Zoological Journal of the Linnean Society, 2022, **195**, 65–87. With 6 figures.

Taxonomic challenges posed by discordant evolutionary scenarios supported by molecular and morphological data in the Amazonian *Synallaxis rutilans* group (Aves: Furnariidae)

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Received 12 October 2020; revised 5 July 2021; accepted for publication 30 July 2021

Alpha taxonomy endeavours to propose a coherent vision of existing species and, simultaneously, to individualize the natural entities useful to understand evolutionary processes. This ideal is especially difficult when available data lack congruence. Here we address the polytypic species *Synallaxis rutilans* (ruddy spinetail), a suboscine passerine widely distributed in the Amazon Basin and whose taxonomy could, potentially, aid our understanding of processes shaping its biodiversity. Combining genetic [genomic ultraconserved elements (UCE) and mtDNA] and morphological data, we demonstrate that while delimitation of genetic lineages and their phylogenetic relationships are strongly associated with classic Amazonian geographic barriers, such as rivers, different coloration patterns appear to be more associated with local selection processes for phenotype. Employing an evolutionary approach, whereby the species is considered a taxonomic category, rather than a nomenclatural rank, we propose to recognize five species: *S. amazonica*, *S. caquetensis*, *S. dissors*, *S. omissa* and *S. rutilans*. The taxonomic arrangement proposed here permits better understanding of the similarities and differences among taxa from different areas of endemism, and represents patterns of genetic and morphological diversity resulting from distinct processes acting across certain time frames.

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This arrangement draws attention to the importance of understanding the evolutionary processes operating in the complex and constantly changing Amazonian landscape.

ADDITIONAL KEYWORDS: Amazon – phylogenetics – species delimitation – spinetail.

INTRODUCTION

The processes underlying the origin and diversification of Amazonian biodiversity are of considerable interest but remain poorly understood. Evaluation of these processes depends on sound taxonomic arrangements for use in assessment of the patterns that have shaped the distribution of the complex fauna and flora of the region. For example, areas of endemism among upland forest birds are often used as references for biogeographic studies or as targets for conservation (Haffer, 1969; Cracraft, 1985; Silva *et al.*, 2005; Naka & Brumfield, 2018), but defining these areas depends on how taxa are delimited. Timing of population divergence and establishment of phylogenetic relationships among taxa from different areas of endemism are now commonly used to understand the processes that have given rise to the staggering natural diversity of Amazonia (Ribas *et al.*, 2012, 2018; Smith *et al.*, 2014), but again these depend on how species are defined. Taxonomic studies, especially reviews of the alpha taxonomy of different Amazonian populations, are the unique means to define units of analysis that are the basis for inferring diversification processes and have the potential to enable more accurate biogeographic analyses, as well as to inform conservation policies for the region.

Although morphological approaches have performed an important role in the history of avian taxonomy, they do not adequately resolve the complexity underlying both the mechanisms of speciation and the decision-making processes of taxonomists (Raposo & Kirwan, 2017; Raposo *et al.*, 2017). This has led to several proposed strategies and approaches for making taxonomic decisions, associated with different sources of data and evidence. These approaches, often referred to as integrative taxonomy (e.g. Dayrat, 2005; Will *et al.*, 2005; Padial *et al.*, 2010; McKay *et al.*, 2014), are related to conceptual frameworks such as that of de Queiroz (2007) and have been applied to, supposedly, better reflect the multiplicity of factors relevant to taxonomy. However, such approaches do not dispense with a need to analyse on a case-by-case basis, otherwise they fail to reflect the idiosyncracies of species formation and maintenance in different organisms, and variability in the empirical data available in each case.

The *Synallaxis rutilans* group (Passeriformes: Furnariidae) is an avian lineage that might particularly benefit from an integrative taxonomic approach. Its distribution is confined to Amazonia and it has been potentially subject to many of the intricate patterns and processes governing this biome. However, in common with many Amazonian passerines, this group has a long taxonomic history with many subspecies having been described by early 20th century museum workers lacking relevant experience of vocal, behaviourial and biogeographic processes. Currently, the group comprises the species *Synallaxis rutilans* Temminck, 1823 and its nominotypical subspecies, and the following subspecies generally considered to be valid according to Peters (1951), Remsen (2003) and Dickinson & Christidis (2014): *Synallaxis rutilans omissa* E.J.O. Hartert, 1901; *Synallaxis rutilans amazonica* Hellmayr, 1907; *Synallaxis rutilans tertia* Hellmayr, 1907; *Synallaxis rutilans caquetensis* Chapman, 1914; *Synallaxis rutilans confinis* J.T. Zimmer, 1935; and *Synallaxis rutilans dissors* J.T. Zimmer, 1935. The first taxonomic analysis of this group was undertaken by Hellmayr (1907), who described two subspecies, *S. r. amazonica* and *S. r. tertia*, and lumped *S. omissa*, originally described as a species by E.J.O. Hartert (1901), within *S. rutilans*. Thereafter, three further subspecies were subsequently described: *S. r. caquetensis* by Chapman (1914) and *S. r. dissors* and *S. r. confinis* by Gyldenstolpe (1930). Although a number of systematic revisions of the group have been undertaken (Cory & Hellmayr, 1925; Gyldenstolpe, 1930; Peters, 1951; Vaurie, 1980), only the most recent works (Ridgely & Tudor, 1994; Remsen, 2003) have suggested that *S. omissa* could represent a separate species. Finally, none of the recent publications concerning evolution and relationships among the Furnariidae (Irestedt *et al.*, 2009; Moyle *et al.*, 2009; Derryberry *et al.*, 2011; Batalha *et al.*, 2013; Ohlson *et al.*, 2013; Claramunt, 2014; Tobias *et al.*, 2014) has included samples from the distributions of most subspecies of *S. rutilans*. An integrative taxonomic revision of this lineage is, therefore, sorely needed to clarify its systematics, as well as to characterize the patterns responsible for diversity within the group.

The objective of the present work is to present a taxonomic revision of the *Synallaxis rutilan*s group, using both morphological and molecular characters, employing a methodological approach to defining species limits via an integrative scenario based on the concept of taxognosis of Dubois & Raffäelli (2009). We also present a lectotype designation for *Synallaxis rutilans* Temminck, 1823.

MATERIAL AND METHODS

MOLECULAR DATA

Taxon sampling

We sampled 82 individuals of *Synallaxis rutilans* from throughout its distribution in the Amazon Basin (see Supporting Information, Table S1). All tissue samples relate to voucher specimens deposited in ornithological collections of the Museu Paraense Emílio Goeldi, Belém (MPEG), Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA), Lousiana State University Museum of Zoology, Baton Rouge (LSU), Museu de Zoologia da Universidade de São Paulo (MZUSP) and the American Museum of Natural History, New York (AMNH). These vouchers were analysed morphologically and they represent all of the morphotypes known in the group.

We obtained mtDNA sequences for all 82 individuals, but because the mtDNA behaves as a single locus and does not recombine, it fails to account for part of the lineage history. To obtain a genomic perspective on the relationships among the main mtDNA lineages and morphotypes detected, we also obtained genomic data using probes for ultraconserved elements (UCE) for 17 selected samples, including at least one sample per area of endemism (AE) and representatives of the morphological variation found in the group.

As outgroups, we used four specimens of *S. cherriei* Gyldenstolpe, 1930, the sister-species of *S. rutilans* according to Derryberry *et al.* (2011), for the mitochondrial dataset and four of *S. albigularis* Sclater, 1858 for the genomic dataset, as this was the phylogenetically closest species with UCE data available (see below).

DNA extraction and sequencing

DNA was extracted using the Wizard Genomic DNA Purification Kit (Promega) following the manufacturer's protocol. We used published DNA primers to amplify and sequence two mitochondrial genes (*COI*, cytochrome *c* oxidase subunit 1; *ND2*, NADH dehydrogenase subunit 2) (Sorenson *et al.*, 1999). Polymerase chain reaction (PCR) and sequencing reactions followed standard procedures. All sequences were manually checked and aligned using GENEIOUS v.R7.1.9 (Kearse, 2012). Based on preliminary analysis of the mtDNA matrix, we selected a subset of samples for subgenomic sequencing. We employed a capture sequence protocol using a probe set targeting 2321 loci of UCE (Harvey *et al.*, 2017). DNA extracts for selected samples were sent to Rapid Genomics (Gainesville, FL) for sequencing, which followed the standard protocol described in Faircloth (2012).

Phylogenetic analysis, dating and genetic distances based on mtDNA

To reconstruct phylogenetic relationships among all individuals we employed MrBayes 3.2.6 (Ronquist *et al.*, 2012). Both mtDNA genes were concatenated and the best partition scheme and substitution models were selected by PartitionFinder 2.1.1 using the Bayesian information criteria (BIC) (Lanfear *et al.*, 2017). Two parallel simultaneous runs were performed, for a total of 2×10^7 generations, with the trees being sampled every 1000 generations. To recover the time tree, we employed BEAST 1.8.2 (Drummond *et al.*, 2012), calibrating the tree using the time of diversification between *Synallaxis cherriei* and *S. rutilans* under a normal distribution in the prior tmrca (the most recent common ancestor) with mean 2.8 Myr and stdev 0.6 (Derryberry *et al.*, 2011). These diversification times were based in a multilocus approach (three mtDNA and three nuclear genes) for the Furnariidae (Derryberry *et al.*, 2011) and agree with fossil calibrated ages obtained in a larger phylogeny of the Tyranni (Harvey *et al.*, 2017). In addition, we also changed the ucld.mean prior from the default setting to a uniform distribution with initial value of 0.01, and lower distribution set to 0 and upper to 0.1, which roughly corresponds to the 2% rate of substation per million years expected for avian protein coding mtDNA regions (Weir & Schluter, 2008). Posterior distribution, effective sample size (ESS) values and burn-in to reach stationarity from both analyses were checked using TRACER 1.7 (Rambaut *et al.*, 2018). The haplotype network was obtained with TCS v.1.21 (Clement *et al.*, 2000). We calculated corrected genetic distances using MEGA 6 (Tamura, 2013).

Ultraconserved elements (UCE) processing and analyses

Raw data were processed via the Phyluce script pack (Faircloth, 2016) (Supporting Information, Table S1). Raw sequences were cleaned for adapter contamination and low-quality reads using illumiprocessor (Faircloth, 2013) and Trimmomatic (Bolger *et al.*, 2014). We assembled the clean reads employing the Trinity RNASeq assembler r2013311110 (Grabherr *et al.*, 2011) with a *de novo* method. UCE loci were identified in the contigs assembled by Trinity after a comparison with the UCE probes used to capture DNA fragments. To recover the phylogenetic relationships among these samples we performed a maximum likelihood analysis in RAxML v.8.2 (Stamatakis, 2014) and Bayesian inference analyses in ExaBayes v.1.4 (Aberer *et al.*, 2014), using the concatenated matrix with three treatments for missing data: a complete matrix, in which only loci shared by all individuals were used; and two matrices where missing data were allowed, namely a 95% and 75% complete matrix. This allowed inclusion of loci shared by at least 95% or 75% of individuals, respectively. The maximum likelihood

tree was obtained using RAxML by searching the best tree and then recovering the bootstrap support for each node using the autoMRE algorithm. Bayesian inference was performed in two parallel runs, for a total of 2×10^7 generations. *Synallaxis albigularis* was used as the outgroup.

Morphological data

We analysed 477 specimens (247 males, 188 females, 41 unsexed) at 29 different institutions, including the syntypes, holotypes and paratypes of all taxa in the *Synallaxis rutilans* group. The complete list of analysed material is presented in the Supporting Information Table S1. All biometric data and analyses of plumage coloration were made by the first author (R.S.).

Specimen material was analysed both with respect to morphometrics and plumage coloration. Morphometric data sampled were: bill length (exposed culmen, from the feathers to the tip) and depth (at the nares); wing length (relaxed chord); and tail length (of the central pair of rectrices). The first three measurements were taken using electronic callipers (accurate to 0.05 mm) and the last using a metal ruler (accurate to 0.1 mm) and by counting the number of rectrices.

The software *Statistica 12* (StatSoft, 2013) was used to generate descriptive analyses (means, standard deviation, minimum and maximum values), a principal component analysis (PCA), multivariate analysis of variance (MANOVA) and Scheffe test (post hoc), observing the normality and homoscedasticity (Levene's test) assumptions of the data. A significance level of 5% was adopted in all of our analyses. To be considered a morphometric character diagnostic between species, a given feature must represent a separate state and, in the case of continuous variables, there must be no overlap between their ranges (i.e. maximum and minimum values).

