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Short Communication

Investigating the utility of traditional and genomic multi-locus datasets to resolve relationships in *Lipaugus* and *Tijuca* (Cotingidae)

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ABSTRACT

Rapid diversification limits our ability to resolve evolutionary relationships and examine diversification history, as in the case of the Neotropical cotingas. Here we present an analysis with complete taxon sampling for the cotinga genera *Lipaugus* and *Tijuca*, which include some of the most range-restricted (e.g., *T. condita*) and also the most widespread and familiar (e.g., *L. vociferans*) forest birds in the Neotropics. We used two datasets: (1) Sanger sequencing data sampled from eight loci in 34 individuals across all described taxa and (2) sequence capture data linked to 1,079 ultraconserved elements and conserved exons sampled from one or two individuals per species. Phylogenies estimated from the Sanger sequencing data failed to resolve three nodes, but the sequence capture data produced a well-supported tree. *Lipaugus* and *Tijuca* formed a single, highly supported clade, but *Tijuca* species were not sister and were embedded within *Lipaugus*. A dated phylogeny confirmed *Lipaugus* and *Tijuca* diversified rapidly in the Miocene. Our study provides a detailed evolutionary hypothesis for *Lipaugus* and *Tijuca* and demonstrates that increasing genomic sampling can prove instrumental in resolving the evolutionary history of recent radiations.

1. Introduction

The tree of life contains numerous rapid radiations (Rokas and Carroll, 2006). In birds, these radiations occur at multiple taxonomic levels and temporal scales. For example, the majority of modern avian orders arose rapidly in a 16-million-year window following the K-Pg boundary (Hackett et al., 2008; Jarvis et al., 2014). At more recent timescales, several groups within the perching birds or passerines exhibit extraordinary bursts of diversification (e.g., Burns et al., 2014; Moyle et al., 2009). Rapid radiations result in phylogenies defined by long terminal branches and short internodes. Resolving such relationships may be empirically intractable (Patel et al., 2013), but increasing genomic sampling can be useful in some cases. For example, the use of thousands of ultraconserved elements (UCEs) and even whole genomes has improved resolution of difficult nodes early in the radiation of Neoaves (McCormack et al., 2013; Jarvis et al., 2014). Genomic datasets including UCEs have also proven useful for resolving more recent relationships in some groups (e.g., Ješovnik et al. 2017; Pie et al., 2019; Andersen et al., 2019). To assess the efficacy of genomic data for resolving a relatively recent and rapid radiation, we compared phylogenies from two genetic datasets of different sizes (eight Sanger sequencing loci and over a thousand sequence capture loci) in a clade of nine closely related species (*Lipaugus* and *Tijuca*) of Neotropical passerine birds.

The closely related genera *Lipaugus* (seven species) and *Tijuca* (two species) occur within the "core-cotingas" clade of Cotingidae (subfamily Cotinginae; Berv and Prum, 2014; Tello et al., 2009). All species in both genera are forest birds that are restricted to narrow elevational ranges that are either exclusively montane (*L. uropygialis*, *L. fuscocinereus*, *L. weberi*, *L. lanioides*, *L. streptophorus*, *T. atra*, *T. condita*) or

