



RESEARCH ARTICLE

Biogeography of a neotropical songbird radiation reveals similar diversification dynamics between montane and lowland clades

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Funding information

American Museum of Natural History; Conselho Nacional de Desenvolvimento Científico e Tecnológico; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior; Fundação de Amparo à Pesquisa do Estado de São Paulo; Museum of Comparative Zoology, Harvard University; Universidad de los Andes; Fundação de Amparo à Pesquisa do Estado do Amazonas; Louisiana State University; National Science Foundation

Handling Editor: Lars Chatrou

Abstract

Aim: Continental evolutionary radiations provide opportunities to understand how landscape evolution and biotic factors interact to generate species diversity. Additionally, understanding whether diversification dynamics differ between montane and lowland environments is a long-standing question with few comparative analyses in the Neotropics. To address these questions, we investigated the biogeographical patterns and the evolutionary processes underlying the diversification of a songbird genus, and compared diversification dynamics of clades occurring in lowland and montane Neotropical habitats.

Location: Neotropical montane and lowland forests.

Taxon: *Arremon* (Aves: Passerellidae).

Methods: We sequenced genomic data (ultra-conserved elements, UCEs) of 92 individuals (including historical skin specimens) comprising 47 of 50 currently recognized subspecies in the genus and collected habitat association data to (1) build the most complete phylogenetic hypothesis for the genus to date using maximum likelihood and Bayesian methods with a concatenated matrix, and a multi-species coalescent method based on quartets; and (2) reconstruct the evolution of their ancestral ranges, habitat association and diversification rates.

Results: All phylogenetic methods recovered essentially the same topology with strong support values for most interspecific nodes revealing relationships among species. We found evidence for a montane and humid ancestral range in Central America in the late Miocene and a later expansion into the lowlands of Central America, as well as into the lowlands and mountains of South America. Despite some temporal



variation in diversification rate, we found overall similar diversification dynamics between montane and lowland clades.

Main conclusion: Species diversity within the genus is likely underestimated by the current taxonomic arrangement. The colonization of lowlands and dry forests, and expansion across South America, may have provided new geographical and ecological opportunities for speciation resulting in high species diversification. Overall diversification dynamics were comparable between montane and lowland clades, contrasting with previous studies focused on such comparisons for Neotropical birds.

KEYWORDS

Andes, biodiversity, genomics, speciation, systematics, ultra-conserved elements

1 | INTRODUCTION

The study of evolutionary radiations, defined as a 'dramatic proliferation of taxa in a clade' (Simões et al., 2016), may help elucidate how a substantial part of Earth's biodiversity was generated. Most radiations are driven by a combination of biotic factors, intrinsic to the organisms, as well as abiotic factors, related to changes in the landscape where these organisms occur (Simões et al., 2016). Thus, radiations allow us to explore different aspects of evolution and to understand the rise of biodiversity hotspots.

The Neotropics is arguably one of the most prolific regions in terms of radiations (Abreu-Jr et al., 2020; Harvey et al., 2020). This is partly due to its complex geo-climatic history, including major landscape changes such as the closure of the Isthmus of Panama, the Andean uplift and the climatic cycles of the Pleistocene, which promoted biotic interchanges, isolated populations causing speciation and provided the environmental conditions for adaptation and range evolution of ecologically diverse organisms (Hoorn et al., 2010; Smith & Klicka, 2010; Thom et al., 2020). The resulting highly diverse biota provides extensive opportunities to study speciation and diversification dynamics (e.g. how diversification rates vary in time) across distinct landscapes. For example, organisms living in mountains are thought to be especially prone to speciation due to topographic heterogeneity and steep ecological and elevational gradients, whereas lowland species are often seen as older and more widespread, implying reduced opportunity for speciation (Antonelli, Kissling, et al., 2018; Graves, 1988). However, overall information regarding differences in diversification dynamics in lowlands and mountains is relatively scarce and controversial, as few clades occupy both kinds of habitats and provide enough sampling and taxonomic resolution (i.e. more refined species limits) to allow robust comparisons.

A study of diversification in montane and lowland Neotropical bird clades found higher speciation rates for Andean groups during the Pleistocene relative to lowland taxa, and attributed this result to the fact that habitat configuration, hence population connectivity and gene flow were likely more affected by glacial cycles in the mountains (Weir, 2006). However, the perception of lower diversification rates in the Neotropical lowlands may be an artefact

due both to undersampling across this vast, often inaccessible, and understudied region, especially in Amazonia (Ritter et al., 2019), as well as by a trend of phenotypic conservatism/crypticness in apparently homogeneous habitats, such as the understorey of humid forests (Buainain et al., 2021). In contrast, similar speciation dynamics were found for montane and lowland clades in a recent study of a Neotropical plant genus (Vargas et al., 2020). More studies of radiations involving complete sampling of closely related montane and lowland clades with comparable taxonomic resolution are essential to understand generalities in terms of how diversification dynamics may vary across the Neotropical lowlands and highlands.

The genus *Arremon* occurs in Neotropical mountains and lowlands, including humid and dry forests, from Mexico to Argentina, and comprises 19 [described/recognized] species and ~50 subspecies (Howard et al., 2014). There are three montane clades (hereafter 'brunneinucha' with 11 taxa, 'torquatus' with 14 taxa and 'crassirostris' with three taxa) and one large predominantly lowland group with 22 taxa, which is assumed to be monophyletic, hereafter the 'lowland *Arremon*' (Cadena et al., 2007). Species are mostly allopatric, but some occur in parapatry (Figure 1; Billerman et al., 2020). Even though species of *Arremon* occupy distinct habitats, they are all territorial, inhabit the interior or edge of forests, in the undergrowth, hopping on or near the ground, in dense cover where they forage in pairs unobtrusively, looking for insects and seeds. Most species nest on or near the ground (up to 1.5 m), have a roofed or open cup nests, have similar body sizes and share eco-morphological traits such as bill shape (Billerman et al., 2020; Ridgely & Tudor, 2009).

Given its distribution encompassing many different biomes and several lowland and montane habitats throughout Central and South America, *Arremon* is an ideal model to evaluate the role of abiotic (e.g. geological and climatic events) and biotic (adaptation to dry and humid, montane and lowland forests) factors in driving diversification in the Neotropical region. Because its major clades have a distinct distribution pattern, each being almost exclusively distributed either in lowlands or mountains, the genus provides a unique opportunity to compare diversification dynamics between these two habitat types. Much has been accomplished regarding species delimitation and distribution in the montane *Arremon* (Cadena

