

1 **Extreme genetic structure and dynamic range evolution in a montane**
2 **passerine bird: implications for tropical diversification**

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17 **Abstract**

18 **Aim:** Employ phylogeographic analyses of a widespread species complex to examine the role of historical and
19 evolutionary processes in the origin and maintenance of high species diversity in the Neotropical montane region.
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21 **Location:** Neotropical highlands.
22

23 **Taxon:** *Henicorhina* wood-wrens (Aves, Troglodytidae).
24

25 **Methods:** We collected mtDNA sequence data for 288 individuals thoroughly covering the range of the *Henicorhina*
26 *leucophrys* complex from Mexico to Bolivia. Sequences were employed to characterize population structure, infer
27 phylogenetic relationships among populations and their divergence times, examine lineage accumulation through time,
28 and identify presumptive species using coalescent methods. We also explored the origin of elevational and latitudinal
29 replacements involved in spatial changes in species assemblages in the Andes.
30

31 **Results:** We found remarkable genetic structure within the complex, which consists of numerous lineages reaching
32 >12% sequence divergence; most divergent populations occur in areas separated by topographic barriers but several of
33 them, typically not sister to each other, co-occur with elevational segregation on mountain slopes or replace each other
34 with latitude along the Andes. Some close relatives occur in areas separated by thousands of kilometers, with more
35 distant relatives occupying intervening areas. The complex likely originated in the Mexican highlands and expanded
36 extensively in South America while diverging rapidly at a constant rate into many different lineages which have
37 persisted for millions of years. Coalescent analyses consistently revealed that the complex may comprise more than 30
38 species; while we do not suggest these presumptive species should be recognized by taxonomists in the absence of
39 additional data, *H. leucophrys* is a distant outlier among New World birds in terms of high lineage diversity within a
40 single recognized species.
41

42 **Main Conclusions:** Our study captured wood-wren lineages in the act of building up diversity via divergence and
43 persistence in allopatry, achievement of secondary sympatry, and coexistence at the landscape scale mediated by
44 ecological and evolutionary divergence. Although dispersal by wood-wrens is restricted at present and this likely
45 accounts for strong population structure across topographic barriers, their ranges have been dynamic, managing to
46 disperse over much of the montane Neotropics. Phases of expansion and contraction of ranges and localized extinctions
47 of populations likely account for phylogeographic patterns which are precursors to the origin of new species and the
48 accumulation of diversity in tropical mountains.
49

50 **Key words:** Andes, elevational replacement, range expansion, speciation
51

52 Introduction

53 Mountains in the tropics contribute disproportionately to regional species richness given their area in comparison to
54 lowlands, and are often considered global hotspots of biological diversity and endemism (Stattersfield *et al.*, 1997;
55 Orme *et al.*, 2005; Fjelds  *et al.*, 2012). Tropical mountains exhibit particularly high beta diversity (i.e. species
56 turnover in space) because (1) species assemblages shift along elevational gradients, and (2) related species occupy
57 similar elevations in different mountains or in sectors of a mountain separated by geographic barriers. While
58 knowledge of the biodiversity of mountains has advanced conceptually (Graham *et al.*, 2014; Bertuzzo *et al.*, 2016;
59 Badgley *et al.*, 2017) and empirically (e.g., Patterson *et al.*, 1998; Jankowski *et al.*, 2009; McCain, 2009; Price *et al.*,
60 2014; Peters *et al.*, 2016; Quintero & Jetz, 2018), accounting for species richness in montane systems remains difficult.
61 In particular, although climate and available energy have an imprint globally on the distribution of life (Francis &
62 Currie, 2003; Hawkins *et al.*, 2003), they cannot predict the agglomeration of range-restricted species in tropical
63 mountains (Rahbek & Graves, 2001; Jetz & Rahbek, 2002; Rahbek *et al.*, 2007; but see Ruggiero & Hawkins, 2008).
64 Because the high richness and uniqueness of mountains in the tropics may instead reflect high speciation rates or low
65 extinction rates (Jetz *et al.*, 2004; Badgley *et al.*, 2017), considering evolutionary processes is crucial to a better
66 understanding of montane diversity (Graham *et al.*, 2014; Laiolo *et al.*, 2018; Quintero & Jetz, 2018).