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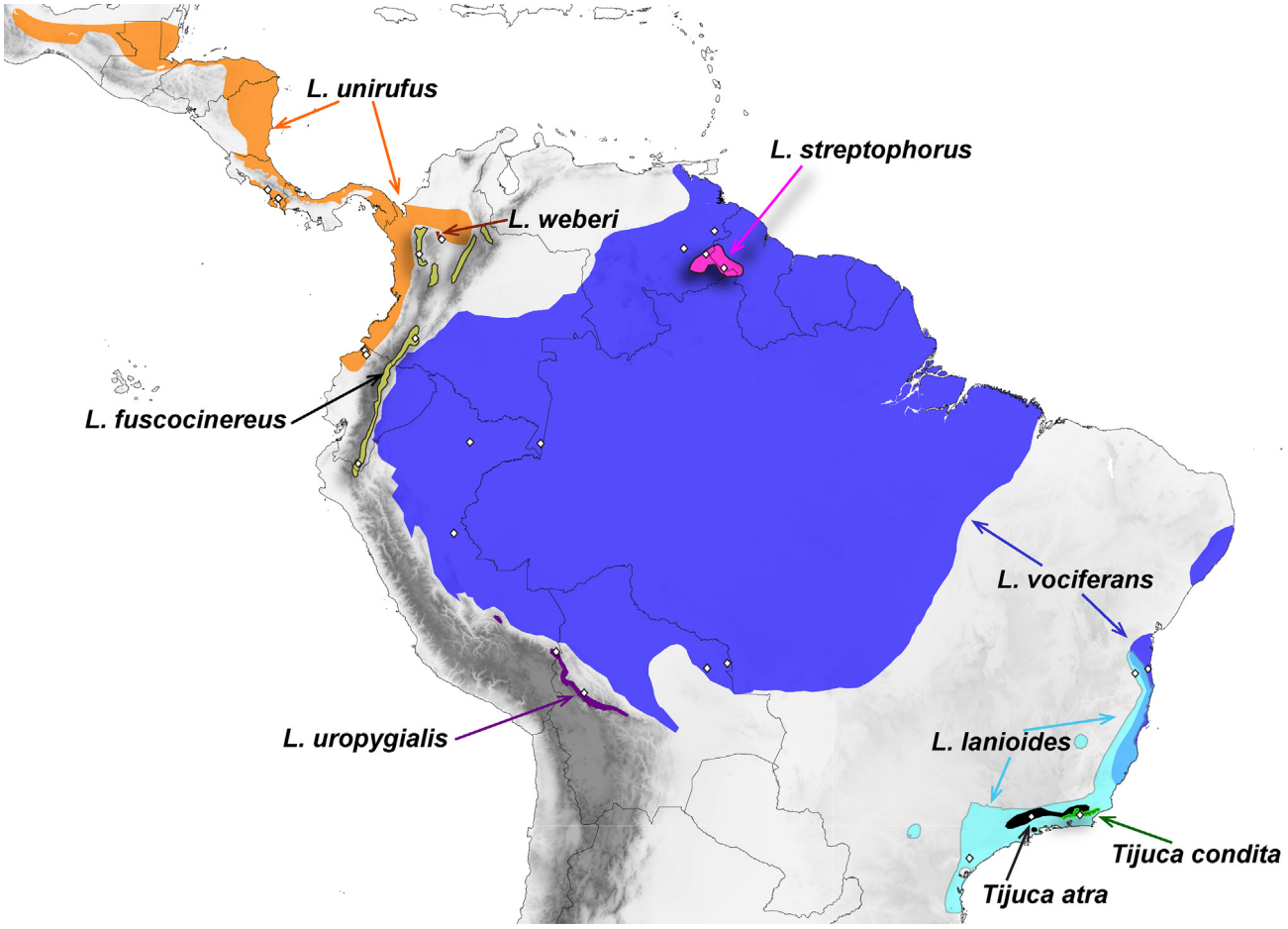

Fig. 1. Distribution map of *Lipaugus* and *Tijuca* across Neotropical montane and lowland forests, and locations of sampled individuals (open diamonds). Two *Lipaugus* pihas are widespread across the lowland rainforests on opposite sides of the Andes: *L. vociferans* (Amazonia and Atlantic Forest) and *L. unirufus* (Chocó and Central America). Three species are restricted to Andean cloud forests: *L. weberi, L. fuscocinereus*, and *L. uropygialis*. The only *Lipaugus* species with sexual dichromatism, *L. streptophorus*, is restricted to the Eastern Tepui mountains. Three species are endemic to the Atlantic Forest: *L. lanioides, T. condita,* and *T. atra*.

