Universidade de São Paulo, Brazil; AMNH, American Museum of Natural History, USA.

Table A2. Collection localities of *Dendrocolaptes platyrostris* and of other taxa for the genetic analyses, sample identification, vouchers, and locality of plumage data collection

Species	Locality (habitat)	Genetic data: sample size and tissue identification[TISSUE]	Vouchers for tissue samples[VOUCHER]	Plumage versus genetic comparison: plumage data, locality and sample size[PLUMAGE]
Dendrocolaptes platyrostris	1 – Ubajara, Ceará (CE). 3°51'S, 40°56'W (Caatinga)	N = 1. LGEMA 11443[B]	Photo[P]	Baturité, CE. 4°17'S, 38°55'W, N = 6
	2 – National Park (NP) Serra das Confusões, Piauí (PI). 9°40'S, 44°8'W (Caatinga)	N = 7. All LGEMA: P1853[M], P2181[M], P2277[M], P2278[M], P2329[M], P2379[M], P2431[M]	LFS 353[F] All MZUSP: 77719, 77720, 77721, 77722, 77723.	Locality: Idem genetic data. N = 7
	3 – Bonito, Bahia (BA). 11°56'S, 41°15'W (Caatinga)	N = 1. LGEMAP2272[B]	Photo[P]	Fazenda Mocambo e Iracema (Chapada Diamantina), BA. 12°25'S, 41°21'W. N = 3
	4 – Brasilândia de Minas, Minas Gerais (MG). 16°59'S, 46°0'W (Cerrado)	N = 6. B1718[B], B2055[B], B2058[B], B2064[B], B2083[B], B2278[B]		Arinus, MG. 15°55'S, 46°4'W, N = 3
	5 – Felixlândia, MG. 18°44'S, 44°48'W (Cerrado)	N = 1. B1625[B]		Excluded from the plumage versus genetic analysis
	6 – Bocaiúva, MG. 17°5'S, 43°48'W (Cerrado)	N = 2. B1790[B], B2215[B]		Excluded from the plumage versus genetic analysis
	7 – Simonésia, MG. 20°7'S, 42°00'W (Atlantic forest)	N = 1 B431[B]		NP Caparaó, Espírito Santo (ES). 20°26'S, 41°24'W. N = 3
	8 – Araponga, MG. 20°39'S, 42°32'W (Atlantic forest)	N = 1. B930[B]		NP Caparão, N = 3
	9 – NP Itatiaia, Rio de Janeiro. 22°25'S, 44°36'W. (Atlantic Forest)	N = 1. LGEMA P1326[B]	Photo[P]	Locality: Idem genetic data. N = 10
	10 – Três Lagoas, Mato Grosso do Sul. 20°46'S, 51°43'W (Cerrado)	N = 1. LGEMA11444[M]	GBN2[F]	Locality: Idem genetic data. N = 6
	11 – Morro do Diabo State Park, São Paulo (SP). 22°30'S, 52°18'W (Atlantic forest)	N = 5. All LGEMA: P1496[B], P1901[B], P1912[B], P1948[B], P1952[B]	Photo[P]	Locality: Idem genetic data. N = 2
	12 – Barreiro Rico, SP. 22°38'S, 48°13'W (Atlantic forest)	N = 1. P1696[M]	FMH 050054[F]	Victoria, SP. 22°46'S, 48°2'W. N = 3
	13 – Morro Grande State Park, SP. 23°42'S, 46°59'W (Atlantic forest)	N = 8. All LGEMA: P1033[B], P2066[B], P2480[B], P2520[B], P2544[B], P2553[B], P2668[B], P2699[B],		Eng. Ferraz, SP, 23°58'S, 46°36'W, N = 8

Locality	Tissue (genetic)	Voucher	Plumage
14 – Burí, SP. 23°39'S, 48°32'W (Atlantic forest)	N = 1. LGEMAP862[M]	MZUSP 75589	Locality: Idem genetic data. N = 1
15 – Pinhalão, Paraná (PR). 23°46'S, 50°3'W (Atlantic forest)	N = 1. LGEMAP885[M]	MZUSP 75622	Locality: Idem genetic data. N = 1
16 – Wenceslau Braz, PR. 22°5'S, 48°47'W (Atlantic forest)	N = 1. LGEMAP957[M]	MZUSP 75690	Locality: Idem genetic data. N = 1
17 – Ortigueira, PR. 24°12'S, 50°55'W (Atlantic forest)	N = 1. LGEMA11429[M]	GBN IIA092[F]	Locality: Idem genetic data. N = 1
18 – Rancho Queimado, Santa Catarina (SC). 27°40'S, 49°1'W (Atlantic forest)	N = 1. LGEMAP1750[B]		Hansa, SC, 26°26'S, 49°14'W, N = 3
19 – Arroio do Padre, Pelotas, Rio Grande do Sul (RS). 31°31'S, 52°23'W (Atlantic forest)	N = 2. LGEMAP1736[B], LGEMAP1738[B]	Photo[P]	Sinimbú, RS, 29°32'S, 52°32'W, N = 2
20 – San Antonio, Concepción, Paraguay. 23°33'S, 56°56'W. (Atlantic forest and Cerrado)	N = 1, Genbank AY442990 (Irestedt, Fjeldsa & Ericson, 2004)		Not considered
Dendrocolaptes picumnus	Amazonas, Brazil	N = 4. All LGEMA*: P355 (= LSUB 35687)[M], P360 (= LSUB 35704)[M], P368 (= LSUB 35727)[M], P369 (= LSUB 35728)[M]	
Dendrocolaptes certhia	Amazonas, Brazil	N = 1. LGEMA9791[M]	
Dendrocolaptes sanctithomae		N = 1. Genbank EF212895 (Weir & Schluter, 2007)	
Xiphocolaptes promeropirhynchus		N = 1. Genbank AY089798 (Aleixo, 2002)	

TISSUE – tissue type. B, blood; M, muscle. Tissue samples are deposited at the Laboratório de Genética e Evolução Molecular de Aves (LGEMA) of the Universidade de São Paulo (São Paulo, Brazil), at the Laboratório de Biodiversidade e Evolução Molecular (B) of the Universidade Federal de Minas Gerais (Belo Horizonte, Brazil), or at the Louisiana State University Museum of Natural Science (LSUB), Baton Rouge (USA). VOUCHER – P, photo available from authors; F, indicates collector and field number when specimens have not been catalogued. Collectors: LFS, Luis Fabio Silveira; GBN, Renato Gaban Lima; FMH, Fernando d'Horta. *Samples deposited in two collections. PLUMAGE – Whenever plumage data were extrapolated from the nearest location, this locality is given. Otherwise, the locality of the plumage data is the same locality of the genetic data.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Model parameters used to simulate genetic datasets under different demographic scenarios and to evaluate the goodness of fit of the observed mitochondrial DNA control region sequences of *Dendrocolaptes platyrostris*. Variables t_1 and t_2 represent divergence times (years). For models with two historical events (models 4a to 6b), t_1 is the most recent event and t_2 is the oldest event. Migration rates in proportion of the effective population that migrates each generation. Significance of combined *P*-values was evaluated at the 1% level, after using the sequential Bonferroni correction (Quinn & Keough, 2002). Rejected models are denoted with an italicized combined *P*-value.

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