Plumage analysis used Smithe's chart (1974, 1981) to define colours. We scored the coloration of 12 different feather tracts, namely: the throat; breast; abdomen; flanks; forehead; crown; supercilium; face (including malar/ear-coverts/cheek); back; rectrices; wing-coverts; and remiges (following the topography of Proctor & Lynch, 1993: 49, 51). When two different colours could be identified, the 'first colour' named is the main colour and the 'second colour' preceded by the symbol '±' (meaning more or less present) the subsidiary colour, with more variation. Unsexed specimens, juveniles and those in moult and/or damaged, were not considered in the analyses.

Smithe (1974, 1981) refers to colours using codes and names, and for some colours (only in the 1974 edition) hue, value and chroma measurements are presented. The codes used by Smithe (1974, 1981) consist of numbers (and sometimes associated letters), but there is no quantitative relationship between the numbers and colours. In turn, hue, value and chroma measurements are little used in the technical literature. These measurements were made using a spectrophotometer and are presented only for the colours in the 1974 edition. We sought to transform colours into numbers that reflect the differences between them, which in turn might enable a more detailed analysis and comparison of the plumage of the analysed specimens. Considering the discussion in Smithe (1974), the *Naturalist's color guide* (Smithe, 1974, 1981) was subject to spectrophotometry analysis. The copies of Smithe (1974, 1981) used to analyse specimens were visualized using an Ocean Optics USB 2000 + UV-VIS spectrophotometer under controlled conditions. Three measurements of each colour in the catalogue were made and their arithmetic mean generated, as within each patch of colour there is some variation, presumably due to printing irregularities. The resultant mean values were subject to Pavo R package (Maia *et al.*, 2013), which calculated 23 colorimetric variables for each patch. As the objective of this analysis was to compare different colours, saturation, hue and brightness were all measured, i.e. the same variables used by Smithe (1974) to refer to colours in his catalogue. Finally, after logging base 10 for brightness and hue, the summed value of the three variables replaced the reference number of each catalogue colour identified for each feather tract on each specimen. The values of all feather tracts were summed for each individual, to reach a total value for the colours of each specimen. This permitted us to create a quantitative identity for each individual.

The program QGIS 2.4.0 (QGIS Development Team, 2014) was utilized to generate the maps and all specimen data were georeferenced based on the original label information and, in some cases, using the geographical coordinates in Paynter (1982, 1997), Stephens & Traylor (1983, 1985), Paynter & Traylor (1991) and Vanzolini (1992).

Finally, we must mention the specimens collected in Brazil by the Olalla family (Carlos Olalla and his sons, Alfonso, Ramon, Manuel and Rosalino), which are principally held in the American Museum of Natural History, New York. Although there has recently been an effort to resolve questions concerning the accuracy of the label data associated with Olalla specimens (Wiley, 2010), there are still problems regarding their localities. As already reported (e.g. Vaurie, 1965, 1967), this issue becomes even more problematic when attempting to correctly define on which bank of an Amazonian river a specimen was actually collected. Consequently, specimens collected by the Olalla family were examined but excluded from

our analyses. A detailed work on the Ollala collection is being prepared by R.S., to provide a critical revision of the data related to the *S. rutilans* group, precisely to identify the localities and collection dates.

Distance matrix analyses

Correlations between geographical, phenotypic and genetic distances were tested considering each individual analysed. A Mantel test (Mantel, 1967) was performed for peer-to-peer comparisons, based on a Pearson correlation coefficient and significance level of 5%. Partial Mantel tests were also performed to evaluate the correlation of genetic/phenotypic distance and geographic distance between populations, in this case defined using the clades resulting from the cladistic analysis identified by the areas of endemism with which they are associated. The Mantel test was performed using the XLSTAT 19.02 program (Addinsoft, 2017).

Geographic distance was calculated using Geographic Distance Matrix Generator 1.2.3 (Ersts, 2017). Phenotypic distance was calculated based solely on plumage data. Morphometric data were excluded from phenotypic distance analysis given the absence of data for many specimens due to damaged parts, especially the loss of the central rectrices, compromising tail length. Concerning genetic distance, see 'Phylogenetic analysis, dating and genetic distance' above.

Taxonomy

Taxognosis

Dubois & Raffaëlli (2009: 15) proposed 'taxognosis' as a general term for taxon definition, and this concept is adopted herein to define specific limits in the *Synallaxis rutilans* group. To present our hypothesis of taxognosis in the *S. rutilans* group we use an evolutionary approach whereby the species is considered a taxonomic category rather than a nomenclatural rank. According to Dubois (2017: 65) 'A taxonomic category is a set of taxa that share certain biological, historical or other particularities', whereas '. . . nomenclatural rank is a level in a hierarchy of taxa'. This use of species is appropriate for the purpose of evolutionary study and biodiversity conservation.

Faced with a complex and dynamic evolutionary scenario, and in order to make taxonomic decision-making as objective and replicable as possible, a species delimitation method was developed following Dubois (2017) who described taxognosis considering two main types: *physiognosis*, as a taxognosis that does not refer to a cladistic hypothesis; and *cladognosis*, as taxognosis that refers to a cladistic hypothesis.

Regarding physiognosis, the first criterion is represented here by the presence or absence of a 'diagnosis' defined in Dubois (2017: 71), but used with modifications, as follows: morphological characters that are shared by all members of the taxon and absent in all non-members, independent of any cladistic hypothesis. In cases of the presence of diagnosis, the score attributed to the taxon was equal to 1, and in case of absence the score was –1. A second criterion is based on DNA and is related to Bayesian inference considering presence (1) or absence (–1) of genetic structure in the genomic data.

Considering cladognosis, we used the coinognoses defined by Dubois (2017: 71) as 'a cladognosis based directly on the hypothesised cladistic relationships between taxa, without explicit reference to characters or character states'. The coinognosis in this study was based on presence (1) or absence (–1) of phylogenetic structure based on mtDNA corresponding to areas of endemism. A second criterion is based on morphological characters and called 'mapping tree'. This criterion is based on plumage data mapped to a phylogenetic tree (resulting from mtDNA analysis). The score attributed to the taxon was equal to 1 when the character state is shared by all members of the clade and absent in all members of its closest sister-group, but not necessarily absent in all other non-members.

The analysed groups were defined from geographical distribution of the clades obtained by phylogenetic analysis and their relation to areas of endemism. The definitions listed above are summarized in Table 1. After performing the analysis described above, the following formula was applied to equalize the weight of the values between physiognosis and cladognosis, and to restrict the results between –1 and 1 ($-1 \leq x \leq 1$), where: $\sum$, summation; Ph, physiognosis; Cl, cladognosis; *N*, number of features.

$$((\sum \mathrm{Ph})/N\mathrm{Ph}) + (\sum \mathrm{Cl})/N\mathrm{Cl}))/2$$

After applying the above formula, two scenarios for taxognosis were considered: negative results ($-1 \leq x < 0$) *without* specific recognition; and equal to zero or positive results ($0 \leq x \leq 1$) *with* specific recognition. These parameters were established because negative results occur when just one aspect among all traits considered is present in the analysed clade. On the other hand, zero or positive results are those where at least the totality of the physiognosis or cladognosis traits analysed are present.

Among clades considered species and those without taxonomic recognition there is the possibility of different values (between –1 and 1) which permit this information to be used in decision-making; for example, to define conservation or management units. These may differ from the taxonomic categories defined herein, albeit without the need to modify alpha taxonomy of the group as discussed by, among others, Tobias *et al*. (2010).

Table 1. Methodological approach used for taxognosis of the *Synallaxis rutilans* group

Categories	Subcategories	Data	Features (*N*Fea)
Physiognosis (Ph)	Diagnosis	Plumage and morphometry	Morphological analyses
	Bayesian inference	nuclearDNA	Genetic structure
Cladognosis (Cl)	Coinognosis	mtDNA	Phylogenetic structure
	Mapping tree	Plumage	Morphological analyses

Taxonomic data

Concerning presentation of taxonomic data, the list of synonyms proposes to present strictly nomenclatural information, and is based on Dubois's (2000: 58) definition of synonymy *sensu stricto*, i.e. '. . . a list of nomina and references including only the original morphonym of a nomen in the original publication where it was first made nomenclaturally available with their authors and dates.'

The diagnoses presented for the species defined as taxonomic categories are not, of necessity, linked to a cladistic hypothesis and are not restricted to comparison with the nearest group as defined by the phylogenetic analysis, as is commonly the case in new species descriptions (e.g. the 15 new species described in del Hoyo *et al.*, 2013). In this sense, the diagnosis presented here for each taxon follows the definition already used in the context of the taxognosis which is '. . . based on character states that either are considered to be differential for the taxon, i.e., shared by all members of the taxon and absent in all non-members, or the variable combination of which is differential (in cases of polythetic diagnoses)' (Dubois, 2017: 71). It is important to note that the diagnoses presented fulfil, as far as possible, the role of being intentional, relevant, objective and non-arbitrary, as proposed by Simpson (1961) and highlighted by Dubois (2017) as characteristics necessary for diagnoses used in pattern-based taxonomy. In addition to the diagnosis, complete morphological descriptions of the taxa considered valid are also presented, including variations within the analysed populations. For distributional data, we used Dickinson & Christidis (2014), where necessary complemented by data from the analysed material.

RESULTS

MOLECULAR DATA

MtDNA phylogeny and haplotype networks

We sequenced 994 base pairs (bp) for the *ND2* gene, and 545 bp for *COI* of all individuals. The best model of sequence evolution was HKY+G for *ND2* and HKY+I for *COI*. MrBayes and BEAST analyses recovered the same topology, i.e. monophyly of *Synallaxis rutilans* with seven geographically structured lineages distributed across known Amazonian areas of endemism (Cracraft, 1985; Silva *et al.*, 2005). The tree topology recovered two major groups, north and south of the Amazon River (Fig. 1). The northern group, with moderate support (posterior probability, PP = 0.9) comprises two lineages: one east of the Negro River, in the Guiana AE (individuals 1–17), and the other west of the Negro River, in the Napo AE (individuals 18–22). The southern group, which is well supported, includes two clades, separated by the Xingu River. The eastern clade is further subdivided by the Tocantins River, in the Xingu AE (individuals 23–25) and Belém AE (26–30). The western clade is subdivided by the Madeira, in the Inambari AE (individuals 31–49), and then by the Tapajós River, in the Rondônia AE (individuals 50–64) and Tapajós AE (individuals 65–82).

Diversification events among the lineages commenced in the Pleistocene 0.91 Mya [95% highest posterior density (HPD) = 0.51–1.42 Mya], followed by the split of the Guiana and Napo lineages 0.72 Mya (0.4–1.15 Mya). South of the Amazon River, the first split occurred 0.67 Mya (0.38–1.07 Mya), followed by diversification of the Inambari lineage 0.48 Mya (0.26–0.77 Mya). The last two diversification events occurred almost simultaneously, with the Belém and Xingu lineages splitting 0.39 Mya (0.19–0.66 Mya) and those in the Tapajós and Rondônia AE 0.36 Mya (0.18–0.58 Mya).

The statistical parsimony (TCS) analysis recovered three different networks, representing lineages found in the Guiana AE, Napo AE and one connecting all lineages south of the Amazon River. All populations, except for the Guiana, Xingu and Belém, show evidence of recent expansion, with one or two haplotypes being shared by most individuals and several 'satellite' haplotypes.