lowland (*L. vociferans* and *L. unirufus*). The two lowland species collectively inhabit almost all major areas of lowland Neotropical rainforest, whereas the montane species occur in restricted geographic ranges in the Tropical Andes, Eastern Tepuis, and Brazilian Atlantic Forest (Fig. 1). For instance, *L. weberi* occurs in an estimated 100–300 square kilometers between 1,425 and 1,900 m in the northern Central Andes of Colombia (Cuervo, 2014), and *T. condita* is restricted to less than 200 square kilometers between 1,375 and 2,000 m in central Rio de Janeiro, Brazil (Alves et al., 2008). In part due to the scarcity of samples of these range-restricted taxa, the evolution of the group is poorly understood.

In the most complete phylogenetic study of the cotingas to date, Berv and Prum (2014) used Sanger sequencing data from six loci and seven of the nine species of *Lipaugus and Tijuca* to confirm these two genera form a single clade. Their *Tijuca* sample (an individual of *T. atra*), however, was embedded within *Lipaugus* with low support for a sister relationship to *L. lanioides* (posterior probability, hereafter pp, = 0.62). Their tree supported a sister relationship between the two sampled Andean species (*L. fuscocinereus* and *L. uropygialis*) (pp = 1.0) and a sister relationship between *L. unirufus* and a clade containing all other sampled species (pp = 1.0), but all other nodes in the *Lipaugus-Tijuca* clade received low support (pp ≤ 0.62). Their dated tree indicated that most diversification events occurred within a 5-million-year time period (see Supplementary Appendix, Berv and Prum, 2014). Rapid diversification, in addition to incomplete taxon sampling, probably accounts for the current uncertainty of relationships within *Lipaugus* and *Tijuca*.

Here, we obtain data from the two previously unsampled species, *L. weberi* and *T. condita*, and increase genomic sampling to over a thousand loci to estimate species-level phylogenetic relationships within *Lipaugus* and *Tijuca*. This study provides an empirical example of genome-scale data better resolving relationships within a rapid radiation than more traditional multi-locus Sanger sequencing data, and also presents a new phylogenetic framework for biogeographical and comparative work in this group.

2. Materials and methods

2.1. Taxon sampling and DNA sequencing

Our eight-locus, Sanger sequencing dataset included 34 individuals representing all nine species of *Lipaugus* and *Tijuca* (Table S1). For the only polytypic species within this group, *L. unirufus*, we sampled the two subspecies currently recognized (*unirufus* and *castaneotinctus*). We included multiple individuals per species for all ingroup taxa (except for *T. condita*, for which only one sample was available), and sampled six outgroups from other cotingid lineages. We used standard methods to extract and sequence loci (ND2, ND3, CYT-*b*, G3PDH, MYO, BF5, RAG-1 and −2) for all samples, supplemented with sequences already published in GenBank when possible. Raw sequences were edited in Sequencher v 5.2 (Gene Codes Corporation, Ann Arbor, MI) and aligned using Muscle (Edgar, 2004). We found no evidence of nuclear pseudogenes (i.e. numts) in mtDNA sequences. Details are presented in supplementary methods.

For a sample of 14 individuals, including at least one representative of each *Lipaugus-Tijuca* species and one outgroup (Table S1), we targeted 2,417 conserved genomic regions to generate our genomic dataset (hereafter "sequence capture dataset"). We used a custom-designed array to capture 2,321 UCEs with their flanking sequence as well as 96 exon and intron markers commonly used in avian phylogenetics (Harvey et al., 2017). DNA library enrichment and sequencing was outsourced to RapidGenomics LLC (Gainesville, FL). Sequences were demultiplexed, assembled and aligned using the PHYLUCE pipeline (Faircloth, 2016). We retained loci that were more than 100 basepairs in length and had an average depth of 15 or more reads across samples.