67 Dozens of studies have used phylogenetic and population genetic perspectives to probe into evolutionary processes
68 underlying patterns of avian diversity in the Neotropical mountains. Birds have diversified rapidly in the Andes, with
69 pivotal roles of features of the landscape (e.g., low-lying valleys, high-elevation passes) and of climatic changes as
70 drivers of divergence (P rez-Em n, 2005; Weir, 2006; Cadena *et al.*, 2007; Ribas *et al.*, 2007; Sedano & Burns, 2010;
71 Chaves *et al.*, 2011; Guti rrez-Pinto *et al.*, 2012; Valderrama *et al.*, 2014; Benham *et al.*, 2015; S nchez-Gonz lez *et*
72 *al.*, 2015; Winger & Bates, 2015; Prieto-Torres *et al.*, 2018). Allopatric differentiation of lineages separated by barriers
73 to dispersal is predominant (Hazzi *et al.*, 2018), whereas evidence for speciation in parapatry along mountain slopes
74 remains elusive (Patton & Smith, 1992; Garc a-Moreno & Fjelds , 2000; Cadena *et al.*, 2012; Caro *et al.*, 2013). Thus,
75 the replacement of closely related species along elevational gradients, a salient geographic pattern in tropical avifaunas
76 (Terborgh, 1971, 1977), appears to result largely from populations coming into secondary contact after allopatric
77 divergence (Diamond, 1973; Cadena, 2007; Freeman, 2015). However, with hundreds of bird species living in the
78 Neotropical mountains, much remains to be learned about the histories of individual clades and about how such
79 histories collectively resulted in the patterns of diversity we observe today.

80 Before conducting analyses seeking to characterize and account for patterns of diversity one must have proper
81 knowledge of what species exist and where they occur (Fine, 2015). Traditionally, the species-level taxonomy of birds
82 was considered well-known (Scheffers *et al.*, 2012), with suggestions that the inventory of species was essentially
83 complete by the mid 20th century (Mayr, 1946). This, however, proved incorrect: multiple avian species have been
84 discovered and described over recent decades, and analyses of novel data sets (notably, of vocal and genetic variation)
85 have revealed that species-level diversity was seriously underestimated (Fjelds , 2013). The extent to which avian
86 taxonomy will require revision depends on how one delimits species (Tobias *et al.*, 2010; Gill, 2014; Toews, 2015;
87 Barrowclough *et al.*, 2016; Remsen, 2016), but clearly there are more species of birds than traditionally thought,
88 particularly in the tropics. Although problems with species delimitation are unlikely to affect assessments of patterns
89 in local (alpha) diversity of birds, inadequate knowledge of species limits may seriously influence perceptions of
90 patterns in species turnover in space and hence regional and global patterns of diversity (beta and gamma diversity).
91 Alternative approaches for species delimitation may also influence inferences about biogeographic history (Smith *et al.*,
92 2018).

93 Birds in which species diversity is likely greater than traditionally thought are those in which plumages vary subtly
94 (in which case one would expect species recognition to be based more on vocal cues), and in which ecologically
95 relevant traits (body size, habitat, dispersal ability) may be conducive to population isolation (Burney & Brumfield,
96 2009; Salisbury *et al.*, 2012; Smith *et al.*, 2014; Harvey *et al.*, 2017a). Here, we analyze the phylogeography of the
97 Grey-breasted Wood-wren complex (*Henicorhina leucophrys*, Troglodytidae), a group of small, drably colored and
98 highly vocal songbirds of forest interior, with poor dispersal abilities. Because the complex is broadly distributed from

99 Mexico to Bolivia and restricted to montane forest habitats, it is an appropriate system in which to ask questions
100 relevant to understanding the role of evolutionary processes in establishing patterns of diversity in Neotropical
101 mountains. We used extensive geographic sampling to reconstruct the phylogenetic relationships of populations in the
102 complex and to characterize patterns of genetic variation with the goals of (1) gaining insight about the tempo and
103 mode of evolutionary differentiation and on the role of colonization of new regions in diversification, (2) understanding
104 the role of geographic isolation in the differentiation of lineages, and (3) exploring the origin of elevational
105 replacements leading to changes in species assemblages with elevation. We also examined the extent to which current
106 taxonomy adequately reflects true diversity and reflected on the influence of cryptic differentiation for inferences about
107 diversification processes and patterns of diversity in the tropics.