Ultraconserved elements (UCE) data and phylogenetic inference

We recovered 1543 loci for the complete matrix, with a mean locus length of 599.55 base pairs, and a total of 5972 parsimony informative (PI) sites, or a mean of 3.87 PI sites per locus. The incomplete matrices, 95% and 75%, respectively, possess 2079 and 2269 loci, with mean locus length of 594.5 and 588.25 base pairs, and

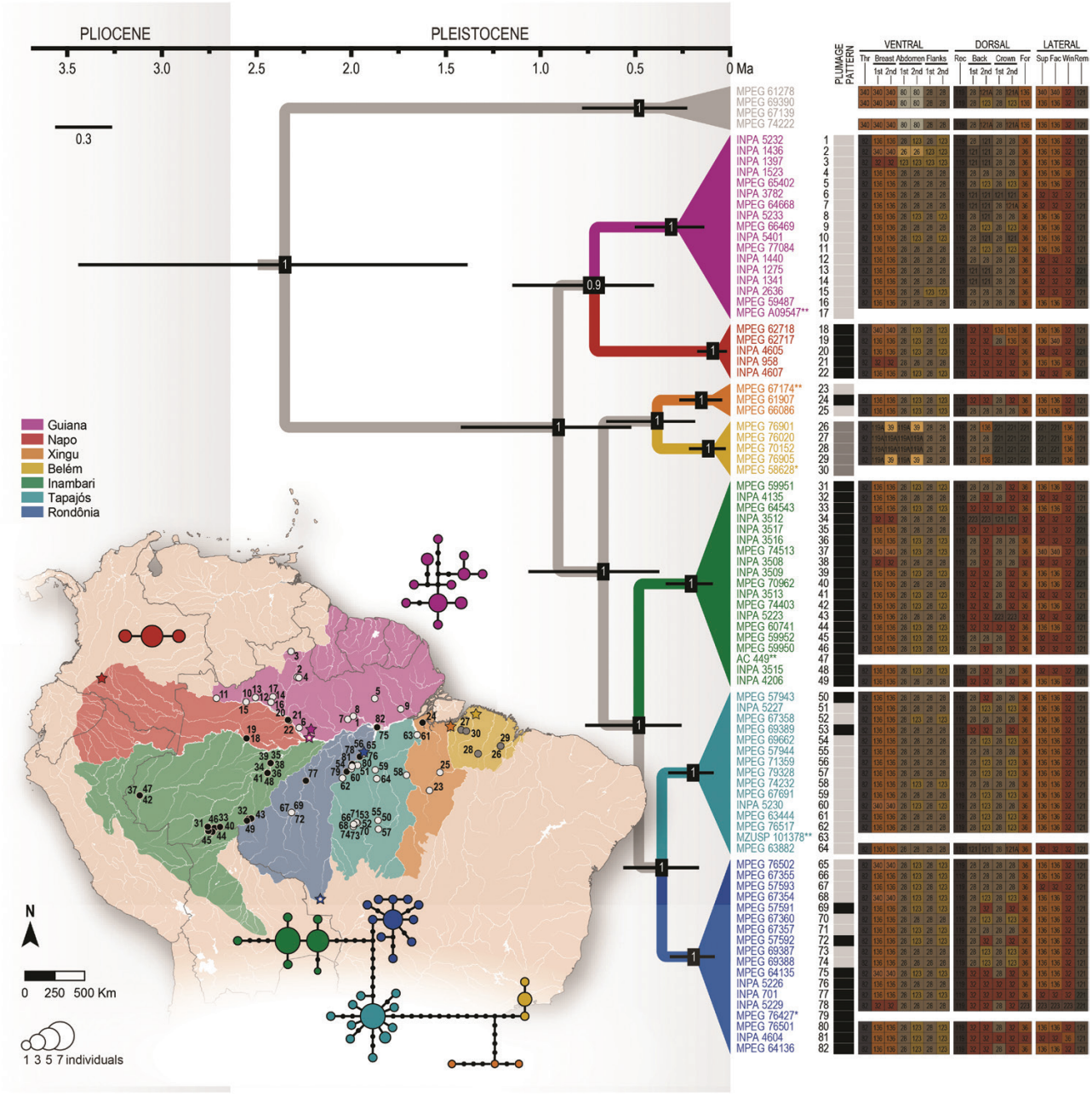

Figure 1. Map showing the distribution of sequenced individuals, phylogenetic time tree and plumage analyses for the *Synallaxis rutilans* group. The areas of endemism recognized by Silva *et al.* (2005) are highlighted on the map, and distribution points are numbered in accordance with individuals in the tree. The phylogenetic time tree is based on 1539 bp of concatenated *ND2* and *COI* genes. Posterior probability values and the 95% HPD are indicated at each node. Thr, throat; Rec, rectrices; For, forehead; Sup, supercilium; Fac, face; Win, wing-coverts; Rem, remiges; 1st, first colour (main colour); 2nd, second colour (variation ±); 36 (e.g.), colours in Smithe's catalogue; *, specimen damaged or immature; **, specimen analysed without Smithe's catalogue; MPEG A, spirit collection specimen; dark grey circles in map and patches in table, specimens with grey plumage pattern; light grey circles and patches, specimens with olive plumage pattern; black circles and patches, specimens with rufous plumage pattern; purple star, type locality of *S. r. dissors*; red star, type locality of *S. r. caquetensis*; red star with white spot, type locality of *S. r. confinis*; blue star, type locality of *S. r. amazonica*; blue star with a white spot, type locality of *S. r. tertia*; orange star, type locality of *S. r. rutilans*; yellow star, type locality of *S. r. omissa*.

a total of 7961 and 8602 PI, with a mean of 3.83 and 3.79 per locus.

Topologies and bootstrap support were similar for all analyses of all matrices (Supporting Information, Figs S1, S2). All mtDNA lineages represented in the UCE dataset by more than one individual were recovered with high support in all analyses. Phylogenies obtained using the UCE dataset agree with the mtDNA analysis in recovering well-supported clades north and south of the Amazon River, with the northern clade comprising four individuals in two distinct lineages, the Guiana AE and Napo AE. Within the southern clade, the UCE topology corroborates the sister-group relationship between individuals from the Xingu and Belém AE with high support (Supporting Information, Figs S1, S2). Relationships among the remaining southern lineages were poorly resolved (Supporting Information, Figs S1, S2). Thus, the genomic dataset corroborates the principal relationships recovered by the mtDNA analysis, indicating that no widespread gene-flow has occurred since the origin of the mtDNA clades that might homogenize phenotypes and disrupt phylogenetic signal in the genomic dataset, a situation that has been observed in other Amazonian species complexes (Thom *et al*. 2018).

Morphological data

Morphometric data

For the morphometric data analysis, the clades obtained in the cladistic analysis were considered as groups and named according to the areas of endemism. The data are presented according to the clade sequence of the cladistic analysis (Fig. 1). We found significant differences, albeit not diagnostic, among clades. The data are not diagnostic due to overlap between the range of values for all of the variables analysed. However, it bears mention that according to the descriptive statistical analysis presented in Table 2, maximum values were always recorded in the Belém AE.

Despite the lack of diagnosability, the MANOVA revealed that the morphometric data differ significantly (F (24.890) = 7.25, P < 0.001) among different populations/clades resulting from the mtDNA analysis. A Scheffe test, undertaken subsequently, indicated that bill length is significantly longer in the Belém AE, compared to all other areas (P < 0.03), except the Xingu (P = 0.59); and that tail length is significantly shorter in the Napo AE versus all other areas (P < 0.01). It is also noteworthy that the MANOVA indicated significantly different data for males versus females (F (4250) = 4.64, P = 0.001), with males having deeper bills (P < 0.001) and longer wings (P = 0.002), according to the Schefee test, undertaken a posteriori. Figure 2 illustrates the PCA, used as an exploratory analysis of the data, wherein the first two components (Factors 1 and 2) were responsible for 64.6% of the variation, with wing length (83%) the variable that most contributes to explain variation in Factor 1 data, whilst tail length (70%) most contributed to explain variation in Factor 2 data. Figure 2 highlights the morphometric data of the Napo population area with unrestricted distribution, but concentrated in the lower-left quadrant, with variation distinct from the other populations, whose distributions are not restricted but are focused on the upper and lower right quadrants.

Plumage data

Three colour patterns were identified: grey, in which the forehead, supercilium and face are Vandyke brown (221); olive, wherein the crown and back possess olive tones (dark brownish olive, 129; raw umber, 123), offering a clear contrast between the crown and the forehead, as well as the supercilium and face, which are reddish brown (forehead, supercilium and face amber, 36 or chestnut, 32); and rufous, in which the crown and back are chestnut (32), showing practically no contrast with the amber (36) forehead and amber (36) supercilium and face (see Figs 1, 3; Table 3).

Grey-patterned birds do not show any trace of rufous on the head (forehead, supercilium and face) and 100% of analysed specimens from the Belem AE are so characterized. This pattern does not occur in any other area and there are no intermediates. The olive pattern characterizes 100% of specimens analysed from the Guiana area of endemism, but unlike grey-patterned birds, specimens with the same morphological pattern do occur in other areas of endemism. The rufous pattern characterizes 100% of specimens analysed from the Napo AE but, like the olive pattern, specimens with the same morphology occur in other areas of endemism, including in sympatry with olive-patterned specimens. Figure 4 illustrates this and presents the percentage of occurrence of olive and rufous patterns in each of the areas of endemism where no single pattern is exclusive. Finally, outside the Guiana and Napo AEs there are individuals with intermediate plumage between the olive and rufous patterns, having the upperparts more or less chestnut (32) (as in rufous-patterned birds), but the crown olive (129) (as in olive-patterned birds). For the purpose of analysis, these individuals were classified as rufous pattern.

Among grey-patterned birds, there is also plumage variation in the underparts and upperparts, but not on the head, which characterizes the morphological diagnosis of this population. Some individuals have the underparts and back hair-brown (119A), whereas others have the underparts and back more or less

Table 2. Descriptive statistics for morphometric data pertaining to the *Synallaxis rutilans* group, considering the clades recovered by the cladistic analysis and named according to areas of endemism. SD, standard deviation; min, minimum values; max, maximum values; *N*, number of specimens. The maximum and minimum values for each group are highlighted in bold

		Guiana	Napo	Xingu	Belém	Inambari	Tapajós	Rondônia
Bill length	**mean**	13.17	13.59	13.83	13.08	13.18	13.07	13.21
	SD	0.52	0.53	0.61	0.62	0.51	0.52	0.59
	min	12.14	12.23	12.26	11.90	**11.70**	12.06	12.18
	max	14.84	14.50	**15.09**	14.21	14.12	14.00	14.63
	N	107	49	73	26	65	27	90
Bill depth	**mean**	4.40	4.34	4.40	4.40	4.31	4.50	4.39
	SD	0.24	0.19	0.23	0.19	0.26	0.22	0.25
	min	**3.82**	3.93	4.00	3.97	**3.82**	3.99	**3.82**
	max	5.09	4.70	**5.12**	4.77	5.00	4.87	5.01
	N	102	47	69	26	55	21	76
Wing length	**mean**	57.99	59.02	58.76	57.87	58.24	59.76	58.72
	SD	2.06	2.16	1.94	1.48	1.88	1.69	1.79
	min	**51.77**	53.90	54.94	54.31	54.28	54.50	53.13
	max	63.22	63.73	**64.86**	60.77	63.49	63.01	63.88
	N	109	52	72	24	67	24	89
Tail length	**mean**	65.91	66.12	65.86	58.00	65.80	63.44	64.05
	SD	3.38	2.59	3.23	3.88	2.75	2.45	2.84
	min	56.00	60.34	58.00	**52.00**	61.00	59.00	54.00
	max	**74.50**	72.00	**74.50**	69.00	72.00	68.00	70.00
	N	74	37	56	16	50	18	66
Rectrices		10	10	10	10	10	10	10

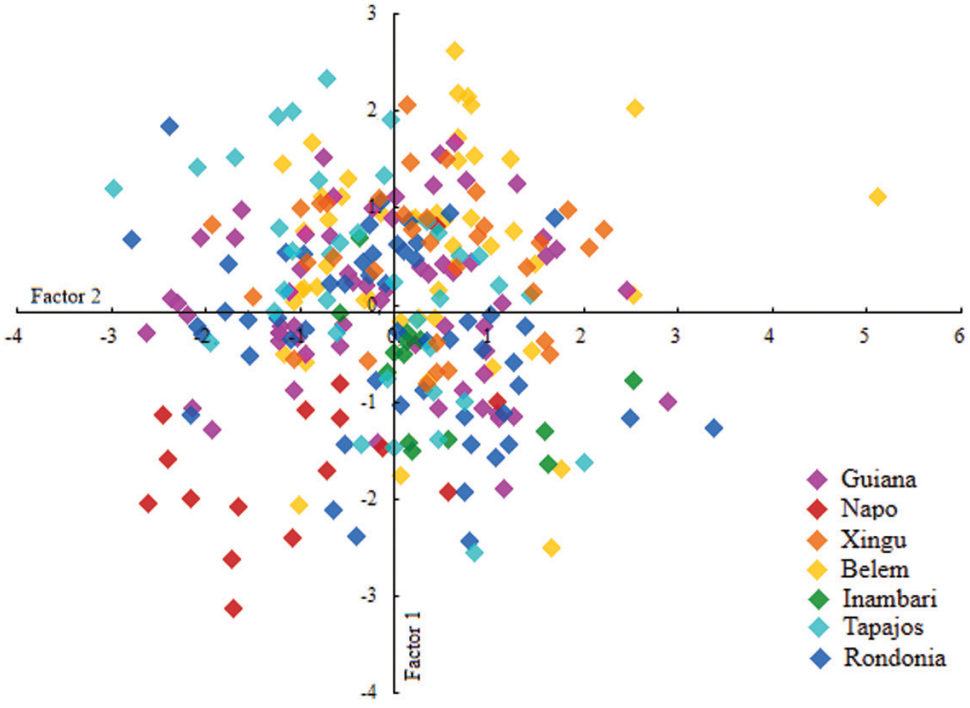

Figure 2. Scatterplots illustrating the results of the PCA for the morphometric data pertaining to populations of the *Synallaxis rutilans* group as clades resulting from the cladistic analysis performed using mtDNA.