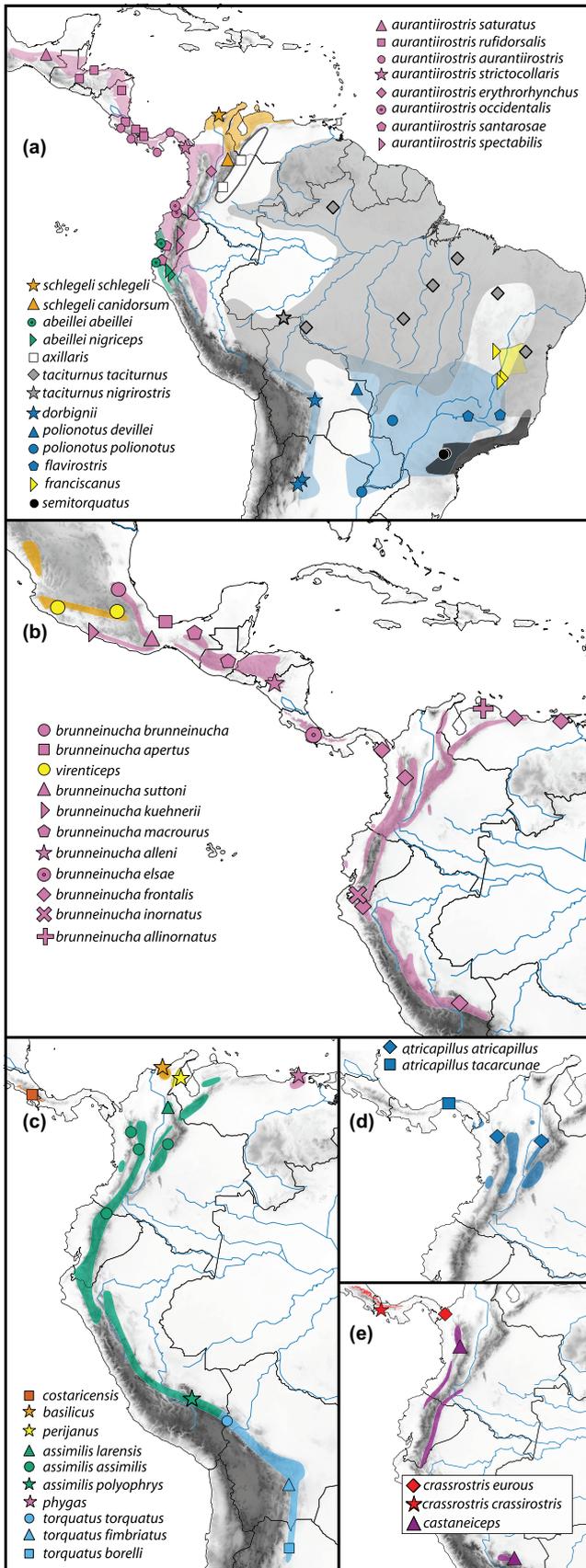


FIGURE 1 Maps of geographical distributions of the *Arremon* taxa shown separately by major groupings: (a) 'lowland *Arremon*'; (b) 'brunneinucha'; (c) and (d) 'torquatus'; and (e) 'crassirostris'. Polygons show current range coloured by species according to the classification of BirdLife international (<http://datazone.birdlife.org>), symbols represent the tissue samples used in this study coded by their current taxonomic classification. Maps were projected using WGS84 web Mercator

Trujillo-Arias et al., 2017). In addition, phylogenetic relationships among major clades and among many taxa have not been confidently estimated (Cadena et al., 2007; Flórez-Rodríguez et al., 2011; Klicka et al., 2014), due to insufficient genetic or taxonomic sampling or rapid radiation precluding the resolution of polytomies. This resulted in conflicting topologies with low statistical support, precluding the study of spatial and temporal patterns of diversification in a comparative framework.

Here, including almost all species and subspecies recognized within the genus, with a broad geographical sampling of widespread taxa, we employ genomic, distribution and habitat association data to estimate phylogenetic relationships, range evolution, diversification rates and evolution of habitat association in *Arremon*. Based on our well-supported phylogeny and biogeographical reconstruction, we ask (1) how did the evolution of habitat association affected diversification in the group (i.e. what is the proportion of lineages that occupy different habitats compared to the ancestor? Is there an association between changes in diversification rates and habitat association?); (2) whether there is temporal and spatial congruence among diversification events and geologic and climatic events, focusing on Andean uplift and connectivity between Central and South America; and (3) whether diversification dynamics were different in lowlands and mountains. We focus our discussion on the broad biogeographical patterns, a more detailed discussion on the systematics of each major clade will be presented in a future study.

2 | MATERIALS AND METHODS

2.1 | Phylogenomic analyses

We sampled 92 individuals, including 15 historical samples (skin specimens) of *Arremon* (Figure 1, Supporting Information: Figures S1–S3, Table S1), representing 18 of 19 species, and 47 (94%) of 50 recognized subspecies (Dickinson & Christidis, 2014; Navarro-Sigüenza et al., 2013). The genus *Atlapetes*, which is part of a large clade sister to *Arremon*, was used as outgroup (Klicka et al., 2014). We obtained genomic data using a probe set targeting 2321 loci of Ultra Conserved Elements (UCE) (Faircloth et al., 2012; see Supporting Information for more details).

Based on a concatenated matrix, we employed (1) a maximum-likelihood (ML) analysis in IQ-TREE (Nguyen et al., 2014). The best-fit substitution model was inferred in ModelFinder (Kalyaanamoorthy et al., 2017) and node support was inferred with UltraFast Bootstrap

et al., 2007; Cadena & Cuervo, 2010; Cadena & Loiselle, 2007; Navarro-Sigüenza et al., 2008), but several of the lowland *Arremon* taxa remain poorly studied (but see Buainain et al., 2017, 2020;



(Hoang et al., 2017) and SH-aLRT branch test (Guindon et al., 2010); (2) A Bayesian Inference (BI) analysis in EXABAYES (Aberer et al., 2014). Four independent runs with 2,000,000 Markov chain Monte Carlo (MCMC) each were performed, sampling every 500 generation. Stationarity and convergence of the independent runs were inferred using Tracer 1.6 (Rambaut et al., 2014). A consensus tree was generated combining the four runs. For the species-tree analysis (ST), we employed a multi-species coalescent approach in SVDQUARTETS (Chifman & Kubatko, 2015) implemented in PAUP* 4.0a (build 165) (Swofford, 2002) with independent gene trees for each UCE locus. All possible quartets were evaluated. Bootstrap support values were estimated using 10,000 replicates. Node support was considered strong in ML when UFBoot ≥ 95 and SH-aLRT ≥ 80 ; in BI when posterior ≥ 0.95 ; and in ST when bootstrap ≥ 80 .

2.2 | Divergence time estimations

We used TREEPL (Smith & O'Meara, 2012) to produce a time-calibrated phylogeny under a penalized likelihood framework. Penalized likelihood uses a semi-parametric approach that allows for different rates on different branches but has a smoothing parameter, chosen using cross-validation, that affects how much rate differences over the tree are penalized (Smith & O'Meara, 2012). To select the trees to be used as input for TREEPL, we wrote a custom script that interleaves the posterior samples of the four independent Exabayes runs performed with UCE data and excludes the first 25% of the trees in each run as burn-in. It then searches for the most frequent topology in the last 100 posterior samples. Finally, it selects 100 random trees with this same most frequent topology. These trees were then pruned using PHYTOOLS (Revell, 2012) to include one randomly selected terminal per lineage and used as input for TREEPL. Lineages were delimited based on monophyletic groups corresponding to previously named taxa, which typically are phenotypically distinct. We opted for this provisional arrangement because current taxonomic treatments for the group likely underestimates its real diversity (Buainain et al., 2016, 2017) and might impact subsequent analyses (Moen & Morlon, 2014). For more details on lineage delimitation, see Supporting Information.