108 **Methods**

109 **Study system**

110 *Henicorhina* wrens (Troglodytidae) range widely in the Neotropical region. Traditionally, taxonomists recognized two
111 widespread species, the White-breasted Wood-Wren (*H. leucosticta*) and the Grey-breasted Wood-Wren (*H.*
112 *leucophrys*). Two species with restricted ranges, Bar-winged Wood-Wren (*H. leucoptera*) from southern Ecuador and
113 northern Peru (Fitzpatrick *et al.*, 1977), and Munchique Wood-Wren (*H. negreti*) from western Colombia (Salaman *et*
114 *al.*, 2003), were later described. More recently, another narrow endemic formerly considered a subspecies of *H.*
115 *leucophrys*, Hermit Wood-Wren (*H. anachoreta*) from northern Colombia, was elevated to species status (Cadena *et*
116 *al.*, 2016). Preliminary data on phylogenetics and population structure of wood-wrens based on mitochondrial DNA
117 sequences suggest that both *H. leucosticta* and *H. leucophrys* are paraphyletic (*H. leucoptera* is nested within *H.*
118 *leucosticta* and *H. anachoreta* is nested within *H. leucophrys*), and both comprise multiple distinct lineages (Dingle *et*
119 *al.*, 2006; Becker *et al.*, 2007; Caro *et al.*, 2013; Aguilar *et al.*, 2014; Smith *et al.*, 2014). However, no comprehensive
120 analysis of genetic variation across the range of either widespread species has been conducted.

121 Wood-wrens segregate ecologically by elevation. Overall, *H. leucosticta* is a lowland species replaced in montane areas
122 by *H. leucophrys*; their replacement is sharp and likely mediated by interspecific competition (Jankowski *et al.*, 2010).
123 In the isolated Cordillera del C6ndor of southern Ecuador and northern Peru, *H. leucophrys* also replaces *H.*
124 *leucosticta* in montane areas but is absent from higher elevations where *H. leucoptera* occurs (i.e. the three species
125 turn over along the elevation gradient; Fitzpatrick *et al.*, 1977; Dingle *et al.*, 2006). Likewise, in part of the western
126 slope of the Colombian Andes, *H. negreti* replaces *H. leucophrys* (subspecies *brunneiceps*) at higher elevations, and is
127 in turn replaced by nominate *H. leucophrys* east of the ridgeline on the eastern slope of the cordillera (Salaman *et al.*,
128 2003). In addition, two populations of *H. leucophrys* differing in mtDNA sequences, morphology, and songs are
129 parapatrically distributed along an elevational gradient in Ecuador (Dingle *et al.*, 2008; Dingle *et al.*, 2010), but
130 nuclear gene flow indicates they are conspecific (Halfwerk *et al.*, 2016). A similar scenario with populations differing
131 genetically, morphologically and vocally, and turning over along an elevational gradient exists in the Sierra Nevada de
132 Santa Marta, northern Colombia (Caro *et al.*, 2013; Burbidge *et al.*, 2015); because there is little to no hybridization,
133 these populations are now treated as separate species, with *H. anachoreta* sharply replacing *H. leucophrys* at higher
134 elevations (Cadena *et al.*, 2016).

135 **Sampling**

136 We focused on the *H. leucophrys* complex, i.e. the clade defined by the most recent common ancestor of populations
137 referable to *H. leucophrys* in current taxonomy and *H. anachoreta* (Dingle *et al.*, 2006; Caro *et al.*, 2013). Although *H.*
138 *negreti* was not sampled in previous molecular analyses, we consider it part of the complex based on phenotypic traits
139 (Salaman *et al.*, 2003) and our data (see below). The *H. leucophrys* complex is widespread in Neotropical mountains,
140 ranging from Mexico to Bolivia (Figure 1); as currently circumscribed, it consists of 19 taxa including *H. anachoreta*,
141 *H. negreti*, and 17 subspecies of *H. leucophrys* (Kroodsmas & Brewer, 2005). For phylogeographic analyses, we sought
142 to sample as thoroughly as possible across geography and taxonomy. Combining sequences generated for this study
143 and published sequences available in GenBank (total 288 individuals), we managed to cover nearly all of the
144 distribution range of the complex and all named taxa, with multiple individuals and localities per taxon whenever