Figure 3. Specimens of the *Synallaxis rutilans* group illustrating the patterns grey, olive, and rufous in plumage from left to right: ventral, lateral and dorsal views: MPEG 38618, Alto Turiaçu, Maranhão, Brazil; MPEG 59487, Barcelos, Amazonas, Brazil; and MPEG 56645, Juruti, Pará, Brazil.

Table 3. Plumage colour patterns of the *Synallaxis rutilans* group based on Smithe (1974) and topography according to Proctor & Lynch (1993). () signifies that the indicated colour is not present in the relevant specimen but occurs in the population concerned; / indicates 'or'; ± indicates a greater or lesser presence of the colour preceding the symbol. 1st, main colour; 2nd, second colour, associated with variation (±)

Reference			MPEG 38618	MPEG 59487	MPEG 56645
Pattern			Grey	Olive	Rufous
Ventral	**Throat**		119	119	119
	Breast	**1st**	119A	36 (340/32)	36 (32/340)
		2nd	(± 39)	-	-
	Abdomen	**1st**	119A	28 (26/123)	28
		2nd	(± 39)	(± 123)	(± 123)
	Flanks	**1st**	28 (119A)	28 (123)	28
		2nd	-	(± 123)	(± 123)
Dorsal	**Rectrices**		119	119	119
	Back	**1st**	119A	28 (121)	32 (28/223)
		2nd	(± 36)	(± 123/121)	(± 32)
	Crown	**1st**	221	28 (121)	32 (36/28/121/223)
		2nd	-	(± 123/121/121A)	(± 32/36)
	Forehead		221	36 (32)	36 (32/223)
Lateral	**Supercilium**		221	36 (32)	36 (340/32/223)
	Face		221	36 (32)	36 (340/32/223)
	Wing-coverts		36	32 (36)	32 (36)
	Remiges		121	121 (221)	121 (221)

cinnamon (39) or amber (36). Such variation was interpreted by Gyldenstolpe (1930) as ontogenetic, but our analysis of juvenile specimens did not confirm this hypothesis, as shown in Figure 5, because material of this age showed all of the characteristic features of both patterns – grey and olive. We found no correlation between plumage variation in grey-patterned birds and geography, as in some extreme cases plumage variation occurs at the same locality (e.g. MPEG 38616, with rufous present on the breast, abdomen and back, and MPEG 38618 without any trace of rufous, were collected at Alto Turiaçu, Maranhão, Brazil, on the same day; see Fig. 6).

The data also suggest no relationship with sexual dimorphism, as males and females can show any extreme in the range of variation. Instead, the variation in grey-patterned birds, wherein some individuals have the underparts and back hair-brown (119A), and others have the underparts and back more or less cinnamon (39), appears to be more associated

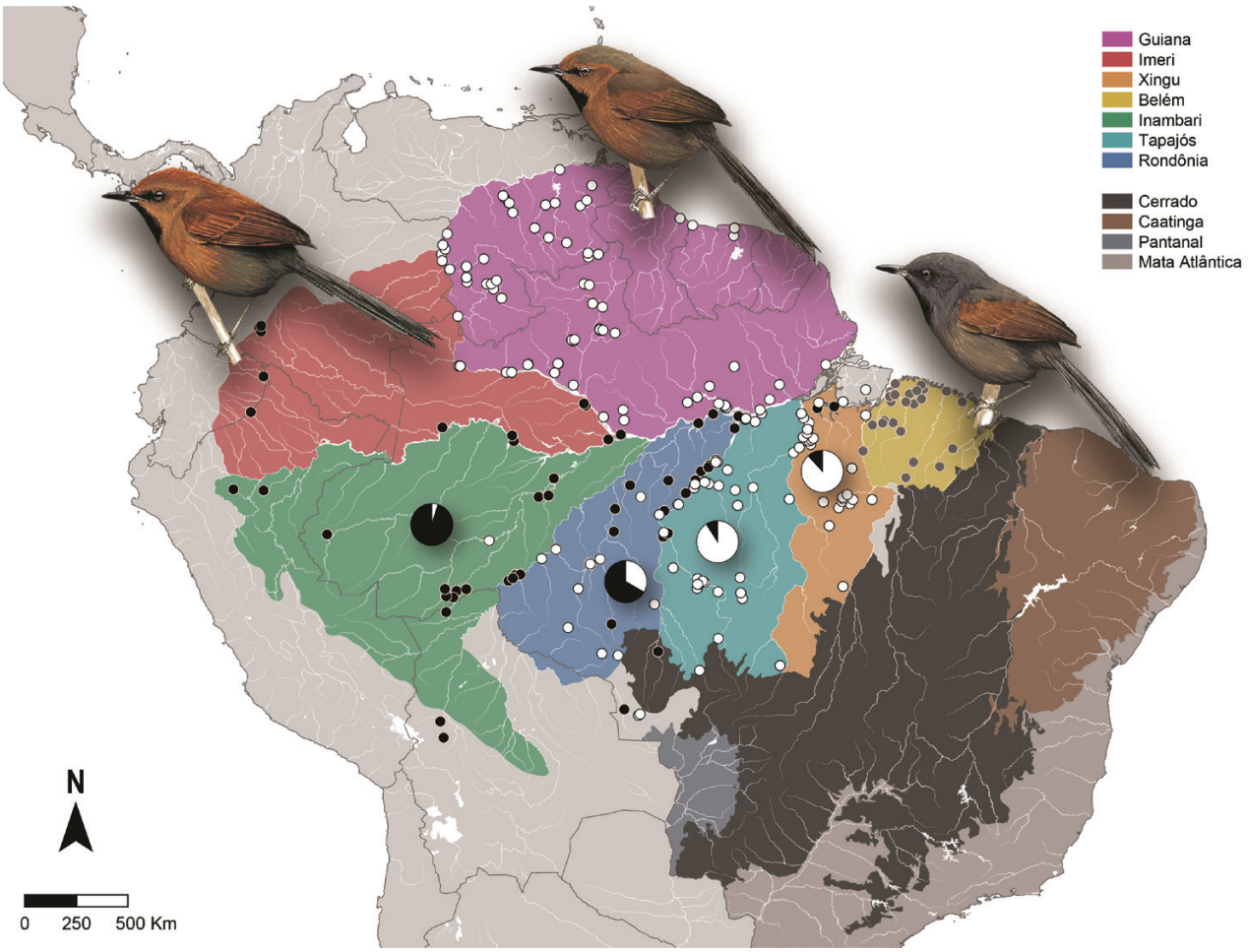

Figure 4. Plumage distribution and geographic variation in the *Synallaxis rutilans* group. Dark grey circles, specimens with grey-patterned plumage; pale grey circles, specimens with olive-patterned plumage; black circles, specimens with rufous-patterned plumage. Concerning intermediate individuals, any specimen with rufous present on the upperparts was classified in the 'specimens with rufous-patterned plumage' group. *Illustrations of birds with the typical plumage of: *S. caquetensis* (on the left); *S. dissors* (centre above); *S. omissa* (right). Area of endemism (AE) and distribution of species of the *Synallaxis rutilans* group: purple, Guiana EA, *S. dissors*; red, Napo EA, *S. caquetensis*; orange, Xingu EA, *S. rutilans*; yellow, Belém EA, *S. omissa*; and green, Inambari EA, blue, Rondônia EA and turquoise, Tapajós EA, *S. amazonica*. *Illustrations from del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E, eds. 2017. *Handbook of the birds of the world alive*. Barcelona: Lynx Edicions (retrieved on 10.11.2017 from http://www.hbw.com).

with polymorphism than ontogeny, geography or sexual dimorphism.

Divergenge analyses

The results of the Mantel tests revealed a significant but weak correlation between most of the datasets (Tables 4 and 5). Significant results were obtained between the genotypic/phenotypic, geographic/genotypic and geographic/phenotypic distances, but no significance was obtained when a partial Mantel was performed using geography as a reference for the genetic and phenotypic distances concomitantly.

Taxonomy

Taxognosis

Table 6 presents the analysis for taxognosis in the *Synallaxis rutilans* group. The analysis was conducted both for the clades identified by the cladistic analysis and for the taxa currently considered valid *sensu* Peters (1951), Remsen (2003) and Dickinson & Christidis (2014). It should be mentioned that this analysis recovered two clades for which no names are available. Thus, specimens from the Inambari AE are hereafter referred to as clade 'Unnamed Inambari'; and those from the Tapajós AE area as clade 'Unnamed Tapajós'.

Figure 5. Specimens of the *Synallaxis rutilans* group showing the grey (left-hand bird in each image) and olive patterns in juvenile plumage, from left to right, ventral, lateral and dorsal views: MZUSP 44653, Capim, Pará, Brazil; and MZUSP 93965, Boa Vista, Roraima, Brazil.

Figure 6. Specimens of the *Synallaxis omissa* showing the absence of correlation between plumage variation and geography, from left to right, lateral and ventral views: MPEG 38616, collected at Alto Turiaçu, Maranhão, Brazil, on 2 October 1986, with rufous present on the breast, abdomen and back; MPEG 36916, from Carutapera, river Curupi, Maranhão, Brazil, collected on 5 November 1984, with rufous present on the breast, abdomen and back; MPEG 38618, collected at Alto Turiaçu, Maranhão, Brazil, on 2 October 1986, the same day of MPEG 38616, without any trace of rufous.

As shown in Table 6, we recognize as species the following: *Synallaxis dissors*, for the Guiana clade, until now *S. r. dissors*; *Synallaxis caquetensis*, for the Napo clade, until now *S. r. caquetensis* and *S. r. confinis*; *Synallaxis omissa*, for the Belém clade, until now *S. r. omissa*; *Synallaxis rutilans*, for the Xingu clade; and *Synallaxis amazonica*, for the Inambari (no available name, but referred to as Unnamed Inambari here), Tapajós (no available name, but referred to as Unnamed Tapajós here) and Rondônia clades (until

now *S. r. amazonica* and *S. r. tertia*, considering the type locality of both nomina).

The differences between *S. omissa* and *S. rutilans* deserve comment. Although they are sibling groups, the morphological characters of *S. omissa* are especially distinct, with little variation, and are unequivocally diagnostic in relation to all other species, whereas *S. rutilans* is polymorphic and, as evidenced by the data, there is no morphological diagnosis between *S. amazonica*, *S. caquetensis*, *S. dissors* and *S. rutilans*, whereas there is a consistent diagnosis for all of these taxa compared to *S. omissa*. Figure 4 shows the frequency of individuals with red and brown plumage in the different populations of *S. rutilans* and *S. amazonica*, evidencing the geographic variation in morphology and its association with the patterns present in *S. dissors* and *S. caquetensis*, located at the extremities of the range of the *S. rutilans* group, excluding *S. omissa*.

Given this scenario, we hypothesize that *S. omissa* is the product of evolutionary pressures distinct from those acting on the other species of the *S. rutilans* group, probably due to the unique conditions of the geographically isolated Belém AE, especially its relatively small size and location in south-eastern Amazonia, constrained by the phytophysiognomies associated with transitional environments between upland Amazonian forest and the more arid vegetation of the Cerrado and Caatinga biomes (see Fig. 4).

Synallaxis dissors and *S. caquetensis*, despite being completely diagnosable compared to each other and geographically isolated by the Amazonas/Solimões and Negro Rivers, cannot be diagnosed in relation to populations of *S. rutilans* and *S. amazonica*, because both the rufous plumage of *S. caquetensis* and olive of *S. dissors* are present to a greater or lesser extent in the polymorphism exhibited by populations of *S. rutilans* and *S. amazonica*, as previously mentioned.