We calibrated the 100 trees in the crown age of *Arremon* using the range of 8.4–7.5 million years ago (mya). The first date is based on an analysis performed in BEAST 2 (Bouckaert et al., 2019) using sequences of the mitochondrial Cytochrome b (cytb) gene and the widely used 2.1% per million year substitution rate (Figure S4) (Weir & Schluter, 2008). The second date (~7.5 mya) was found for the same node by an independent study employing a biogeographical calibration (Barker et al., 2015). We used the option 'prime' to select the best optimization for the analyses and used the cross-validation option to select the best rate-smoothing value. TREEPL was run for all 100 trees and the results were summarized in TREEANNOTATOR (Rambaut & Drummond, 2019) using the maximum clade credibility criterion. We used this time-calibrated tree for subsequent analyses.

2.3 | Reconstruction of ancestral habitat association

To trace the evolution of habitat association (montane vs. lowland, humid vs. dry) along the phylogeny, we performed stochastic mapping of ancestral character reconstruction. Habitat association data were obtained from literature (Table S2). We classified each lineage as follows: (1) montane (foothills and higher elevation), lowland or both; and (2) humid, dry habitat or both. We used the function make.simmap in 'phytools' package (Revell, 2012) in R environment (R Core Team, 2019), with the best-fit transition rate model, to generate 10,000 simulations to obtain posterior probabilities.

2.4 | Reconstruction of ancestral ranges

To estimate geographical range evolution, we used the BIOGEOBEARS package in R environment (Matzke, 2014). Because we aimed to evaluate the influence of the Andean uplift and the connectivity between Central and South America on the diversification of the genus, we considered four areas in our matrix: Central America, South America west of the Andes, South America east of the Andes and Andes. We evaluated the fit of data under three different models DEC, DIVALIKE and BAYAREALIKE using AICc values.

2.5 | Diversification rate analyses

To compare lowland and montane diversification, we assessed dynamics in diversification rate for the following: (1) the whole genus; (2) lowland and montane clades separately; and (3) all four main clades independently. To evaluate whether there were shifts in diversification rates along the phylogeny, we used Bayesian analysis of macroevolutionary mixtures (BAMM) (Rabosky, 2018) with 95% maximum clade credibility, posterior probability and Bayes factor criteria. We produced plots of speciation (λ), extinction (μ) and net diversification ($\lambda - \mu$) rates through time to examine the patterns of temporal variation in rates. We computed marginal clade-specific rates of speciation and extinction, and generated density plots to test whether different clades had different rate distributions.

We also evaluated rate variation using alternative approaches, which unlike BAMM, provide formal statistical tests for rate variations, but do not accommodate rate heterogeneity along branches. First, we used the gamma statistics in the 'Laser' package in R (Rabosky, 2017) to check whether the data significantly deviated from a null model of constant rate. We then evaluated the fit of each clade to different constant rate (pureBirth and birthdeath), multi-rate (yule2rate) or density-dependant variable-rate models (DDX and DDL). We tested the model fit of the data regarding three models of variable speciation and extinction rates: (1) SPVAR (exponentially declining speciation and constant extinction); (2) BOTHVAR (both speciation and extinction are variable) and (3) EXVAR (constant

speciation and exponentially declining extinction). Finally, we described the accumulation of diversity with lineages through time (LTT) plots constructed using 'ape' (Paradis et al., 2004) in R.

3 | RESULTS

3.1 | Phylogenetic relationships and divergence times

The final dataset contained 2201 UCE loci, and each locus was present in at least 90% of specimens. All phylogenetic reconstructions produced essentially the same topology with minor differences at the tips and strong support for most nodes (Figure 2, Figures S1–S8). We recovered four main clades congruent with the 'brunneinucha', 'torquatus', 'crassirostris' and 'lowland *Arremon*' groups. The first divergence event separates the lowland clade from the three montane clades in the upper Miocene (8.4 mya, CI = 8.3–8.4, Figure 2, Figure S9), followed by rapid diversification among the three montane clades during the following 1 myr (Figure 2). Most of the remaining diversification events occurred during the Plio-Pleistocene in the last 4.5 myr.

Within the lowland clade, diversification started at 4.6 (CI = 4.5–4.6) mya and the first divergence separated off a clade including all subspecies of *A. aurantirostris*, except for *A. a. spectabilis*, a taxon from the eastern Andean foothills. Despite its very similar phenotype to *A. a. aurantirostris* taxa, *A. a. spectabilis* was instead embedded in the *flavirostris/polionotus/dorbignii* clade from the foothills and lowlands east of the Andes, and was not related to *A. aurantirostris* from west of the Andes (Figures 1a and 2). Among the remaining 'lowland *Arremon*', the first divergence separated off *A. abellei*, from the dry lowlands of both slopes of the Peruvian and Ecuadorian Andes, and the next separates *A. schlegeli* of the dry forests of northern South America, from a clade occurring east of the Andes (Figures 1a and 2).

Within the montane clade, the first divergence gave rise to the 'brunneinucha' clade, including the remarkably phenotypically distinct *A. b. virenticeps*. This clade started to diversify at 3.4 (CI = 3.3–3.4) mya, and is divided into two main clades, north (upper clade in Figure 2) and south of the Isthmus of Tehuantepec in Southern Mexico (Figures 1b and 2). Within the 'torquatus' clade, diversification started synchronically with the lowland clade at 4.5 (CI = 4.4–4.6) mya. Accordingly, *A.*

costaricensis from Central America is sister to all the remaining taxa (Figures 1c1,c2 and 2). The next split involved *A. atricapillus* from Panama and the Colombian Andes, which is sister to two clades, one including the Central Andean taxa (*A. assimilis*) and the other including the Northern (upper clade in Figure 2) and Southern Andean clades. The placement of *A. poliophrys* from the Central Andes was ambiguous being sister to *A. a. assimilis* in BI and ML trees but closer to the Northern+Southern clades in the ST. *Arremon assimilis larensis* from northern Colombia and western Venezuela is closer to other northern Andean species than to remaining subspecies of *A. assimilis*. Finally, diversification within the 'crassirostris' clade started only at 1.4 (CI = 1.3–1.4) mya, with *A. crassirostris eurous* from Eastern Panama being more closely related to *A. castaneiceps* from the Andes than to the nominate *A. c. crassirostris* from Central America (Figures 1d and 2).