145 possible (Figure 1; Supplementary Table 1). Sampling in Middle America covered all the major montane areas where
146 members of the complex occur; within South America sampling was especially thorough in Venezuela, Colombia and
147 Ecuador, and less so in the southern part of the range (i.e. Peru and Bolivia). As outgroups for phylogenetic analyses,
148 we used specimens of *H. leucosticta* and *H. leucoptera*, and of species of *Microcerculus*, *Campylorhynchus*,
149 *Cistothorus*, *Troglodytes*, *Cantorchilus* and *Cyphorhinus* (see Barker, 2017 for an overview of relationships among
150 wren genera), for a grand total of 300 individuals considered in analyses.

151 DNA extraction and sequencing

152 We extracted DNA using DNeasy tissue extraction kits (Qiagen, Valencia, CA) following the manufacturer's protocol.
153 We then amplified an 842 base-pair region of the mtDNA gene ATPase 6/8 using primers described by Joseph et al.
154 (2004). We chose to sequence this region because it has been employed in earlier studies of *Henicorhina* (Dingle et al.,
155 2006; Dingle et al., 2008; Caro et al., 2013), which enabled us to include published sequences in analyses. Fragments
156 were amplified via polymerase chain reaction (PCR) in 12.5 µl reactions with denaturation at 94 °C for 10 min, 40
157 cycles of 94 °C for 30 s, 54 °C for 45 s, and 72 °C for 2 min, followed by 10 min elongation at 72 °C and 4 °C soak.
158 PCR products were sequenced at the Barrick Museum of Natural History (University of Nevada, Las Vegas),
159 Universidad de los Andes (Bogotá, Colombia), or the High-Throughput Genomics Unit at the University of
160 Washington. Chromatograms were aligned using Sequencher v4.9 (GeneCodes Corporation, Ann Arbor, MI).

161 Analyses

162 Gene trees

163 Before phylogenetic analyses, we determined the best-fit model of evolution to be GTR + G with jModeltest v2. 1. 7
164 (Posada, 2008). We then used Bayesian (BEAST v1.8.4; Drummond et al., 2012) and maximum-likelihood (RAxML v
165 8.2.4; Stamatakis, 2006) methods to estimate phylogenetic trees. For the Bayesian analyses we ran 50 million
166 generations, sampling trees and parameters every 5000 generations. A relaxed uncorrelated lognormal clock with a rate
167 of 2% and a birth-death speciation tree prior (Ritchie et al., 2017) were applied. We confirmed likelihood stationarity
168 and adequate effective sample sizes above 200 for all estimated parameters using Tracer v1.6.0
169 (<http://tree.bio.ed.ac.uk/software/tracer>). The parameter values of the samples from the posterior distribution on the
170 maximum clade credibility tree were summarized after discarding the first 5 million generations (10%) as burn-in
171 using TreeAnnotator v1.8.4 (Drummond et al., 2012). Maximum-likelihood analyses were conducted using a
172 GTRGAMMA model and run for 1000 nonparametric rapid bootstrap replicates to provide an assessment of nodal
173 support.

174 Both Bayesian and maximum-likelihood analyses were first done with a dataset containing all ATPase sequences (n =
175 300), then repeated with a reduced data set containing only individuals having unique haplotypes (n = 184), and then
176 reduced further by removing all non-*Henicorhina* taxa (i.e. outgroups). Trees constructed using the latter data set (n
177 = 178) were set aside for use in species delimitation analyses described below. To visualize and annotate trees and to
178 produce figures, we employed R packages ggtree (Guangchuang et al., 2017) and phytools (Revell, 2012), and QGIS v
179 2.18.20 with the Qgis2threejs plugin (<http://qgis.osgeo.org>).

180 Species delimitation

181 Given uncertainty about species diversity in the *H. leucophrys* complex, we employed two coalescent approaches using
182 mtDNA data to identify distinct lineages which may be considered presumptive species worthy of additional study
183 with other sources of information (Carstens et al., 2013; Sukumaran & Knowles, 2017): (1) multi-rate Poisson Tree
184 Processes (mPTP v0.2.0; Kapli et al., 2017) and (2) a Bayesian implementation of the General Mixed Yule Coalescent
185 Model (bGMYC v1.0.2; Reid & Carstens, 2012). The trees generated by BEAST using the unique haplotype dataset
186 were used as input for these analyses.