Table 4. Results of a Mantel test for the matrices of genetic, phenotypic and geographical distances. Significant values are highlighted in bold: *P*, level of significance; R, Pearson correlation values; and the asterisk (*) a partial Mantel test

Distance Matrix			R	P
Genetic	Phenotypic		0.056	**0.0001**
Geographic	Phenotypic		0.195	**0.0001**
Geographic	Genetic		0.320	**0.0001**
Genetic	Phenotypic	Geographic*	-0.007	0.5820

Table 5. Result of the analysis among populations undertaken via a binary correlation matrix where the values '0' and '1' were attributed to sites inside and outside endemic areas (clades). Significant values are highlighted in bold: *P*, level of significance; R, Pearson correlation values; asterisk (*) partial Mantel test; and asterisks (**) fewer than five individuals

Clado	Distance Matrix			R	P
Rondonia	Genetic	Geographic		0.056	**0.0030**
	Phenotypic	Geographic		0.110	**0.0001**
	Genetic	Phenotypic	Geographic*	0.050	**0.0000**
Belem**	Genetic	Geographic		-0.026	0.1580
	Phenotypic	Geographic		0.013	0.3140
	Genetic	Phenotypic	Geographic*	0.056	**0.0010**
Napo	Genetic	Geographic		-0.037	**0.0460**
	Phenotypic	Geographic		0.006	0.6720
	Genetic	Phenotypic	Geographic*	0.056	**0.0001**
Inambari	Genetic	Geographic		-0.057	**0.0020**
	Phenotypic	Geographic		0.022	0.0930
	Genetic	Phenotypic	Geographic*	0.057	**0.0001**
Tocantins	Genetic	Geographic		0.103	**0.0001**
	Phenotypic	Geographic		-0.105	**0.0001**
	Genetic	Phenotypic	Geographic*	0.067	**0.0001**
Xingu**	Genetic	Geographic		-0.014	0.5530
	Phenotypic	Geographic		0.017	**0.0010**
	Genetic	Phenotypic	Geographic*	0.056	**0.0001**
Guiana	Genetic	Geographic		0.077	**0.0001**
	Phenotypic	Geographic		0.014	0.2990
	Genetic	Phenotypic	Geographic*	0.055	**0.0001**

Table 6. Taxognosis results for the *Synallaxis rutilans* group. AE, areas of endemism; Dia, diagnosis; Bay, Bayesian inference, based on genetic structure; Coi, coinognosis, based on phylogenetic structure; Map, mapping tree. [1] Names applied to the clades recovered by cladistic analysis, based on the endemic areas nomenclature of Silva *et al.* (2005); [2] valid names for clades identified by the cladistic analyses; [3] *S. rutilans confinis* J. T. Zimmer, 1935, is an available name for the Napo clade, but is a junior synonym of *S. rutilans caquetensis* Chapman, 1914; [4] *S. rutilans tertia* Hellmayr, 1907, is an available name for the Rondônia clade, but is a junior synonym of *S. rutilans amazonica* Hellmayr, 1907, following the First Reviser action in Vaurie (1980: 117)

Groups	Taxognosis				Results		
AE	Physiognosis		Cladognosis		Score	Species limits	Valid names[2]	Taxonomic proposal
Clades1	Dia	Bay	Coi	Map				
Guiana	-1	1	1	1	0.5	Species	*S. r. dissors*	*S. dissors*
Napo	-1	1	1	1	0.5	Species	*S. r. caquetensis* and *S. r. confinis*	*S. caquetensis*[3]
Xingu	-1	1	1	1	0.5	Species	*S. r. rutilans*	*S. rutilans*
Belem	1	1	1	1	1.0	Species	*S. r. omissa*	*S. omissa*
Inambari	-1	-1	1	-1	-0.5	Not species	Unnamed Inambari	*S. amazonica*[4]
Tapajos	-1	1	1	-1	0.0	Species	Unnamed Tapajós	*S. amazonica*[4]
Rondônia	-1	-1	1	-1	-0.5	Not species	*S. r. amazonica* and *S. r. tertia*	*S. amazonica*[4]

Taxonomic data

The *Synallaxis rutilans* group can be considered a superspecies (*sensu* Mayr, 1931), given that our work seeks only to designate taxonomic categories, not nomenclatural ranks (for the distinction, see: Dubois & Raffaëlli, 2012; Dubois, 2017). The *S. rutilans* superspecies differs from all other *Synallaxis* in having the throat blackish neutral grey (82) and all five pairs of rectrices sepia (119). The species are presented in order of their historical description.

Synallaxis rutilans Temminck, 1823

Synallaxis rutilans Temminck, 1823: 227, fig.1 (lectotype, by present designation, ZMB 9078, from Cametá, Pará, Brazil, examined by us; see *Remarks 1* and *2* for designation and comments).

Diagnosis: Synallaxis rutilans differs from *S. omissa* in having the forehead, supercilium and face amber (36). However, *S. rutilans* lacks any morphological diagnosis compared to *S. amazonica*, *S. caquetensis* and *S. dissors*, as both the rufous pattern of *S. caquetensis* and olive pattern of *S. dissors* occur in *S. rutilans*, including individuals with intermediate plumage, which are also present especially in *S. amazonica*.

Description: Throat sepia (119); breast amber (36), varying individually between robin rufous (340) and chestnut (32); abdomen and flanks olive brown (28), varying individually between clay color (26) and raw umber (123), with elements of raw umber (123) as a secondary colour; rectrices sepia (119); back and crown olive brown (28), varying individually to Vandyke brown (121), with elements of raw umber (123) and Vandyke brown (121) as the secondary colour; forehead amber (36) varying individually to chestnut (32); supercilium and face amber (36), varying individually to chestnut (32); wing-coverts chestnut (32), varying individually to amber (36); remiges Vandyke brown (121), varying individually to Vandyke brown (221); bill length 12.2–14.5 mm; bill depth 3.9–4.7 mm; wing length 53.9–63.7 mm; tail length 60.3–72.0 mm, with ten rectrices (see Tables 7, 8).

Distribution: Understorey of terra firme forest in Brazil, *S. rutilans* occurs from the left bank of the Tocantins River to the right bank of the Xingu River, in north-east to south-east Pará and north-east Mato Grosso. Distribution represented in Figures 1 and 4 by orange colour of the Xingu AE.

Remarks 1: We examined specimens RMNH 88788 and ZMB 9078, both of which have been considered syntypes of *Synallaxis rutilans* Temminck, 1823

Table 7. Plumage colour of the species of *Synallaxis rutilans* group according to Smithe (1975, 1981) and topography according to Proctor & Lynch (1993)

		CHARACTERS										
Taxa	Reference	Throat	Breast	Abdomen	Flank	Rectrices	Back	Crown	Forehead	Supercilium	Face	Wing-coverts	Remiges
S. dissors	AMNH 248587	119	36	28	28	119	28	28	36	36	36	36	121
S. caquetensis	AMNH 116376	119	32	28	28	119	32+28	28+32	36	32	32	32	121
S. rutilans	AMNH 248588	119	36	28	28	119	28	28	36	36	32	32	121
S. omissa	AMNH 523598	119	119A	119A	119A	119	119A	221	221	221	221	36	121
S. amazonica	AMNH 523587	119	32	28	28	119	32+28	28+32	36	32	32	32	121

(Hellmayr, 1907; Dekker, 2003). According to the handwritten data on the base of the wooden pedastel on which the specimen is mounted (which matches the original label), RMNH 88788 is believed to have reached the museum via 'Verreaux' (presumably referring to the Maison Verreaux) and to have been collected in Peru. However, this information does not match that presented by Dekker (2003: 9) in the avian type catalogue of the Naturalis Biodiversity Center in Leiden, wherein the provenance of RMNH 88788 is stated to be 'Brazil'. The specimen in question corresponds in plumage and posture to that in Temminck (1823: 227, fig.1), the original description of *S. rutilans*, wherein he mentioned only 'Brésil', not Peru, thereby leaving some doubts concerning the true status of this specimen as a type. With respect to ZMB 9078, this was collected by Friedrich Wilhelm Sieber at Cametá, Pará, Brazil, sometime between 1800 and 1812, on behalf of J. C. H. G. von Hoffmannsegg (1776–1849) (Sylke Frahnert, *in litt.*). In 1809, von Hoffmannsegg was instrumental in founding the Berlin museum (now the Museum für Naturkunde) and donated his entire private collection to the new institution (Pinto, 1979). This material was studied by, among others, C. J. Temminck (1778–1858) and as a result, specimen ZMB 9078 became one of the syntypes of *S. rutilans* Temminck, 1823, perhaps the only one (Hellmayr, 1907). Considering the above, we designate ZMB 9078 as a lectotype of *S. rutilans* Temminck, 1823 and consequently RMNH 88788 becomes a paralectotype, thereby avoiding any nomenclatural consequences should RMNH 88788 prove not to be a syntype (see discussion in relation to the type locality, below).

Remarks 2: In the original description of *S. rutilans* Temminck (1823) mentioned only 'Brésil'. The type locality was restricted to Cametá, Pará, Brazil, by Cory & Hellmayr (1925), who treated ZMB 9078 as the sole syntype of *S. rutilans*. However, RMNH 88788, with locality Peru, has also been considered a syntype of *S. rutilans* Temminck, 1823 (Dekker, 2003). The Code (ICZN 1999) states that 'if the syntypes originated from two or more localities (including different strata), the type locality encompasses all of the places of origin' (Article 73.2.3). Cory & Hellmayr's (1925) restriction of type locality, not being based on a lectotype designation, carries no weight under the Code, and Peru must be considered part of the type locality of *S. rutilans* Temminck, 1823. Based on our analysis of the *S. rutilans* group, this makes defining the nominate taxon problematic, because the type series of *S. rutilans* would represent a composite series as 'Peru' encompasses populations of *S. caquetensis*, meaning that there is a taxonomic requirement (Article 74.7.3

Table 8. Descriptive statistics of morphometric data of the *Synallaxis rutilans* group. SD, standard deviation; min, minimum values; max, maximum values; *N*, number of specimens; mm, millimetres

Taxa	Bill length (mm)			Bill depth (mm)			Wing length (mm)			Tail length (mm)			
	mean ± SD	min–max	*N*	mean ± SD	min–max	*N*	mean ± SD	min–max	*N*	mean ± SD	min–max	*N*	Rectrices
S. dissors													
Overall	13.2±0.5	12.1–14.8	129	4.4±0.3	3.8–5.1	122	57.9±2.1	51.8–63.5	131	65.8±3.3	56.0–74.5	92	10
Females	13.0±0.5	12.1–14.8	57	4.3±0.2	3.8–4.9	51	57.6±1.6	54.3–60.8	56	65.8±3.4	56.0–74.5	46	10
Males	13.3±0.5	12.4–14.4	67	4.5±0.2	3.8–5.1	66	58.3±2.2	52.9–63.5	70	66.1±3.0	58.0–73.0	44	10
S. caquetensis													
Overall	13.1±0.6	11.9–14.2	25	4.4±0.2	4.0–4.8	25	57.8±1.5	54.3–60.8	23	57.3±2.7	52.0–61.0	15	10
Females	13.1±0.6	12.1–14.2	11	4.4±0.3	4.0–4.8	11	57.5±1.8	54.3–59.8	9	57.4±1.4	56.0–60.0	5	10
Males	13.0±0.6	11.9–14.2	14	4.4±0.1	4.2–4.6	14	58.1±1.3	55.8–60.8	14	57.2±3.2	52.0–61.0	10	10
S. rutilans													
Overall	13.6±0.5	12.2–14.5	49	4.3±0.2	3.9–4.7	47	59.0±2.2	53.9–63.7	52	66.1±2.6	60.3–72.0	37	10
Females	13.6±0.5	12.5–14.4	26	4.3±0.2	3.9–4.7	27	58.0±1.9	53.9–62.8	27	66.4±2.6	62.0–72.0	22	10
Males	13.7±0.6	12.2–14.5	22	4.4±0.2	4.1–4.7	19	60.1±1.8	56.2–63.7	24	65.9±2.5	60.3–69.0	14	10
S. omissa													
Overall	13.8±0.6	12.3–15.1	73	4.4±0.2	4.0–5.1	69	58.8±1.9	54.9–64.9	72	65.9±3.2	58.0–74.5	56	10
Females	14.1±0.6	12.9–15.0	26	4.3±0.2	4.0–5.0	25	58.2±1.9	55.3–64.9	27	66.4±3.4	58.0–74.5	20	10
Males	13.7±0.6	12.3–15.1	47	4.4±0.2	4.0–5.1	44	59.1±1.9	54.9–63.9	45	65.6±3.1	58.5–72.0	36	10
S. amazonica													
Overall	13.2±0.6	11.7–14.6	161	4.4±0.2	3.8–5.0	133	58.8±1.8	53.1–63.9	159	64.5±2.9	54.0–72.0	117	10
Females	13.1±0.6	12.2–14.3	63	4.3±0.3	3.8–4.9	50	58.3±1.8	54.1–62.2	62	64.2±2.9	59.0–72.0	41	10
Males	13.2±0.6	11.7–14.6	84	4.4±0.2	3.9–5.0	70	59.3±1.7	55.2–63.9	84	64.5±2.9	54.0–71.5	66	10

of the Code) to objectively define the type locality and the taxonomic allocation of the nomen (Dubois & Ohler, 1996; Frétey *et al.*, 2018), justifying the lectotypification. The designation above of ZMB 9078 as lectotype of *S. rutilans* Temminck, 1823, also ensures nomenclatural stability, as it restricts the type locality (Articles 73.2.3 and 76.2 of the Code) of *S. rutilans* Temminck, 1823, to Cametá, Pará, Brazil, at 02°15'S, 49°30'W (see: Paynter & Traylor, 1991). As a result of designating this lectotype, RMNH 88788 becomes a paralectotype (Article 74.1.3).