3.2 | Ancestral habitat association

The best fit ancestral reconstruction model was the one with equal forward and reverse transition rates (symmetric) for the montane–lowland habitat association dataset, and the one with equal transition rates among all three states for the humid–dry dataset (Table S3). The most recent common ancestor of all *Arremon* species was most likely associated with montane and humid habitats (Figure 3a,b). Colonization of the lowlands occurred between 8.4 and 4.5 mya exclusively in the 'lowland *Arremon*' clade. Diversification in this lowland clade took place during the last 4.6 myr and included a few independent recolonizations of montane habitats (mostly foothills) by *A. taciturnus*, *A. axillaris*, *A. semitorquatus*, *A. dorbignii* and *A. a. spectabilis*. The occupation of dry habitats occurred five times independently (i.e. in distinct lineages) during the Pleistocene, exclusively within the lowland clade (within the *A. abellei*, *A. schlegeli* and *flavirostris/polionotus* species complexes, and within *A. franciscanus* and *A. taciturnus*) (Figure 3b). See Table S3 for more details on transition rates.

3.3 | Ancestral range estimation

The best-fit model was DEC (dispersal–extinction cladogenesis) (Table S4). The ancestral distribution for the genus is optimized west

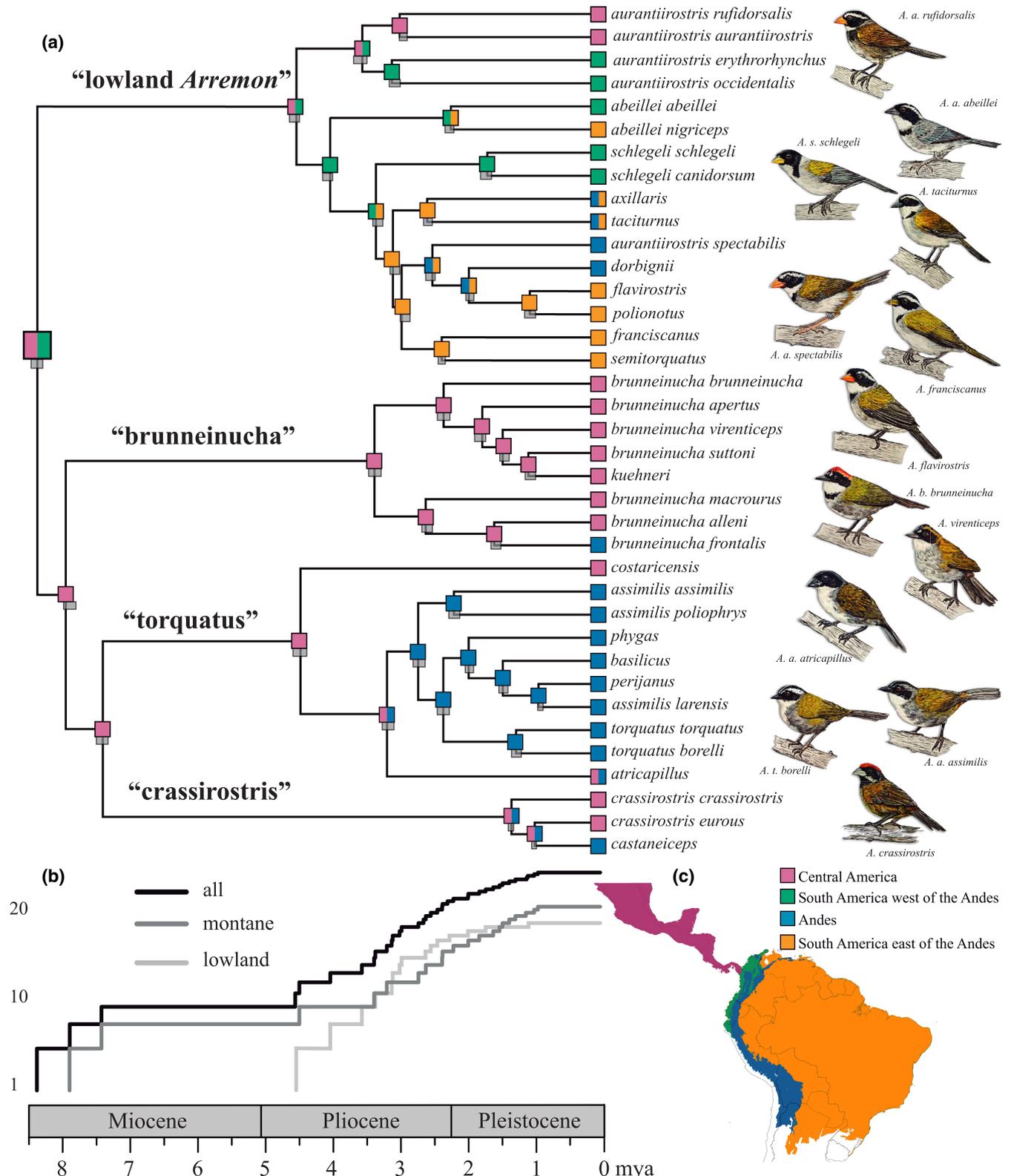
FIGURE 2 (a) Phylogenetic relationships and divergence times among taxa within the *Arremon* genus. The topology shown was recovered by Bayesian inference (BI) with 2201 concatenated loci (UCE sequences) and a 90% complete matrix. All nodes had maximum support values. Divergence times were estimated using TREEPL with 100 random trees that had the most frequent topology in the last 100 samples from the posterior of the four independent runs. Grey bars under the tree nodes represent CIs of estimated divergence times. Colours at the tree tips represent the most likely distribution areas of current lineages based on posterior probability, while colours on the tree nodes represent the most likely ancestral ranges estimated under the DEC model in BIOGEOBEARS. Nodes or tips with more than one colour represent ancestors or current lineages that occur in more than one area. Geographical location of these areas can be seen on panel (c). All nodes defining the relationships among the main lineages are highly supported in at least three of the four metrics used to evaluate the phylogenetic methods (BI, ML, ST), except for the placement of *A. a. Polyophrys*, which was supported by the BI and one ML metric (SH-aLRT). (b) Lineages through time (LTT) plots (bottom left) in log values of cumulative number of lineages. Curves are coloured to represent the whole *Arremon* radiation (black), montane (dark grey) and lowland (light grey) clades. The LTT plots were calculated using the fully supported, time-calibrated UCE tree. More detailed topologies, the full BI, maximum likelihood (ML) and species trees (ST) with node support can be found in Figures S1–S8. Bird illustrations by Hevana Lima. Some of taxa shown in Figure 1 are omitted from the phylogenetic tree because they were not sustained as distinct lineages (e.g. they were not monophyletic)



of the Andes, in South and Central America (Figure 2). The ancestral distribution of the 'lowland *Arremon*' was also reconstructed in Central America and South America west of the Andes. Ancestral ranges restricted to South America first appear around 4 mya in the large lowland clade sister to the *A. aurantirostris* species complex. The colonization of the lowlands east of the Andes occurred between 4

and 3 mya, following a split between *A. schlegeli* and all other eastern lineages. A few lineages (*A. taciturnus*, *A. axillaris*, *A. a. spectabilis* and *A. dorbignii*) re-colonized the Andes (mostly the foothills) independently.