2.2. Alignment partitioning

For the Sanger sequencing dataset, we simultaneously assessed the appropriate partitioning scheme and the best model of nucleotide substitution for each inferred partition using PartitionFinder 1.1.1 (Lanfear et al., 2012). We also assessed models without partitioning to reduce complexity for some species tree analyses. The closest available model to the inferred best model was used in subsequent analyses. Partitioning schemes and substitution models are described in Table S2. For the sequence capture dataset, we partitioned by locus.

2.3. Gene tree inference

We inferred gene trees for each locus using standard Bayesian and maximum likelihood methods. We estimated Bayesian gene trees for the Sanger sequencing loci in MrBayes 3.2.2 (Ronquist et al., 2012). We ran four independent MCMC runs with incrementally heated chains (0.175) and sampled every 1,000 steps for 10 million generations. The first 25% of the posterior sample was discarded as burn-in. We checked for sufficient mixing and appropriate values of effective sample size (> 200) of all parameters. Maximum likelihood gene tree inference for both Sanger sequencing and sequence capture loci was conducted in RAxML 7.0.3 (Stamatakis et al., 2008). For computational reasons, we applied the GTRCAT model of nucleotide substitution, an efficient approximation of the GTR model with rate heterogeneity among sites, and we conducted and halted rapid bootstrapping automatically using the RAxML autoMRE option.

2.4. Species tree and divergence time estimation

We first estimated species trees from the concatenated Sanger and sequence capture datasets, partitioned by locus, using RAxML as described above. For the Sanger dataset, we next used the Bayesian gene tree - species tree approach implemented in *BEAST (Heled and Drummond, 2010) to simultaneously estimate the tree topology and divergence times. We used a birth-death model for the species tree because we expect the study clade is old enough to have experienced extinction. We applied a lognormal relaxed clock and calibrated evolutionary rates for six of the eight sampled loci using published estimates from prior studies in other passerine birds (Table S3). We completed two runs of 500 million MCMC generations, sampling every 20,000 steps. We assessed mixture and convergence, combined samples from the two runs, and discarded 25% of the posterior sample as burn-in to obtain a maximum clade credibility (MCC) tree.

Due to the large size of the sequence capture dataset, we used a summary species tree approach implemented in ASTRAL 4.7.6 (Mirarab et al., 2014) to infer species trees from unrooted gene trees estimated for each sequence capture locus in RAxML. We utilized the best scoring trees from the maximum likelihood gene tree analyses and performed 100 replicates of multi-locus bootstrapping using the sets of bootstrap trees from RAxML. We did not investigate the timing of divergence events using the sequence capture data, in part because substitution rate heterogeneity within and across UCE loci complicates time calibration of phylogenies in the absence of fossil or geological calibration points (both of which are lacking for this group). We instead focused on dates inferred from the Sanger sequence data for which prior information is available on substitution rates. However, because the tree topology estimated from the genomic dataset might be more accurate than that identified by *BEAST using the Sanger data, we also ran a dating analysis in which the tree topology was fixed to the RAxML and Astral estimate from sequence capture data. Settings were otherwise identical to those used for simultaneous estimation of tree topology and divergence times described above, with two runs again combined to obtain a MCC tree and associated posterior support values.

3. Results

3.1. Dataset characteristics

Our genetic sampling for the Sanger sequencing dataset was complete for 20 of the 26 ingroup samples processed. We were unable to amplify RAG-1 for two *L. u. castaneotinctus* samples and one *L. vociferans* sample, and recovered partial RAG-1 sequence data for samples of *L. fuscocinereus* and *L. lanioides*. For the same two *L. u. castaneotinctus* samples, we were unable to amplify RAG-2 and BF5. Details on the Sanger sequencing dataset are reported in Table S4.

We recovered an average of 2,069 of the 2,417 targeted sequence capture loci with an average coverage of 190x per locus across the 13 ingroup individuals. The final sequence capture dataset used for all phylogenetic analyses consisted of the 1,079 loci that were recovered from all 14 samples. For each sample, the number of loci recovered and information on average read depth and sequence length are reported in Table S5.