Synallaxis omissa E.J.O. Hartert, 1901

Synallaxis omissa E.J.O. Hartert, 1901: 71 (holotype AMNH 523598, adult female from Pará, Brazil, examined by us; see *Remarks 4, 5* and *6* for comments).

Diagnosis: Synallaxis omissa differs from *S. rutilans*, *S. amazonica*, *S. caquetensis* and *S. dissors* in having the forehead, supercilium and face Vandyke brown (221) without any trace of rufous.

Description: Throat sepia (119); breast and abdomen hair-brown (119a) with or without cinnamon (39) elements; flanks olive brown (28) varying individually to hair-brown (119a); rectrices sepia (119); back hair-brown (119a) with variable traces of amber (36); crown, forehead, supercilium and face Vandyke brown (221); wing-coverts amber (36); remiges Vandyke brown (121); bill length 12.3–15.1 mm; bill depth 4.0–5.1 mm; wing length 54.9–64.9 mm; tail length 58.0–74.5 mm, with ten rectrices (see Tables 7, 8).

Distribution: Synallaxis omissa is entirely allopatric with *S. rutilans*, *S. amazonica*, *S. caquetensis* and *S. dissors*, being restricted to the area east of the right bank of the Tocantins River, in south-eastern Pará and northern and western Maranhão, Brazil. The geographic range of the species is restricted to the Belém AE [as defined by Haffer (1969)] and all records of *S. rutilans* in the state Maranhão are attributable to *S. omissa*. Distribution represented in Figures 1 and 4 by yellow colour of the Belém AE.

Remarks 4: According to E.J.O. Hartert (1901), the holotype of *Synallaxis omissa*, AMNH 523598, an adult female, was collected by Joseph Beal Steere (1842–1940), on 19 July 1897. LeCroy & Sloss (2000) highlighted that the correct year of collection was 1879 [not 1897, as reported by E.J.O. Hartert (1901)].

Remarks 5: The original description of *S. omissa* cited the type locality as Pará, Brazil (E.J.O. Hartert, 1901). Subsequently, Paynter & Traylor (1991: 66) considered this to be more precisely defined as 'Belém', and designated the coordinates 0127/4829 (USBGN) for the precise location. Restriction of the type locality of *S. omissa* to Belém, Pará, was corroborated by Papavero *et al.* (2008: 133) and is consistent with the species distribution east of the right bank of the Tocantins River based on the specimens we studied.

Remarks 6: Peters (1951: 91) stated that 'The majority of the specimens of this race lack any trace of rufus on the head and underparts; occasional specimens however are coloured exactly like *S. r. rutilans*', and in fact, as previously reported, the underparts of *S. rutilans* and *S. omissa* can appear similar in respect of those specimens of the latter with cinnamon (39) colour on the breast and abdomen. However, *S. omissa* is diagnosed by the plumage of the head and *contra* Peters (1951), among all of the 317 specimens analysed by us (including those in the Museum of Comparative Zoology, where Peters was curator while preparing his *Check-list of birds of the world* in 1931–52), we have not located any individual of *S. omissa* with the coloration of *S. rutilans* (or *S. dissors* and *S. caquetensis*) on the head. In other words, none of the specimens showed any trace of amber (36) or cinnamon (39) on the head and face, whereas all individuals of *S. rutilans*, *S. dissors* and *S. caquetensis* analysed by us were well marked in this respect. It is important to note that *S. omissa*, although considered a subspecies of *S. rutilans*, has been distinguished to some extent as a unique biological entity by use of a unique vernacular name. Whereas the English name of all other taxa within the *S. rutilans* group is ruddy spinetail, sooty spinetail was used for *S. omissa* by del Hoyo & Collar (2016).

Synallaxis amazonica Hellmayr, 1907

Synallaxis rutilans amazonica Hellmayr, 1907: 14 (holotype, AMNH 523587, an adult female from Itaituba, left bank of the Tapajós River, Pará, Brazil, examined by us; see *Remarks 7* for comments).
Synallaxis rutilans tertia Hellmayr, 1907:15 (holotype, NMW 20198, an adult female from Engenho do Gama, Guaporé River, Mato Grosso, Brazil).

Diagnosis: Synallaxis amazonica differs from *S. omissa* in having the forehead, supercilium and face amber (36). However, *S. amazonica* lacks any morphological diagnosis compared to *S. rutilans*, *S. caquetensis* and *S. dissors*, as both the rufous pattern of *S. caquetensis* and olive pattern of *S. dissors* occur in *S. amazonica*, including individuals with intermediate plumage.

Description: Throat sepia (119); breast amber (36), varying individually between robin rufous (340) and

chestnut (32); abdomen and flanks olive brown (28), varying individually between clay colour (26) and raw umber (123), with elements of raw umber (123) as a secondary colour; rectrices sepia (119); back and crown olive brown (28), varying individually to Vandyke brown (121), with elements of raw umber (123) and Vandyke brown (121) as the secondary colour; forehead amber (36) varying individually to chestnut (32); supercilium and face amber (36), varying individually to chestnut (32); wing-coverts chestnut (32), varying individually to amber (36); remiges Vandyke brown (121), varying individually to Vandyke brown (221); bill length 11.7–14.6 mm; bill depth 3.8–5.0 mm; wing length 53.1–63.9 mm; tail length 54.0–72.0 mm, with ten rectrices (see Tables 7, 8).

Distribution: Understorey of terra firme forest in Brazil, *S. amazonica* occurs from the left bank of the Xingu River, in central Pará, and the right bank of the Amazonas/Solimões River, in Amazonia, south-west to western Mato Grosso, Rondônia, Acre and to eastern Peru and western Bolivia. The distribution of *Synallaxis amazonica* is represented in Figures 1 and 4 by the turquoise, blue and green colours of the Tapajós, Rondônia and Inambari endemic areas, respectively.

Remarks 7: Vaurie (1980: 117) mentioned that 'As first reviser, I select *amazonica* (Hellmayr, 1907: 14) as the name of the rufous populations, rather than *tertia* (Hellmayr, 1907: 15), which Cory & Hellmayr (1925) noted subsequently is 'closely similar' to *amazonica*'. *Synallaxis r. amazonica* Hellmayr, 1907, was described simultaneously with *Synallaxis r. tertia* Hellmayr, 1907, and from the moment that Vaurie (1980) considered these two names to be subjective synonyms he acted in accordance with Article 24.2.2 of the Code, wherein it is stated that determining the precedence of names is the role of the first reviser. We maintain the understanding of Vaurie (1980) that *S. r. tertia* is a junior subjective synonym of *S. r. amazonica*, but we think that *S. r. amazonica* should not be the name applied to 'rufous' populations of the *S. rutilans* group. Populations with diagnostically rufous plumage are named *Synallaxis caquetensis* Chapman, 1914, considering the type locality and the results of our analysis. Thus, in fact, the act of Vaurie (1980) as first reviser fixed the priority of *S. r. amazonica* ahead of *S. r. tertia*, but application of the name *S. r. amazonica* proposed here is distinct from that used by Vaurie (1980) and is not affected by his judgment as first reviser.

Synallaxis caquetensis Chapman, 1914

Synallaxis rutilans caquetensis Chapman, 1914: 621 (holotype AMNH 116376, an adult male from Florência, Caquetá, Colombia, examined by us).
Synallaxis rutilans confinis Zimmer, 1935: 4 (holotype AMNH 312067, an adult male from Igarapé Cacao Pereira, right bank of the Negro River, Brazil, examined by us).

Diagnosis: Synallaxis caquetensis differs from *S. omissa* in having the forehead, supercilium and face amber (36). Compared to *S. dissors*, *S. caquetensis* differs in having the upperparts chestnut (32) and, sometimes, the crown chestnut (32) or amber (36). *Synallaxis caquetensis* cannot be diagnosed morphologically in relation to *S. rutilans* and *S. amazonica*, because the rufous pattern of *S. caquetensis* is replicated to a greater or lesser extent in populations of *S. rutilans* and *S. amazonica*.

Description: Throat sepia (119); breast amber (36), varying individually between chestnut (32) and robin rufous (340); abdomen and flanks olive brown (28), varying individually with elements of raw umber (123) as the secondary colour; rectrices sepia (119); back chestnut (32), varying individually between olive brown (28) and raw umber (223); crown varies individually between olive brown (28), amber (36) and chestnut (32); forehead, supercilium and face amber (36), varying individually to chestnut (32); wing-coverts chestnut (32), varying individually to amber (36); remiges Vandyke brown (121), varying individually to Vandyke brown (221); bill length 11.9–14.2 mm; bill depth 4.0–4.8 mm; wing length 54.3–60.8 mm; tail length 52.0–61.0 mm, with ten rectrices (see Tables 7, 8).

Distribution: North-east Peru, eastern Ecuador, south-east Colombia and north-west Brazil, from the right bank of the Negro River to the left bank of the Amazonas/Solimões. The distribution of *Synallaxis caquetensis* is represented in Figures 1 and 4 by the red colour of Napo AE.

Synallaxis dissors J.T. Zimmer, 1935

Synallaxis rutilans dissors Zimmer, 1935: 4 (holotype AMNH 248587, an adult male from Campos Salles, Manaus, Amazonas, Brazil, examined by us).

Diagnosis: Synallaxis dissors differs from *S. omissa* in having the forehead, supercilium and face amber (36). Compared to *S. caquetensis*, *S. dissors* differs in having the upperparts and crown olive brown (28) or Vandyke brown (121). *Synallaxis dissors* cannot be diagnosed morphologically compared to *S. rutilans* and *S. amazonica*, because the brown pattern of *S. dissors* is also present to a greater or lesser extent in *S. rutilans* and *S. amazonica*.

Description: Throat sepia (119); breast amber (36), varying individually between chestnut (32) and robin rufous (340); abdomen and flanks olive brown (28),

varying individually between clay colour (26) and raw umber (123), with elements of raw umber (123) as the secondary colour; rectrices sepia (119); back and crown vary individually between olive brown (28) and Vandyke brown (121), with some raw umber (123) and Proust's brown (121A) elements as the secondary colour; forehead, supercilium and face amber (36), varying individually to chestnut (32); wing-coverts chestnut (32), varying individually to amber (36); remiges Vandyke brown (121), varying individually to Vandyke brown (221); bill length 12.1–14.8 mm; bill depth 3.8–5.1 mm; wing length 51.8–63.5 mm; tail length 56.0–74.5 mm, with ten rectrices (see Tables 7, 8).

Distribution: Southern Venezuela, French Guiana, Suriname, Guyana and in Brazil from the left bank of the Negro River, across the states of northern Amazonas, Roraima, northern Pará and Amapá. The distribution of *Synallaxis dissors* is represented in Figures 1 and 4 by the purple colour of the Guiana AE.

DISCUSSION

The results obtained here concerning molecular phylogenetic relationships among lineages, and the genetic and phenotypic diversity, provide a strong impression of 'conflict' between the morphological and molecular data. The Mantel tests revealed that when the genotypic and phenotypic data are analysed together, geography cannot explain them both, resulting in a lack of significance. This result is convergent with those of the molecular and morphological data analyses, which did not recover the same groups. Groups obtained in the genetic analysis were not fully concordant with the morphological data. One possible interpretation of this is that geography – both geographic distance and barriers – and varying selective pressures have influenced the genetic and phenotypic variation in different ways and at different times.