The ancestral distribution of the montane clade is reconstructed in Central America. The 'torquatus' clade likely colonized the Andes during the Pliocene (~3 mya) after *A. costaricensis* diverged from the remaining



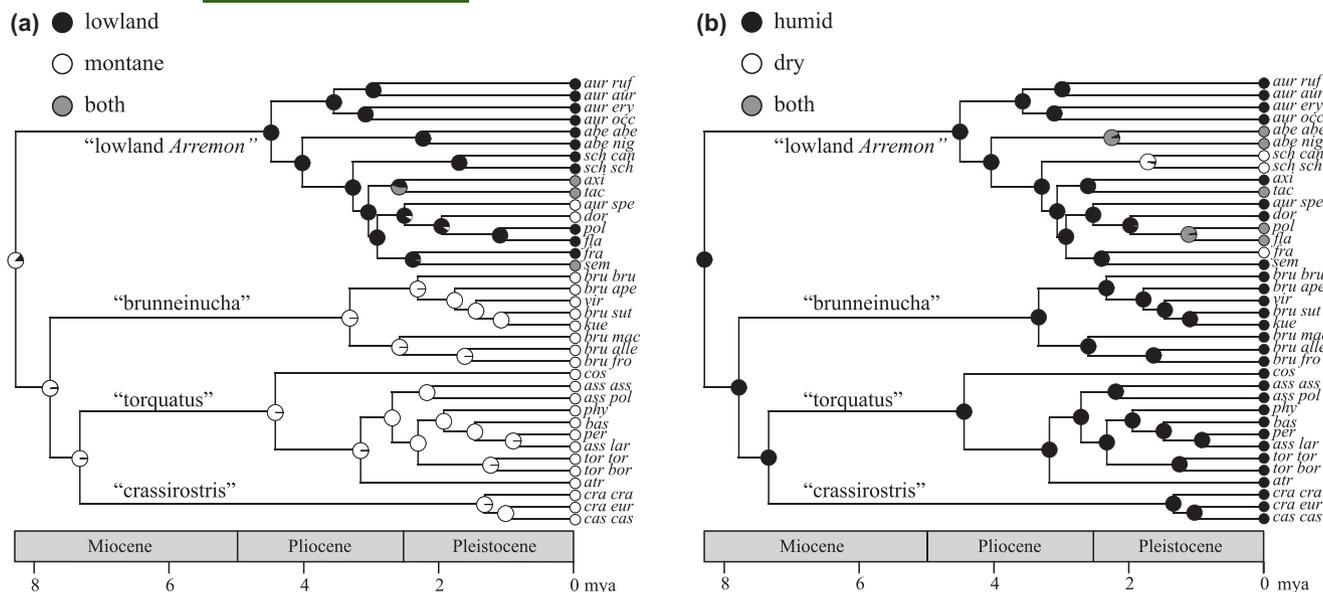


FIGURE 3 Stochastic ancestral character state reconstruction performed for ecological traits in *Arremon*: (a) montane vs. lowland habitat; and (b) humid and dry forests. Pie charts in nodes represent posterior probabilities of ancestral character state sampled from 10,000 simulations. The analyses were based on the fully supported time calibrated UCE tree. Taxon names on the tips are abbreviations using the first three letters of the specific and subspecific epithets. The full names of the taxa at the tips are shown in Figure 2 in the same order

taxa, whereas the 'brunneinucha' clade colonized this region much more recently, sometime during the Pleistocene by the lineage leading to *A. b. frontalis*. According to the optimization, the 'crassirostris' clade occurred in both Central America and the Andes, with the Andean taxon *A. castaneiceps* diverging from its sister lineage about 1.3 mya.

3.4 | Diversification rates

The LTT plots for the entire genus (all lineages, black line in Figure 2, Figure S9) and for the whole montane clade (dark grey line) both showed a steep curve (i.e. high rates of lineage accumulation) near the crown of the radiation (~8–7 mya), followed by a period of either stasis in diversification rate or increased extinctions. At ~4.3 mya, a new pulse of diversification seemingly occurred, coincident with the occupation of South America. Diversification in the montane clade initiated earlier in the radiation and ceased later (in the late Pleistocene) compared to the lowland clade (light grey curve), which resulted in greater number of montane lineages (21) compared to those from the lowlands (16). Despite initiating later (~4.6 mya), diversification rate in the lowland clade was high, especially during the Pliocene (Figure 2, Figure S9).

No shifts in diversification rates were detected by BAMMACROSS the history of the genus *Arremon* (Table S5), thus precluding possible associations with biogeographical or habitat changes. The best shift configuration tree shows high diversification rates near the crown of the radiation, with a subsequent decrease (Figure S11a). The density plot shows high overlap and similar speciation and extinction rates (Figure 4, Figure S10b) among the main clades, and between the lowland and montane clades. We also found very similar mean values of diversification rates among clades (Table S5). The plots of rate through time show

decreasing speciation and constant and low extinction rates, resulting in decreasing diversification rates for all clades (Figure 4, Figure S10c).

The inferred decrease in diversification rate was corroborated by the gamma statistic, which was negative and significant for the whole genus, but not significant ($p = 0.13$) for the 'crassirostris' clade, and borderline ($p = 0.08$) for the clade including all the montane *Arremon* (Table S6). The models that best fit our data were the ones with variable (rather than constant) and declining rates. The density-dependent speciation model (DDL; speciation decreases with cladogenesis) was selected for all clades, except the ones including 'crassirostris' (i.e. all *Arremon* and montane clades), for which the yule2rate was selected with a rate decrease at ~1 mya (Table S6). The model with exponentially declining speciation and constant extinction rate (SPVAR) was selected for all clades (Table S8). Extinction was low (0.001) in all models (Table S6).

4 | DISCUSSION

Based on the most strongly supported phylogenetic hypothesis for the genus *Arremon* (Figure 2) to date, our results suggest the following: (1) Despite currently having a significant part of its diversity in the lowlands and dry habitats, the genus originated in humid montane habitats (Figure 3); (2) the ancestral distribution of *Arremon* was restricted to mountains in Central America, with occupation of South American lowlands and the Andes occurring mostly during the Pliocene (Figure 2) (see discussion at Section 4.3); (3) the mean value, distribution and overall dynamics of diversification rates were similar in lowlands and mountains, but diversification started earlier and has seemingly stagnated later in mountains resulting in higher montane