3.2. Phylogenetic relationships

Our phylogenetic results demonstrated improved resolution with increased sampling of tips and loci (Fig. 2). The well-supported relationships from Berv and Prum (2014), those with posterior probability (pp) > 0.9 (Fig. 2a), are supported by all our analyses. Our Sanger results, which were concordant between concatenated and species tree methods, additionally placed the two species unsampled in that study (Figs. 2b and S1). However, support at several nodes was poor (*BEAST pp ≤ 0.9 and RAxML bootstrap support [bs] ≤ 75) and three nodes were completely unresolved (pp ≤ 0.5). The analyses of the sequence capture dataset, conversely, resulted in a completely resolved tree with high support (ASTRAL and RAxML bs ≥ 90) at all nodes (Fig. 2c). The sequence capture topologies were identical between concatenated and summary species tree methods.

Our sequence capture tree reveals new phylogenetic hypotheses for key relationships in the study group (Fig. 2c). We confirmed that *Lipaugus* is paraphyletic with respect to *Tijuca*, and established that *Tijuca* is also not monophyletic when both species are sampled. We found the three Andean species in the group form a clade, with *L. weberi* sister to the *L. fuscocinereus-L. uropygialis* sister pair. Moving up the tree, single species then branch in sequence, first the Atlantic Forest taxa and then the lowland and Tepui species. Subtended by the oldest of these sequential divergence events, *L. unirufus* subsequently splits into two lineages corresponding to the two subspecies. Many of these relationships are also supported by the Sanger species trees as well as the individual gene trees from the Sanger sequencing dataset (Figs. S2–S5). Sanger sequencing gene trees, however, were characterized by high phylogenetic uncertainty (pp ≤ 0.95 and bs ≤ 75) at multiple internal nodes, leading to topological discordance among loci. Gene tree discordance is not surprising due to the potential for incomplete lineage sorting during the rapid successive speciation in this group, and to the possibility of estimation error resulting from examination of single loci with relatively few informative sites.