Zamudio *et al.* (2016) provided several examples where data sources appear to be in conflict and presented a synthesis of the patterns and processes potentially involved. There are two particularly interesting points here: the first is the 'conflict' of evidence itself; and the second the role of taxonomy in this context. As far as conflict is concerned, this, in fact, is merely illusory. What we have found, after analysing the phylogenetic relationships recovered using both mitochondrial and genomic data, and tests of correlation between genetic, phenotypic and geographical distance matrices, is that distinct biological patterns have arisen in response to different evolutionary pressures and processes.

While phylogenetic patterns and genetic divergence respond strongly to factors such as geographic distance and isolation by riverine barriers, morphological divergence appears less related to distance and barriers, and appears to be due more to differential selective pressures. The phylogenetic and chronological pattern recovered for the group reveals isolation of populations in the Amazonian interfluvia during the last one million years. In this relatively short time period, populations were isolated and probably underwent severe selective pressures mainly in the south-eastern interfluvia, which were subject to stronger climatic change during the Pleistocene (Wang *et al.*, 2017; Silva *et al.*, 2019). The scenario of small isolated populations subject to strong environmental change may have had distinct consequences for the phenotypic and genomic evolution of the group. The isolated populations achieved reciprocal monophyly within each interfluvium relatively quickly, as evidenced by the high support for the mitochondrial clades, but responded differently to selective pressures, with a diagnostic plumage phenotype being fixed only in *S. omissa* in the Belém AE, and marked phenotypic variation being maintained in *S. rutilans* and *S. amazonica* populations, especially in the Rondônia AE. Highly supported nodes in the genomic analysis (Supporting Information Figs S1, S2) evidence the sister-relationship between *S. rutilans* and *S. omissa*, and placement of the latter embedded in the well-supported southern clade, indicating that genomic introgression is not responsible for the phenotypic similarity of the non-sister lineages *S. rutilans* and *S. amazonica*. The phenotypic distinctiveness of *S. omissa* may represent another example of rapid plumage evolution in response to selective environmental pressures. Similar patterns were observed by Amaral *et al.* (2018), even if the processes are perhaps not the same. We should also mention that vocalization data for the *Synallaxis rutilans* group have been analysed, and will be published elsewhere, but variation within the complex was small and does not add significantly to our taxonomic understanding [Vocal variation in the *Synallaxis rutilans* group (Aves: Passeriformes: Furnariidae), in prep.].

An integrative taxonomic proposal must take into account all sources of evidence uncovered by the different (in this case morphological and genetic) analyses employed. Although we apply a methodology that differs from that proposed by Tobias *et al.* (2010), our motivation is similar to that of the latter authors when they stated that '. . . species are not merely another type of clade, but a different type of biological entity altogether. From this perspective, useful information is lost when taxonomy is forced to reflect gene trees by either over-lumping daughter and parent species, or over-splitting inherently paraphyletic taxa, and thereby ignoring the evolutionary reality of the nested lineage…' (Tobias *et al.*, 2010: 727).

To define species limits, our data were integrated into an evolutionary context. By these means, we have sought an approach that is neither subject to, nor restricted to, the tree topologies produced by our phylogenetic analyses, but values the multiple natural influences on the *Synallaxis rutilans* group and, in our opinion, such a decision increases the possibility of producing a consistent and lasting taxonomy for the group. Thus, phylogenetic information produced from molecular data was treated as just one of multiple sources of evidence or, in other words, as a medium rather than the end, as noted by Hörandl (2010: 349) '. . . for evolutionary classifications, a cladogram is actually just the start of the work, not the end. We need to achieve a better understanding of evolutionary processes before formal taxonomic conclusions can be drawn'.

Finally, it is interesting to draw attention to a historical point, namely, that in Vaurie's (1980) revision of the Furnariidae, he already arrived at a number of conclusions similar to those presented here, but these have been underplayed since [e.g. by Remsen (2003)]. Vaurie (1980: 114) stated that '. . . *S. rutilans* varies geographically and the rufous pigment has almost completely vanished in one of its subspecies (*S. r. omissa*)'. He went on to remark that 'Three trends are evident in the geographical variation of *Synallaxis rutilans*; . . . third, in northeastern Brazil, the rufous pigment has vanished from the whole of the plumage with the exception of the rufous area on the upper surface of the wing, although irregular traces of it persist on the back and breast that are better indicated in some individuals than others; these populations, which are fuliginous throughout, are distributed from the right bank of the Tocantins, east to Para and Maranhao' (Vaurie, 1980: 116).

The taxonomic arrangement proposed here allows for a better understanding of the similarities and differences among taxa from different Amazonian areas of endemism, characterizing genetic and morphological diversity patterns that result from distinct processes acting across distinct time-frames. This arrangement raises new evolutionary questions and draws attention to the importance of understanding and preserving evolutionary processes within the complex and constantly changing Amazonian landscape.

ACKNOWLEDGEMENTS

We are grateful to Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for post-doctoral support to R.S (# 2013/26609-1 and 2016/18963–8); the Department of Biology at FFCLRP/USP for infrastructural support of this study during post-doctoral research by R.S.; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a Ph.D. scholarship award to R.S.; the US National Science Foundation for funding the genomic data collection (IOS-1210556 to M.G.H.); the Programa de Pós-graduação in Zoology at the Museu Nacional (PPGZOO) and Department of Vertebrates of the Museu Nacional/UFRJ for supporting this study during doctoral research by R.S.; and the project 'Catalogue of types of Brazilian bird species', funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) via Edital Universal and coordinated by M.A.R. We are especially grateful for a Collection Study Grant from the American Museum of Natural History, New York; an Ernst Mayr Travel Grant in Animal Systematics, Museum of Comparative Zoology, Harvard University, Cambridge, MA; and a Visiting Scholarship Grant from the Field Museum of Natural History, Chicago, all of which supported the work of R.S. in various collections in the USA. CNPq (#440621/2015-1, #312687/2018-4) and FAPESP (#2016/50375-9) also provided research funding to F.A.B. We also thank all of the curators and other scientific staff who permitted access to the collections visited for this study. We also acknowledge the National Laboratory for Scientific Computing (LNCC/MCTI, Brazil) for providing HPC resources of the SDumont supercomputer, which have contributed to the research results reported herein. The authors declare that they have no conflict of interest.

DATA AVAILABILITY

The sequences are available in GenBank under the accession numbers OK076991-OK077075 and MZ956166-MZ956250 and raw reads were deposited at the NCBI Sequence Read Archive in GenBank (PRJNA758374).

REFERENCES

Aberer AJ, **Kobert K**, **Stamatakis A. 2014.** ExaBayes: massively parallel bayesian tree inference for the whole-genome era. *Molecular Biology and Evolution* **31:** 2553–2556.

Addinsoft. **2017.** *XLSTAT (data analysis and statistics software for Microsoft Excel),* version 2017. Paris: Addinsoft.

Amaral F, **Coelho M**, **Aleixo A**, **Luna L**, **Rêgo P**, **Araripe J**, **Souza T**, **Silva W**, **Thom G. 2018.** Recent chapters of Neotropical history overlooked in phylogeography: Shallow divergence explains phenotype and genotype uncoupling in *Antilophia* manakins. *Molecular Ecology* **27:** 4108–4120. http://dx.doi.org/10.1111/mec.14843

Bolger AM, **Lohse M**, **Usadel B. 2014.** Trimmomatic: a flexible trimmer for illumina sequence data. *Bioinformatics (Oxford, England)* **30:** 2114–2120.

Chapman FM. 1914. Diagnoses of apparently new Colombian birds III. *Bulletin of the American Museum of Natural History* **33:** 603–637.

Claramunt S. 2014. Phylogenetic relationships among Synallaxini spinetails (Aves: Furnariidae) reveal a new biogeographic pattern across the Amazon and Paraná river basins. *Molecular Phylogenetics and Evolution* **78:** 223–231.

Clement M, **Posada D**, **Crandall KA. 2000.** TCS: a computer program to estimate gene genealogies. *Molecular Ecology* **9:** 1657–1659.

Cory CB, **Hellmayr CE. 1925.** Catalogue of birds of the Americas. Furnariidae - Dendrocolaptidae. *Publications of the Field Museum of Natural History, Zoological Series* **13:** 1–390.

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

Dayrat B. 2005. Toward integrative taxonomy. *Biological Journal of the Linnean Society* **85:** 407–415.

Dekker RWRJ. 2003. Type specimens of birds in the National Museum of Natural History, Leiden. Part 2. passerines: Eurylaimidae – Eopsaltriidae (Peters's sequence). *Nationaal Natuurhistorisch Museum Technical Bulletin* **6:** 1–142.

del Hoyo J, **Elliott A**, **Sargatal J**, **Christie DA. 2013.** *Handbook of the birds of the world. Special volume. New species and global index.* Barcelona: Lynx Edicions.

del Hoyo J, **Collar NJ. 2016.** *HBW and BirdLife International illustrated checklist of the birds of the world. Volume 2: Passerines.* Barcelona: Lynx Edicions.

de Queiroz K. 2007. Species concepts and species delimitation. *Systematic Biology* **56:** 879–886.

Derryberry EP, **Claramunt S**, **Derryberry G**, **Chesser RT**, **Cracraft J**, **Aleixo A**, **Pérez-Emán J**, **Remsen JV Jr**, **Brumfield RT. 2011.** Lineage diversification and morphological evolution in a large-scale continental radiation: the neotropical ovenbirds and woodcreepers (aves: Furnariidae). *Evolution; International Journal of Organic Evolution* **65:** 2973–2986.

Dickinson EC, Christidis L, eds. 2014. *The Howard and Moore complete checklist of the birds of the world*, *Vol. 2*, *4th edn*. Eastbourne: Aves Press.

Drummond AJ, **Suchard MA**, **Xie D**, **Rambaut A. 2012.** Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* **29:** 1969–1973.

Dubois A. 2000. Synonymies and related lists in zoology: general proposals, with examples in herpetology. *Dumerilia* **4:** 33–98.

Dubois A. 2017. Diagnoses in zoological taxonomy and nomenclature. *Bionomina* **12:** 63–85.

Dubois A, **Ohler A. 1996.** Early scientific names of Amphibia Anura 1. Introduction. *Bulletin du Muséum National d'Histoire Naturelle (A)* **18:** 297–320.

Dubois A, **Raffaëlli J. 2009.** A new ergotaxonomy of the family Salamandridae Goldfuss, 1820 (Amphibia, Urodela). *Alytes* **26:** 1–85.

Dubois A, **Raffaëlli J. 2012.** A new ergotaxonomy of the order Urodela Duméril, 1805 (Amphibia, Batrachia). *Alytes* **28:** 77–161.

Ersts PJ. 2017. *Geographic Distance Matrix Generator (v.1.2.3)*. American Museum of Natural History, Center for Biodiversity and Conservation. Available from http://biodiversityinformatics.amnh.org/open_source/gdmg (accessed on 15 August 2017).

Faircloth BC. 2013. *Illumiprocessor: a trimmomatic wrapper for parallel adapater and quality trimming*. http://dx.doi.org/10.6079/J9ILL.

Faircloth BC. 2016. PHYLUCE is a software package for the analysis of conserved genomic loci. *Bioinformatics (Oxford, England)* **32:** 786–788.

Faircloth BC, **McCormack JE**, **Crawford NG**, **Harvey MG**, **Brumfield RT**, **Glenn TC. 2012.** Ultraconserved elements anchor thousands of genetic markers spanning multiple evolutionary timescales. *Systematic Biology* **61:** 717–726.

Frétey T, **Dewynter M**, **Ohler A. 2018.** Onymotopes in zoological nomenclature: some additional terms, with fixation of a lectonymotope for *Xenopus petersii* Bocage, 1895 (Amphibia, Anura). *Bionomina* **13:** 37–50.

GrabherrMG,**HaasBJ**,**YassourM**,**LevinJZ**,**ThompsonDA**, **Amit I**, **Adiconis X**, **Fan L**, **Raychowdhury R**, **Zeng Q**, **Chen Z**, **Mauceli E**, **Hacohen N**, **Gnirke A**, **Rhind N**, **di Palma F**, **Birren BW**, **Nusbaum C**, **Lindblad-Toh K**, **Friedman N**, **Regev A. 2011.** Full-length transcriptome assembly from RNA-Seq data without a reference genome. *Nature Biotechnology* **29:** 644–652.