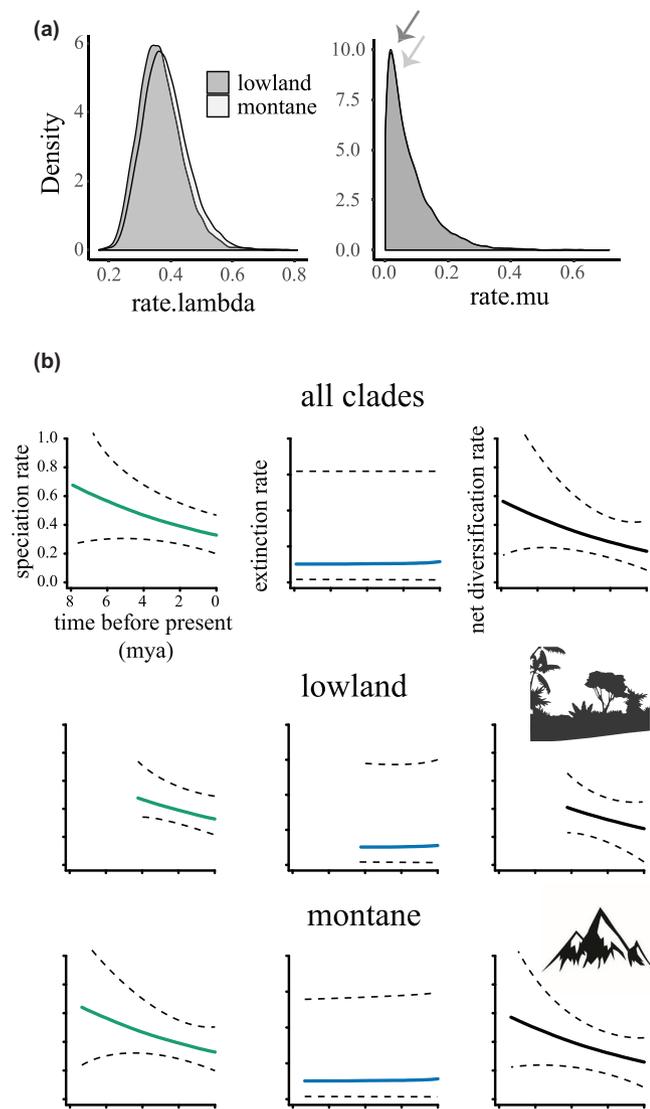


FIGURE 4 Diversification rate variation among the different clades within *Arremon*. Analyses were estimated using Bayesian analysis of macroevolutionary mixtures (BAMM) and the fully supported, time-calibrated UCE tree: (a) density plots with speciation (λ) (left) and extinction (μ) (right) rates calculated and coloured by clade. Grey arrows show the overlapping distribution of rates of the lowland and montane clades; (b) median values (full lines) and 95% confidence intervals (dashed lines) of speciation (green), extinction (blue) and net diversification (black) rates

diversity (Figure 2, Figure S10). Near complete sampling allowed us characterize the *Arremon* diversification pattern and to show that, despite accumulating more montane lineages as a result of more time for speciation, there is no support for the hypothesis of overall higher diversification rates in Neotropical mountains in relation to lowlands.

4.1 | Phylogenetic relationships

The main clades and lineages we recovered are mostly congruent with those documented in previous studies (Cadena et al., 2007;

Cadena & Cuervo, 2010; Dickinson & Christidis, 2014; Navarro-Sigüenza et al., 2008), but the relationships among some of them are novel (Figure 2). Despite the extensive efforts of several authors (Cadena et al., 2007; Flórez-Rodríguez et al., 2011) in increasing the number of loci to resolve the relationships among the four main clades, this is the first time that these relationships are confidently estimated, and the topology found here (Figure 2) is different from the previously proposed hypotheses. Our results confirm the non-monophyly of the formerly recognized genus *Buarremon* (Cadena et al., 2007), which grouped the 'torquatus' and 'brunneinucha' clades separately from 'crassirostris' (formerly in the genus *Lysurus*), thus corroborating a more inclusive and unified definition of *Arremon* (Cadena et al., 2007; Figure 2). The close relationship between 'crassirostris' and 'torquatus' is novel and surprising given that the 'crassirostris' species have nesting behaviour more similar to the 'lowland *Arremon*' species (Greeney, 2018), and plumage coloration pattern more similar to the 'brunneinucha' species (Figure 2). These phenotypic incongruences, coupled with the paraphyly of some species complexes found or confirmed here (e.g. *A. aurantirostris*, *A. crassirostris* and *A. brunneinucha*) (Figure 2), corroborate that phenotypic evolution in *Arremon* was complex, and that phenotypes may sometimes be misleading for taxonomic purposes (Cadena et al., 2007).

In some cases, phylogenetic relationships reflected geographical distributions rather than phenotypes. For example, in the 'lowland *Arremon*', we found that *A. a. spectabilis* is more closely related to other taxa east of the Andes in the *A. flavirostris/A. polionotus/A. dorbignii* complex than to the remaining *A. aurantirostris* subspecies which occur west of the Andes and with which it shares striking carotenoid coloration in the bill and legs as well as plumage features (Figures 1 and 2). Similarly, in the 'torquatus' clade, *A. assimilis larensis*, from the northernmost eastern Cordillera in the Colombian Andes is more closely related to other taxa in northern Andes than to other *A. assimilis* from the central Andes (Figures 1 and 2).

In contrast, however, the northern Andean clade (*A. basilicus/A. perijanus/A. a. larensis/A. phygas*) is more closely related to the geographically distant southern Andean clade (*A. t. torquatus/A. t. fimbriatus*) than to the adjacent Central Andean clade (*A. a. assimilis/A. a. poliophrys*) (Figures 1c and 2), corroborating a disjunct pattern of Andean distribution suggestive of local extinctions, shared among other bird clades (Cadena et al., 2019; Pérez-Emán, 2005).

We found high lineage diversity within currently described species (37 lineages vs. 19 recognized species) (Figure 2, Figures S1–S8), suggesting that the current taxonomic arrangement likely underestimates diversity within the genus. Even though we based our analyses on a propose a provisional 'lineage-based' arrangement, this is only a starting point for a comprehensive taxonomic revision of the genus, which is desirable particularly for 'lowland *Arremon*' and 'brunneinucha'. This is especially relevant considering that several *Arremon* taxa have relatively restricted geographical distributions, and thus refining the species limits in the genus may have important implications for conservation.

4.2 | Ancestral habitat association

The origin and evolution of *Arremon* was largely tied to montane and humid habitats as these habitat types were optimized for the ancestral nodes and retained in most extant species (Figure 3a,b). The occupation of lowlands occurred only once in the evolutionary history of the genus, reinforcing the idea that niche conservatism may play a fundamental role in the interplay between lowland and montane clades, and that some groups track their optimal habitat along historical changes in habitat altitudinal distribution due to climatic changes (Cadena & Loiselle, 2007; Pérez-Emán, 2005). The predominance of diversification within lowlands or mountains is a conspicuous pattern contrasting with previous studies in other Neotropical birds, that recovered multiple transitions between lowland and montane areas associated with speciation (Antonelli, Zizka, et al., 2018; Brumfield & Edwards, 2007) (but see Sedano & Burns, 2010). It is possible that the colonization of the lowlands was enabled by unique set of adaptations, perhaps related to physiological tolerance for higher temperatures, or that lowland-adapted lineages constrained further colonization from montane areas through competitive exclusion (see further discussion in Section 4.3).

The occupation of dry habitats occurred multiple independent times during the Pleistocene within the lowland clade, as observed in other Neotropical taxa (Antonelli, Zizka, et al., 2018), and might be attributed to the historically dynamic spatial distribution of humid and dry habitats, which might have conferred previous exposure and gradual adaptation to new environmental conditions (Antonelli, Zizka, et al., 2018). Although no shifts in diversification rates were detected along the phylogeny, precluding a possible relation with habitat association, multiple *Arremon* lineages evolved into lowland and arid environments, suggesting that range expansion and adaptation to these habitats were relevant for the colonization of an extensive area of the Neotropics (Figures 1a and 2).