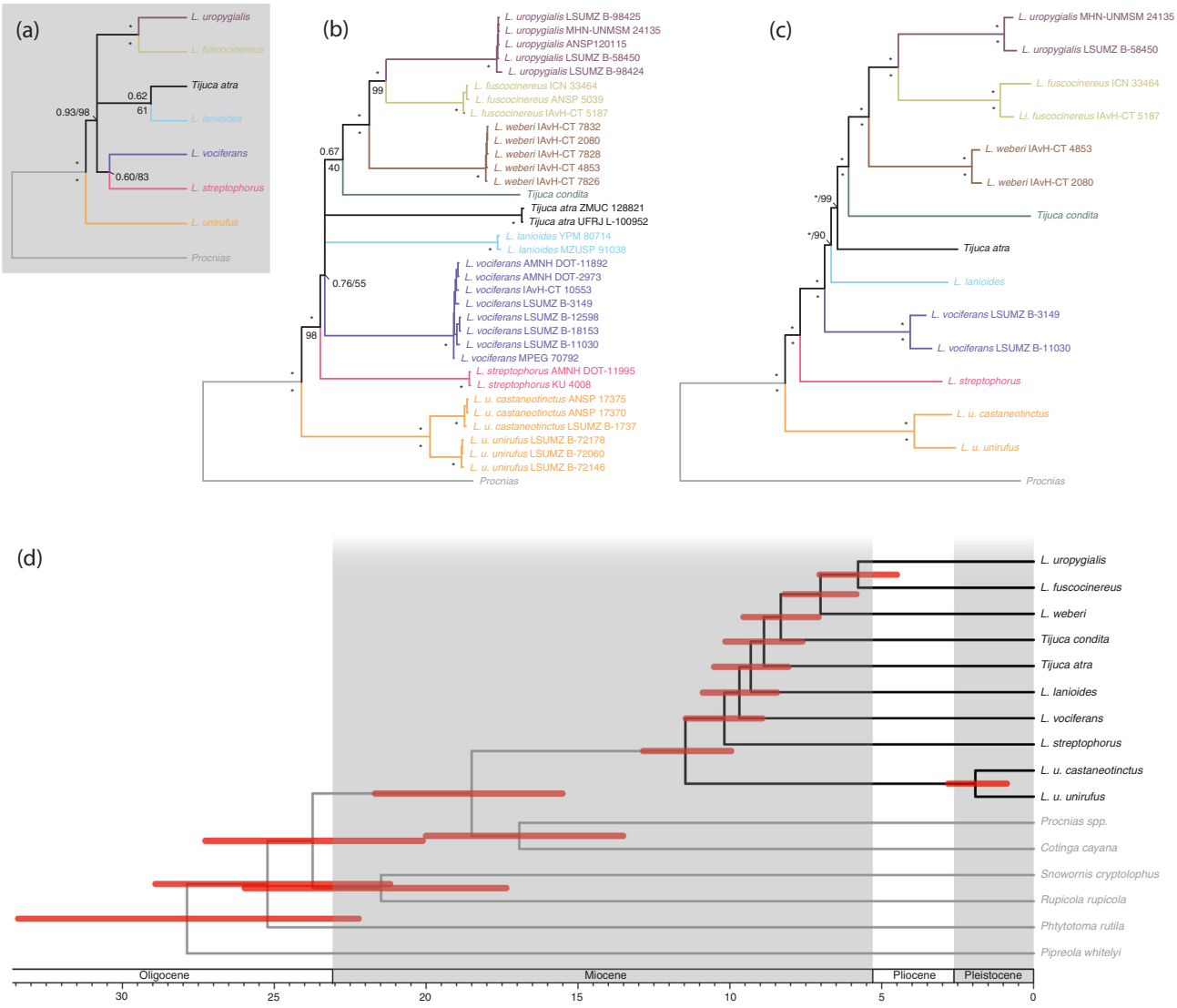

Fig. 2. A comparison of phylogenetic hypotheses for *Lipaugus* and *Tijuca*. Terminal branches leading to species are colored according to the range maps depicted in Fig. 1, sample numbers are provided where necessary to distinguish tips, nodes with < 0.50 posterior probability (pp) are collapsed, and asterisks depict complete support. (a) The phylogeny of Berv and Prum (2014) showing Bayesian pp from *BEAST (above branches or to the left of slashes) and RAxML bootstrap support (bs). (b) The Sanger phylogeny from this study. Branch lengths are from RAxML and values at nodes represent Bayesian pp from *BEAST (above branches or to the left of slashes) and RAxML bs. Support values are not provided for intraspecific relationships and only RAxML bs is provided for terminal taxa because support for those nodes was not estimated in *BEAST. (c) The phylogeny from sequence capture data. Branch lengths are from RAxML and values at nodes represent Bayesian pp from *BEAST (above branches or to the left of slashes) and RAxML bs. (d) The final time-calibrated tree from *BEAST analysis with relationships constrained using the sequence capture topology from (c) and divergence times estimated using the Sanger sequencing data combined with substitution rate estimates from prior studies. Red bars indicate 95% high posterior density of divergence times. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Timing of speciation events