187 For the mPTP analysis we ran five replicate mcmc chains of 10,000,000 generations, sampling every 10,000 with a
188 burn-in of 1,000,000 (10%) using the maximum clade credibility tree obtained as described above. Minimum branch
189 length was calculated using the `minbr_auto` function prior to the analysis. We ran bGMYC with 100 of the 10,000
190 gene trees estimated in the BEAST analysis, after removing 10% as burn-in; this approach accounts for error in gene-
191 tree estimation by integrating over uncertainty in tree topology and branch lengths. For each tree we ran an MCMC
192 chain of 50,000 steps with 40,000 steps of burn-in and a thinning interval of 100 steps. We focused our results and
193 discussion on lineages (i.e. presumptive species) defined using a threshold of 0.5 on probability of membership of
194 individuals (Gehara *et al.*, 2017). However, we also considered more conservative approaches where presumptive
195 species were identified as clusters in the gene tree with posterior probabilities of belonging to the same species ≥ 0.90
196 or ≥ 0.95 , which allowed us to compare our results to similar work on other birds (Smith *et al.*, 2014; Harvey *et al.*,
197 2017b; Smith *et al.*, 2017).

198 *Diversification through time*

199 To describe patterns of lineage accumulation over time, we constructed lineage-through-time (LTT) plots and
200 estimated the gamma statistic (Pybus *et al.*, 2000). We accounted for phylogenetic uncertainty by performing these
201 analyses on a sample of credible trees in the posterior distribution obtained from the BEAST analysis. We employed
202 the 100 trees constructed using only unique haplotypes as input for the bGMYC analyses and trimmed them to
203 include 39 tips corresponding to the presumptive species recognized under the 0.5 threshold. Then we used functions
204 implemented in R packages `ape` (Paradis *et al.*, 2004) and `paleotree` (Bapst, 2012) to build an LTT plot with a 95%
205 confidence interval and to calculate the gamma statistic for each tree. We also examined diversification dynamics
206 employing Bayesian Analysis of Macroevolutionary Mixtures (program BAMM v 2.5.0; Rabosky *et al.*, 2013). Because
207 results were qualitatively similar between methods, we report only those obtained using the simpler approach
208 implemented in `ape`.

209 **Results**

210 We found substantial genetic differentiation among populations in the *H. leucophrys* complex. In total, we recovered
211 172 haplotypes among the 288 individuals analyzed. Several haplotypes were highly divergent from each other, with
212 uncorrected genetic distances between them reaching $>12\%$ (i.e. between individuals from Sierra Madre del Sur of
213 Mexico and from the east slope of the Cordillera Occidental of Colombia). Genetic variation was highly structured
214 spatially, but was not readily accounted for by geographic distance among populations. We did not conduct formal
215 analyses of isolation by distance, but genetic distances among isolated populations from adjacent mountains were often
216 much greater than genetic distances observed over larger distances in more continuous ranges. For instance, mean
217 genetic distances among the five montane areas of Venezuela that we sampled was 7.3% (range 6.1%-8.3%), whereas
218 genetic distances within montane regions extending over comparable distances were much lower, e.g. reaching only
219 3.5% in the Sierra Madre Oriental of Mexico or 1.7% in the Talamanca-Chiriquí mountains of Costa Rica and
220 Panama.

221 Maximum-likelihood and Bayesian phylogenetic analyses recovered similar overall patterns (Figure 2., Supplementary
222 Figures 1-2). The deepest split in gene trees separates clades corresponding to Mexican populations from the Sierra
223 Madre del Sur and the western reaches of the Trans-Mexican Volcanic Belt from a large and strongly supported clade
224 including the remainder of populations in the complex. Within the latter clade, the earliest diverging group occurs in
225 eastern Mexico and consists of three subclades, each corresponding to a unique region within the Sierra Madre
226 Oriental. Sister to this group is a clade divided in two main groups (albeit without strong support, i.e. 0.88 posterior
227 probability, 68% ML bootstrap in analyses using only unique haplotypes): one includes samples from lower Central
228 America (Costa Rica and Panama, subspecies *collina*), whereas the other includes all South American populations of
229 *H. leucophrys*, the Colombian endemic species *H. anachoreta* and *H. negreti*, and a clade formed by samples of *H.*
230 *leucophrys* from Chiapas (Mexico), Guatemala, and El Salvador (subspecies *castanea* and *composita*). The latter clade,
231 of somewhat uncertain affinities within an otherwise South American group (it was recovered as sister to *H. negreti*
232 with 0.95 posterior probability and 56% ML bootstrap in analyses using only unique haplotypes), is the only exception
233 to the pattern in which Mexican and Central American populations are the earliest diverging lineages in the complex.