The Late Miocene initiated a period marked by the decrease in global temperature, fragmentation of tropical biomes, expansion of dry habitats, deserts and grasslands, which is also coincident with a major peak in bird diversification around the globe (Claramunt & Cracraft, 2015; Herbert et al., 2016; Zachos et al., 2001). This period was further followed by the Pleistocene, a period of climatic oscillation between glacial and interglacial cycles that provoked extensive shifts in habitat configuration (Haffer, 1969; Hazzi et al., 2018). Although it is hard to directly associate these events with the evolution of habitat association in *Arremon*, it is possible that a decrease in global temperature and the expansion of drier environments favoured the occupation of these lowland and drier habitats enabling range expansion in the genus.

4.3 | Biogeographical reconstruction

Our estimates of ancestral ranges suggested that the ancestral distribution of the genus included Central America and the South American lowlands west of the Andes (Figure 2). However, historical

connections between South and North America have been dynamic and controversial. These two continents remained largely isolated for long periods of time and their connection occurred gradually over the last ~50mya (Jaramillo, 2018; O'Dea et al., 2016). More recently, the collision between the Panamanian Volcanic Arc with South America at ~12–10 mya resulted in the closure of the Central American Seaway (Jaramillo, 2018; O'Dea et al., 2016). Although the date for a permanent connection is controversial (Montes et al., 2015), sustained migration of terrestrial biota is only detected in the fossil record after ~4.2–3.5 mya, suggesting that the connection was fully and permanently established at this time, allowing easier passage for terrestrial organisms (Jaramillo, 2018; O'Dea et al., 2016).

Thus, considering that at about 8 mya the connection through the Isthmus of Panama might not have been fully established (Jaramillo, 2018; O'Dea et al., 2016), and that *Arremon* species are forest-associated small birds with presumably low dispersal capability, it seems unlikely that the ancestral distribution encompassed both Central and South America at that time. In addition, the South American area optimized to the ancestral node (green in Figure 2) is a lowland area, but the habitat association reconstruction recovered a montane ancestral distribution for the genus (Figure 3a), indicating the Central American mountains as the most likely ancestral range.

The first three diversification events within the genus occurred in a short period of time during the Upper Miocene (~8.4–7.4 mya), probably within Central America (Figure 2). Diversification of both the 'torquatus' and 'lowland *Arremon*' clades started at about 4.6 mya and may have been related to range expansion into South America after the final closure of the Isthmus of Panama, resulting in high speciation both in the Andes and in the lowlands. Expansion into South America was likely one of the most important biogeographical events in the diversification of the genus, (as noted for many other groups; Bacon et al., 2015), given that up to 23 out of 37 of its extant lineages are restricted to South America (Figure 2). The simultaneous occupation of South America by the montane 'torquatus' and 'lowland *Arremon*' clades occurred during a period (last 4.6 my) of intense geological and climatological dynamism, with marked changes in the landscape of the continent (Haffer, 1969; Hoorn et al., 2010). Thus, it is possible that some of the main *Arremon* ancestral lineages were caught in the perfect 'storm' of events at an enhanced time for speciation, resulting in a remarkable recent radiation.

The recent uplift of Central and Northern Andes during the Pliocene probably interrupted an ancient lowland corridor near the Magdalena and Cauca Valleys in southern Colombia (Gregory-Wodzicki, 2000; Montes et al., 2021), influencing the diversification of both montane and lowland biota in northern South American (Brumfield & Edwards, 2007; Hoorn et al., 2010). In *Arremon*, this is congruent with vicariant events early in the diversification of (1) the montane clade 'torquatus', whose taxa occur in 'well-known' biogeographical regions in Central and Northern Andes (Figures 1c and 2), a distribution pattern shared with other bird groups (Cadena et al., 2019; Hazzi et al., 2018), and (2) the 'lowland *Arremon*' clade, as suggested by the trans-Andean divergence at ~3.3 mya,



congruent with other lowland birds (Figures 1a and 2) (Brumfield & Edwards, 2007; Buainain et al., 2021).

Diversification in the 'brunneinucha' clade started later (~3.3 mya) and was centred in Central America (Figures 1b and 2). Its main geographical break separates taxa north and south of the Isthmus of Tehuantepec in southern Mexico. During the mid-Pliocene, tectonic dynamics in this region (Barrier et al., 1998) resulted in a notable reduction of elevations, followed by marine transgressions, which have been linked to diversification in other montane vertebrates with similar distribution and divergence times (Castoe et al., 2009; Tsai et al., 2019).

Many diversification events within *Arremon* date to Pleistocene times (Figure 2), when cycles of climatic changes caused substantial shifts in habitat configuration, resulting in cycles of population isolation and contact (Haffer, 1969). These events have been linked to diversification in lowland *Arremon* species (Buainain et al., 2020; Trujillo-Arias et al., 2017) and are expected to have affected the distribution and diversification of the montane taxa as well (Graves, 1988; Hazzi et al., 2018; Weir, 2006). For example, recent colonization of the Andes by some Central America montane lineages (or vice versa) such as *A. brunneinucha frontalis*, the 'crasirostris' clade (Figures 1 and 2) and possibly *A. atricapillus* (whose Central and South American populations diverged 1 mya, Figure S4) suggests increased Pleistocene connectivity between currently isolated montane habitats, probably due to climate-induced vertical range shifts of montane vegetation (Hazzi et al., 2018). Additionally, recolonization of the Andes by some taxa within lowland clades such as *A. a. spectabilis* and *A. dorbignii* might be related to more favourable conditions during these climatic cycles. Finally, speciation mediated by dispersal events across the Andes through lowpasses during more suitable past climatic conditions has been proposed for other lowland bird species (Brumfield & Edwards, 2007; Cadena et al., 2016). This could be related to diversification events in the *A. abeillei* complex (Figures 1 and 2), which occurs on both sides of the Porculla Valley, one of the Andean regions more susceptible to historical crossings (Cadena et al., 2016).

4.4 | Diversification rates in lowlands and highlands

Mean diversification rates estimated by BAMM are comparable with those of other rapid radiations in birds such as tanagers, tapaculos and ovenbirds (Furnariidae) (Table S5) (Cadena et al., 2020). Despite the lack of shifts in diversification rates in the BAMM analysis, the LTT shows higher diversification rates in the montane versus lowland clade, both early in the radiation of the genus and more recently, during the early Pleistocene, resulting in slightly higher current montane diversity (Figure 2). This is congruent with previous studies that suggest that montane populations, especially in the Andes, were highly susceptible to isolation during glacial cycles due to linear distributions and steep altitudinal gradient (Graves, 1988; Hazzi et al., 2018; Weir, 2006). Nonetheless, Pleistocene climatic

oscillations have also been linked to diversification or to population structure in two 'lowland *Arremon*' groups (Buainain et al., 2020; Trujillo-Arias et al., 2017), and studies on other lowland clades may reveal cryptic diversity, which seems more common in humid lowlands (Buainain et al., 2021). During the period in which the genus occurred both in lowlands and mountains (last 4.6 mya), diversification rates were comparable, with lowland rates even surpassing highland rates between 2 and 3 mya (Figure 2, Figure S10). The colonization of Amazonia, a species-rich area that usually accounts for a large portion of lowland diversity in widespread clades of birds, is very recent and unusually represented by a single species with shallow population structure (Buainain et al., 2020), *A. taciturnus* (grey in Figure 1a), and thus did not significantly contribute to lowland species diversity.