The *BEAST tree estimated using Sanger sequencing loci and constrained to the completely resolved sequence capture topology reveals the dynamics of lineage formation within the *Lipaugus/Tijuca* clade. The lineage leading to *Lipaugus* and *Tijuca* diverged from its shared ancestor with *Procnias* and *Cotinga* in the early Miocene (95% highest posterior density interval [HPD] 22–16 million years ago, hereafter mya) (Fig. 2d). The crown age marking the onset of *Lipaugus-Tijuca* diversification is approximately 11 mya in the mid-Miocene (95% HPD 13–10 mya), and speciation events are clustered during that period with relatively long terminal branches subtending the tips. In fact, six of the eight speciation events in the group occurred during approximately three million years in the last third of the Miocene (95% HPD 13–7.1 mya). These successive speciation events are separated by short internodes with overlapping 95% HPD. The lineages leading to the three Atlantic forest species (*L. lanioides, T. atra,* and *T. condita*) originated during that period, prior to those that lead to the younger, Andean clade. Speciation within the clade of the three Andean species (*L. weberi, L. fuscocinereus, L. uropygialis*) began approximately 7.0 mya (95% HPD 8.2–5.8 Mya), at the end of the Miocene. The divergence between the two *L. unirufus* lineages occurred approximately 2 mya (95% HPD 0.9–2.8 mya), in the early Pleistocene. Divergence times in the *BEAST tree without the topological constraint were highly similar (Fig. S1).

4. Discussion

We resolved unknown and uncertain relationships within the cotingas by increasing both taxonomic and genomic sampling. Our results

confirmed relationships that were strongly supported by prior work (Berv and Prum, 2014). Our traditional Sanger sequencing dataset and complete taxon sampling additionally demonstrated (1) that *Tijuca* spp. are embedded separately within *Lipaugus*, (2) the first support for the genetic distinctness of the two *L. unirufus* subspecies, *L. u. castaneotinctus* and *L. u. unirufus*, and (3) that Andean species fall within a single clade, with *L. weberi* sister to the two larger Andean species. Our larger sequence capture dataset further resolved three recalcitrant nodes and (1) confirmed that *Tijuca* are not sister species and (2) established that branching events in *Lipaugus/Tijuca* involved successive divergences between a single species and a larger group (a "grade") beginning with the early split of the lineage leading to *L. unirufus* from the rest of the group, and followed by those of *L. streptophorus*, *L. vociferans*, *L. lanioides*, *T. atra*, and finally *T. condita*, sister to the Andean clade.

The increasing resolution observed in this study, particularly in the sequence capture dataset, suggests that the reconstruction of relationships in this group was made possible by the addition of more loci. It is possible that differences in phylogenetic methods also played a contributing role. For example, there is evidence that both concatenation and summary species tree methods, such as ASTRAL, can produce well-supported but spurious results in different circumstances. Concatenation fails to account for incomplete lineage sorting and associated gene tree discordance (Edwards et al., 2016), whereas summary species tree methods fail to account for gene tree uncertainty (Gatesy and Springer, 2014). The impacts of these deficiencies in model fit can become more severe as dataset size increases (Kumar et al., 2012). These effects might have led to the well-supported sequence capture trees. However, the impacts of model misspecification can be identified by comparing results across datasets and methods. The highly similar results between concatenated and ASTRAL analyses of the sequence capture dataset, and concordant results between analyses of the sequence capture dataset compared with those based on full gene tree – species tree methods applied to the Sanger sequencing dataset, suggest that the additional relationships resolved in the sequence capture dataset analyses are valid. The improved resolution we observed in *Lipaugus* and *Tijuca* is therefore best explained by increased genomic sampling, and we expect phylogenetic understanding in other groups similar in age would benefit from highly multilocus data.