Gyldenstolpe N. 1930. On a new spine-tail from east Ecuador together with some notes on the forms of the *Synallaxis rutilans*-group. *Arkiv för Zoologi* **25:** 1–20.

Haffer J. 1969. Speciation in Amazonian forest birds. *Science (New York, N.Y.)* **165:** 131–137.

Hartert EJO. 1901. *[Synallaxis omissa n sp.]. Bulletin of the British Ornithologists' Club* **11:** 71.

Harvey MG, **Aleixo A**, **Ribas CC**, **Brumfield RT. 2017.** Habitat association predicts genetic diversity and population divergence in amazonian birds. *The American Naturalist* **190:** 631–648.

Hellmayr CE. 1907. Another contribution to the ornithology of the lower Amazonas. *Novitates Zoologicae* **14:** 1–38.

Hörandl E. 2010. Beyond cladistics: Extending evolutionary classifications into deeper time levels. *Taxon* **59:** 345–350.

ICZN. 1999. *International code of zoological nomenclature*. London: The International Trust for Zoological Nomenclature.

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

Kearse M, **Moir R**, **Wilson A**, **Stones-Havas S**, **Cheung M**, **Sturrock S**, **Buxton S**, **Cooper A**, **Markowitz S**, **Duran C**, **Thierer T**, **Ashton B**, **Meintjes P**, **Drummond A. 2012.** Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics (Oxford, England)* **28:** 1647–1649.

Lanfear R, **Frandsen PB**, **Wright AM**, **Senfeld T**, **Calcott B. 2017.** PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* **34:** 772–773.

LeCroy M, **Sloss R. 2000.** Type specimens of birds in the American Museum of Natural History. Part 3: Passeriformes: Eurylaimidae, Dendrocolaptidae, Furnariidae, Formicariidae, Conopophagidae

and Rhinocryptidae. *Bulletin of the American Museum of Natural History* **257:** 1–88.

Maia R, **Eliason CM**, **Bitton PP**, **Doucet SM**, **Shawkey YMD. 2013.** Pavo: an R package for the analysis, visualization and organization of spectral data. *Methods in Ecology and Evolution* **4:** 906–913.

Mayr E. 1931. Notes on *Halcyon chloris* and some of its subspecies. *American Museum Novitates* **469:** 1–10.

Mantel N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* **27:** 209–220.

McKay BD, **Mays HL Jr**, **Yao CT**, **Wan D**, **Higuchi H**, **Nishiumi I. 2014.** Incorporating color into integrative taxonomy: analysis of the varied tit (*Sittiparus varius*) complex in East Asia. *Systematic Biology* **63:** 505–517.

Moyle RG, **Chesser RT**, **Brumfield RT**, **Tello JG**, **Marchese DJ**, **Cracraft J. 2009.** Phylogeny and phylogenetic classification of the antbirds, ovenbirds, woodcreepers, and allies (Aves: Passeriformes: infraorder Furnariides). *Cladistics* **25:** 1–20.

Naka LN, **Brumfield RT. 2018.** The dual role of Amazonian rivers in the generation and maintenance of avian diversity. *Science Advances* **4:** eaar8575.

Ohlson JI, **Irestedt M**, **Ericson PG**, **Fjeldså J. 2013.** Phylogeny and classification of the New World suboscines (Aves, Passeriformes). *Zootaxa* **3613:** 1–35.

Padial JM, **Miralles A**, **De la Riva I**, **Vences M. 2010.** The integrative future of taxonomy. *Frontiers in Zoology* **7:** 16.

Papavero N, **Overal WL**, **Teixeira DM**, **Hinshaw J. 2008.** The travels of Joseph Beal Steere in Brazil, Peru and Ecuador (1870-1873). *Arquivos de Zoologia* **39:** 87–269.

Paynter RA Jr. 1982. *Ornithological gazetteer of Venezuela*. Cambridge: Harvard University Press.

Paynter RA Jr. 1997. *Ornithological gazetteer of Colombia*. Cambridge: Harvard University Press.

Paynter RA Jr, **Traylor MA. 1991.** *Ornithological gazetteer of Brazil*. Cambridge: Harvard University Press.

Peters JL. 1951. *Check-list of birds of the world*, *Vol. VII*. Cambridge: Harvard University Press.

Pinto OMO. 1979. *A ornitologia do Brasil através das idades. Século XVI a século XIX*, *Vol. XIII*. São Paulo: Empresa Gráfica da Revista dos Tribunais (Brasiliensia Documenta).

Proctor NS, **Lynch PJ. 1993.** *Manual of ornithology: avian structure and function*. New Haven and London: Yale University Press.

QGIS Development Team. 2014. *QGIS Geographic Information System. Open Source Geospatial Foundation Project*. https://qgis.org.

Rambaut A, **Drummond AJ**, **Xie D**, **Baele G**, **Suchard MA. 2018.** Posterior summarization in bayesian phylogenetics using Tracer 1.7. *Systematic Biology* **67:** 901–904.

Raposo MA, **Kirwan GM. 2017.** What lies beneath the controversy as to the necessity of physical types for describing new species? *Bionomina* **12:** 52–56.

Raposo MA, **Stopiglia R**, **Brito GRR**, **Bockman FA**, **Kirwan GM**, **Gayon J**, **Dubois A. 2017.** What really hampers taxonomy and conservation? A riposte to Garnett and Christidis (2017). *Zootaxa* **4317:** 179–184.

Remsen JV Jr. 2003. Family Furnariidae (ovenbirds). In: del Hoyo J, Elliott A, Christie DA, eds. *Handbook of the birds of the world, Vol. 8: Broadbills to Tapaculos*. Barcelona: Lynx Edicions, 162–357.

Ribas CC, **Aleixo A**, **Nogueira AC**, **Miyaki CY**, **Cracraft J. 2012.** A palaeobiogeographic model for biotic diversification within Amazonia over the past three million years. *Proceedings of the Royal Society B. Biological Sciences* **279:** 681–689.

Ribas CC, **Aleixo A**, **Gubili C**, **d'Horta FM**, **Brumfield RT**, **Cracraft J. 2018.** Biogeography and diversification of *Rhegmatorhina* (Aves: Thamnophilidae): implications for the evolution of Amazonian landscapes during the Quaternary. *Journal of Biogeography* **45:** 917–928.

Ridgely RS, **Tudor G. 1994.** *The birds of South America*, *Vol. 2*. Austin: University of Texas Press.

Ronquist F, **Teslenko M**, **van der Mark P**, **Ayres DL**, **Darling A**, **Höhna S**, **Larget B**, **Liu L**, **Suchard MA**, **Huelsenbeck JP. 2012.** MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61:** 539–542.

Silva JMC, **Rylands AB**, **Fonseca GAB. 2005.** The fate of the Amazonian Areas of Endemism. *Conservation Biology* **19:** 689–694.

Silva SM, **Peterson AT**, **Carneiro L**, **Burlamaqui TCT**, **Ribas CC**, **Sousa-Neves T**, **Miranda LS**, **Fernandes AM**, **d'Horta FM**, **Araújo-Silva LE**, **Batista R**, **Bandeira CHMM**, **Dantas SM**, **Ferreira M**, **Martins DM**, **Oliveira J**, **Rocha TC**, **Sardelli CH**, **Thom G**, **Rêgo PS**, **Santos MP**, **Sequeira F**, **Vallinoto M**, **Aleixo A. 2019.** A dynamic continental moisture gradient drove Amazonian bird diversification. *Science Advances* **5:** eaat5752.

Simpson GG. 1961. *Principles of animal taxonomy*. New York: Columbia University Press.

Smith BT, **McCormack JE**, **Cuervo AM**, **Hickerson MJ**, **Aleixo A**, **Cadena CD**, **Pérez-Emán J**, **Burney CW**, **Xie X**, **Harvey MG**, **Faircloth BC**, **Glenn TC**, **Derryberry EP**, **Prejean J**, **Fields S**, **Brumfield RT. 2014.** The drivers of tropical speciation. *Nature* **515:** 406–409.

Smithe FB. 1974. *Naturalist's color guide*. New York: American Museum of Natural History.

Smithe FB. 1981. *Naturalist's color guide*. New York: American Museum of Natural History.

Sorenson MD, **Ast JC**, **Dimcheff DE**, **Yuri T**, **Mindell DP. 1999.** Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. *Molecular Phylogenetics and Evolution* **12:** 105–114.

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics (Oxford, England)* **30:** 1312–1313.

StatSoft Inc. 2013. *STATISTICA (Data Analysis Software System), v.12*. version 12.

Stephens L, **Traylor MA. 1983.** *Ornithological gazetteer of Peru*. Cambridge: Harvard University Press.

Stephens L, **Traylor MA. 1985.** *Ornithological gazetteer of the Guianas*. Cambridge: Harvard University Press.

Tamura K, **Stecher G**, **Peterson D**, **Filipski A**, **Kumar S. 2013.** MEGA**6:** Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* **30:** 2725–2729.

Temminck CJ. 1823. Nouveau recueil de planches coloriées d'oiseaux : pour servir de suite et de complément aux planches enluminées de Buffon, édition in-folio et in-4⁰ de l'Imprimerie royale, 1770. Paris: F. G. Levrault, Livr. 38, 227 pl.

Thom G, **Amaral FR do**, **Hickerson MJ**, **Aleixo A**, **Araujo-Silva LE**, **Ribas CC**, **Choueri E**, **Miyaki CY. 2018.** Phenotypic and genetic structure support gene flow generating gene tree discordances in an Amazonian Floodplain Endemic Species. *Systematic Biology* **67:** 700–718. http://dx.doi.org/doi.org/10.1093/sysbio/syy004

Tobias JA, **Seddon N**, **Spottiswoode CN**, **Pilgrim JD**, **Fishpool LDC**, **Collar NJ. 2010.** Quantitative criteria for species delimitation. *Ibis* **152:** 724–746.

Tobias JA, **Cornwallis CK**, **Derryberry EP**, **Claramunt S**, **Brumfield RT**, **Seddon N. 2014.** Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature* **506:** 359–363.

Vanzolini PE. 1992. *A supplement to the Ornithological gazetteer of Brazil*. São Paulo: Museu de Zoologia da Universidade de São Paulo.

Vaurie C. 1965. Systematic notes on the bird family Cracidae, No. 3. *Ortalis guttata, Ortalis superciliaris* and *Ortalis motmot*. *American Museum Novitates* **2232:** 1–21.

Vaurie C. 1967. Systematic notes on the bird family Cracidae. No. 10. The genera *Mitu* and *Pauxi* and the generic relationships of the Cracini. *American Museum Novitates* **2307:** 1–20.

Vaurie C. 1980. Taxonomy and geographical distribution of the Furnariidae (Aves, Passeriformes). *Bulletin of the American Museum of Natural History* **166:** 1–357.

Wang X, **Edwards RL**, **Auler AS**, **Cheng H**, **Kong X**, **Wang Y**, **Cruz FW**, **Dorale JA**, **Chiang H-W. 2017.** Hydroclimate changes across the Amazon lowlands over the past 45,000 years. *Nature* **541:** 204–207.

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

Wiley RH. 2010. Alfonso Olalla and his family: the ornithological exploration of Amazonian Peru. *Bulletin of the American Museum of Natural History* **343:** 1–68.

Will KW, **Mishler BD**, **Wheeler QD. 2005.** The perils of DNA barcoding and the need for integrative taxonomy. *Systematic Biology* **54:** 844–851.

Zamudio KR, **Bell RC**, **Mason NA. 2016.** Phenotypes in phylogeography: species' traits, environmental variation, and vertebrate diversification. *Proceedings of the National Academy of Sciences of the United States of America* **113:** 8041–8048.

Zimmer JT. 1935. Studies of Peruvian birds. XVIII. Diagnoses of new species and subspecies of Furnariidae from Peru and other parts of South America. *American Museum Novitates* **819:** 1–8.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Table S1. Taxon sampling for molecular data.

Figure S1. Phylogenetic tree of the *Synallaxis rutilans* individuals inferred by RAxML. Node support for the complete, and the 95% and 75% completeness matrices are indicated near the node, asterisk represents maximum support.

Figure S2. Phylogenetic tree of the *Synallaxis rutilans* individuals inferred by ExaML. Node support for the complete, and the 95% and 75% completeness matrices are indicated near the node.