Diversification rates were high early in the radiation of *Arremon* and decreased with time in all clades as shown by BAMM, gamma statistics, and a model with density-dependent speciation (speciation decreases with cladogenesis), which fitted most clades within *Arremon* (Figure S11, Tables S5–S6). The DDL model is commonly found in radiations and many explanations have been proposed (Moen & Morlon, 2014). Considering our extensive sampling, our results are possibly due to (1) high rates near the crown of the radiation, with the first three diversification events happening in a short time interval; (2) gradual decrease in geographical opportunity for allopatric speciation (successively smaller ranges resulted from vicariance events are less susceptible to further fragmentation and environmental barriers if geographical ranges are not further expanded); and (3) strong territorial behaviour associated with little ecological/morphological innovation to avoid competitive exclusion, and/or strong adaptation to specific environments, both of which may prevent further geographical expansion and coexistence during moments of habitat shifts, reducing speciation opportunities. Our ancestral range reconstruction corroborates that even some of the few sympatric taxa such as *A. b. frontalis* and some taxa in the 'torquatus' clade, evolved largely in allopatry, and the current co-occurrence is recent (Figures 1 and 2; Cadena, 2007; Cadena et al., 2007). Thus, predominance of allopatric speciation corroborates a role of decreasing geographical opportunity for speciation. To what extent the subsequent lack of sympatry in the genus is also constrained by competition or by local adaptation remains to be tested. Evidence for both of these hypotheses has been proposed for montane *Arremon* species but remains untested for the lowland groups (Cadena, 2007; Moreno-Contreras et al., 2020; Remsen Jr & Graves IV, 1995).

Despite some temporal asynchrony between diversification in lowland and montane clades (e.g. diversification started earlier within the montane clade; Figure 2), the similarities are notable. Both clades (1) have similar mean values and overlapping distributions of diversification rates (Table S5, Figure 4, Figure S10b); (2) have their rate variation fitting to the same model (Table S6, Figure S11c) (i.e. similar diversification dynamics) and (3) comprise comparable numbers of extant lineages (Figure 2). Overall, this suggests similar diversification dynamics in the lowlands and highlands. It is possible that

different features of the landscape that led to in situ diversification in mountains and lowlands counterbalance each other. For example, Neotropical mountains might be more susceptible to fragmentation per area, due to their latitudinal linearity and steep environmental gradients (Graves, 1988), but the lowlands are more extensive in total area, which allows for significant habitat heterogeneity (Tuomisto et al., 2019) and spatial opportunity for fragmentation, that may be comparable in magnitude to mountains.

5 | CONCLUSIONS

The first well sampled and fully supported phylogenetic hypothesis of the genus *Arremon* indicates a prevalence of allopatric speciation and the importance of biogeographical events that are shared with other Neotropical organisms. Range expansion into South America during a time of landscape dynamism, likely after the final closure of the Isthmus of Panama, may have provided new opportunities for geographical speciation and adaptation to new environments, resulting in high diversification rates both in lowland and montane clades. Thus, we show that despite their spatial and temporal variation, montane and lowland clades have diversification rates with similar mean values, distribution and temporal framework. The evolutionary history of *Arremon* is an example of comparable diversification rates in lowlands and mountains, and does not support the idea that mountains would have consistently higher diversification rates when compared to the lowlands in the Neotropics.

ACKNOWLEDGEMENTS

We thank curators and staff of the collections that granted tissue loans: Alexandre Aleixo and Fatima Lima (MPEG); Cristina Miyaki (LGEMA); Marcos Raposo (MNRJ); Fabricio R. dos Santos (UFMG); J. D. Palacio (IAvH); F. G. Stiles (ICN); Paul Sweet and Thomas Trombone (AMNH); Nate Rice and Jason Weckestein (ANSP); Ben Marks and John Bates (FMNH); Brian Schmidt and Christopher Milensky (USNM); Marlene Freitas (INPA); Fred Sheldon and Donna Dittman (LSUMZ); Carla Cicero and Raurie Bowie (MVZ); Sharon Birks (UWBM); Charles Dardia (CUMV); Jon Fjelds , Kasper Thorup, Jan Kristensen and Knud A. J nsson (ZMUC). We thank Maura Costa for helping with the coding necessary to obtain confidence intervals for divergence times. Research support was provided by Dimensions US-Biota-S o Paulo: Assembly and evolution of the Amazon biota and its environment: an integrated approach, co-funded by the US National Science Foundation to J.C. (DEB 1241066 to J.C.) and FAPESP (2012/50260-6), and by FAPEAM Editais 002/2018 and 005/2019. High-performance computing resources were provided by Louisiana State University and by the National Laboratory for Scientific Computing, Brazil (LNCC). NB was supported by fellowships from CAPES, CNPq and FAPEAM (Fund o de Amparo   Pesquisa do Estado do Amazonas, process no: 062.00104/2020), and received a Collection Study Grant from the AMNH and an Ernst Mayr Grant from the MCZ, Harvard; CCR has a research fellowship from CNPq (311732/2020-8). CDC and JEA were

supported by Convocatoria Publica y Exp n 2019 from Universidad de los Andes (Project:  Evolucionan en concierto el genotipo y el fenotipo? Una evaluaci n de la diferenciaci n entre poblaciones y especies de gorriones de tierras bajas neotropicales?). No permits were needed to conduct this project.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All the genomic data produced are publicly available at NCBI Sequence Read Archive (SRA) under the BioProject (PRJNA818032). The code used for the analyses are available at https://github.com/nnbuainain/biogeography_arremon. Input files for all analyses can be found in supplementary material.

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BIOSKETCH

Nelson Buainain is interested in systematics, taxonomy, biogeography and ecology of birds. Since his early career stages, he has worked in museums and biological collections environments, and tries to integrate traditional and modern scientific approaches to describe and understand the diversity and evolution of Neotropical birds. All authors share the interest to understand the evolution of Neotropical organisms.

Authors' contributions NB and CR designed the study; NB, JA and MF performed the molecular laboratory procedures (DNA extraction and quantification); NB performed all the analyses. MF and BF provided guidance and assistance on UCE processing and data analyses; NB led the writing with contributions of all authors.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Buainain, N., Ferreira, M., Avendaño, J. E., Cadena, C. D., Faircloth, B. C., Brumfield, R. T., Cracraft, J., Ribas, C. C. (2022). Biogeography of a neotropical songbird radiation reveals similar diversification dynamics between montane and lowland clades. *Journal of Biogeography*, 49, 1260–1273. <https://doi.org/10.1111/jbi.14379>