Our highly resolved phylogeny of *Lipaugus* and *Tijuca* reveals a dynamic history resulting in distinct contrasts in diversity among habitats and regions. For example, species in both lowland habitats and in montane habitats occur in multiple locations in our tree, with most of the diversity found in the montane zone. Similar, sometimes evolutionarily rapid shifts between lowland and high-elevation distributions have been observed in other Neotropical birds (e.g., Brumfield and Edwards, 2007). In *Lipaugus*, the two lowland taxa (*L. vociferans* and *L. unirufus*) occur in two clades resulting from the earliest divergence in the group. Following the divergence of the lineage leading to *L. unirufus*, rapid diversification produced the lineages from which all extant montane species arose during an approximately four-million-year period in the last third of the Miocene. The broad HPD intervals of divergence dates in our time calibrated tree and our necessary reliance on substitution rate information rather than fossil calibrations preclude detailed interpretation of the absolute timing of evolutionary events. The mean crown age of our ingroup and outgroup samples, which includes the earliest divergence in Cotingidae (Berv and Prum, 2014), is actually older than mean stem ages for Cotingidae in two recent analyses (Claramunt and Cracraft, 2015, Oliveros et al., 2019), although confidence intervals overlap. Regardless, even if divergences estimates from our tree are inflated, the rapid diversification across South American *Lipaugus* and *Tijiuca* is broadly concurrent with intensification of uplift in Northern and Central Andean orogeny in the mid- to late-Miocene, beginning approximately between 12 and 10 mya (Gregory-Wodzicki, 2000; Hoorn et al., 2010). It seems possible that the formation of novel montane forest habitats during this period influenced the diversification of the species distributed in those habitats.

In the two widely distributed, lowland species in the study group we find contrasting patterns of geographic genetic differentiation. Samples of *L. unirufus* clustered into two distinct sister clades that appear to correspond to two subspecies (*L. u. castaneotinctus* from the southern Chocó and *L. u. unirufus* from Central America) in all mtDNA gene trees, with average sequence divergence in mtDNA of 4.3% (Table S6). These results support a long history of subspecies designation in this species (Hellmayr, 1929; Ridgway, 1906) and undescribed patterns of vocal variation (AMC, pers. obs.) to suggest that *L. unirufus* may contain marked intraspecific diversity. In contrast, we found low intraspecific diversity among our samples of the widespread *L. vociferans*, which agrees with the lack of described phenotypic variation. Despite sampling at localities as distant as 3,800 km apart, average mitochondrial divergence in *L. vociferans* (0.03%, Table S6) was similar to related species with more restricted ranges, such as *L. lanioides* and *L. fuscocinereus* (0.02–0.03%) (Fig. 1). Further geographic sampling within both *L. unirufus* and *L. vociferans* would be useful to more fully characterize geographic diversity in both species.

We demonstrated that *Lipaugus* and *Tijuca* are paraphyletic as currently defined, allowing us to propose a revised classification of this group of cotingas. As suggested previously by the phylogenetic affinities between *T. atra* and *Lipaugus* taxa (Berv and Prum, 2014; Ohlson et al., 2007), the genus *Tijuca* Ferussac 1829 should be subsumed with *Lipaugus* Boie 1828, which has nomenclatural priority. Maintaining the genus *Tijuca* is untenable because *T. atra* (type species of *Tijuca*) is not sister to *T. condita*. To maintain *Tijuca* one would need to erect new genus-level names for *L. unirufus, L. streptophorus,* and *T. condita*, and resurrect *Chirocylla* Sclater and Salvin 1876 (for *L. uropygialis, L. fuscocinereus,* and *L. weberi*) and *Turdampelis* Lesson 1844 (for *L. lanioides*). *Lathria* is not available because it is a junior synonym of *L. vociferans* (Prum, 2001). Therefore, we recommend treating *Tijuca* as a junior synonym of *Lipaugus*, which is masculine. Nine species are hereafter in the genus *Lipaugus*: *L. unirufus, L. streptophorus, L. vociferans, L. lanioides, L. ater, L. conditus, L. weberi, L. uropygialis,* and *L. fuscocinereus*.

CRediT authorship contribution statement

Amie E. Settlecowski: Conceptualization, Investigation, Formal analysis, Data curation, Writing - original draft, Visualization. **Andrés M. Cuervo:** Conceptualization, Methodology, Formal analysis, Data curation, Resources, Writing - review & editing, Project administration. **José G. Tello:** Resources. **Michael G. Harvey:** Formal analysis, Data curation, Writing - review & editing, Visualization. **Robb T. Brumfield:** Resources, Funding acquisition, Writing - review & editing. **Elizabeth P. Derryberry:** Supervision, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2020.106779.

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