234 Basal relationships among major South American lineages were unresolved or poorly supported, yet some patterns in
235 the region are noteworthy. Whereas populations from some isolated montane systems (e.g. the Serranía de Perijá, or
236 the Venezuelan Cordillera de la Costa and Sierra de San Luis) formed distinct clades, this was not the case for the
237 main cordilleras of the northern Andes, resulting in complicated patterns of area relationships. For example, several
238 populations from the western slope of the Andes from Colombia through Ecuador and into northwestern Peru formed
239 a large clade (clade i. in Figure 2), but this clade was not exclusive because it also included some -but not all-
240 populations from the northern sector of the Cordillera Central of Colombia and did not cluster all populations from
241 the western Andes: *H. negreti* and lineages of *H. leucophrys* from the northern and southern sectors of the Cordillera
242 Occidental of Colombia and from western Ecuador occupied different positions in the tree. Likewise, birds from the
243 Cordillera Oriental of the Colombian Andes formed multiple distinct clades seemingly distantly related to each other,
244 and populations from the Central and Southern Andes (i.e. from Bolivia and Peru south of the Marañón Valley or
245 North Peru Low) formed at least two highly divergent clades with differing affinities. Given weak support for deep
246 branches in South America we do not elaborate further on relationships among major biogeographic areas, but do
247 emphasize the complexity of phylogeographic pattern and the strong genetic structure existing over relatively fine
248 spatial scales throughout the continent.

249 Part of the complexity in phylogeographic pattern related to occurrence of phylogenetically distant groups in the same
250 regions can be understood by examining elevational distributions: lineages known to replace each other along
251 elevational gradients in northern South America are not sister to each other (Figure 3). This was true of taxa
252 occurring in the Ecuadorean Andes (*H. l. hilaris* and nominate *H. l. leucophrys*), the Santa Marta mountains (*H. l.*
253 *bangsi* and *H. anachoreta*), and in the western slope of the Colombian Andes (*H. l. brunneiceps* and *H. negreti*). Our
254 data further revealed a previously unknown case of cryptic replacement of mtDNA lineages along an elevational
255 gradient in the Venezuelan Andes. The lineage occurring in the Tamá massif near the Colombia-Venezuela border
256 crosses the Táchira depression to the northeast into the Cordillera de Mérida where we found it from c. 1520 m to c.
257 1920 m. Only a small distance upslope in this range, a different lineage occupied elevations from c. 2100 m to c. 2750
258 m. Divergence in mtDNA sequences between lineages replacing each other with elevation was substantial, in all cases
259 exceeding 5% uncorrected *p* distances (Figure 3).

260 In addition to examples of elevational parapatry, our analyses revealed cases where lineages may meet in contact zones
261 along a latitudinal axis. For instance, two lineages differing in c. 7% uncorrected *p*-distance replace each other along
262 the northern sector of the Cordillera Central of the Colombian Andes. One of these lineages occurs in the northern tip
263 of the cordillera in Antioquia, whereas the other is also found in Antioquia, where we suspect it might range north to
264 the southern extreme of the Aburrá Valley in the outskirts of the city of Medellín. Individuals occupying the northern
265 extreme of the Cordillera Central are most closely allied to geographically distant populations from the western slope
266 of the Andes (i.e. subspecies *hilaris* and *brunneiceps*), which tend to occur at lower elevations and are replaced upslope
267 by nominate *H. leucophrys* in Ecuador or *H. negreti* in southwest Colombia. Several other examples of distinct
268 lineages occurring at different latitudes within mountain systems exist in the Cordillera Oriental of Colombia and
269 along the Andes of Ecuador (Figure 2).

270 Coalescent approaches to delimit species produced consistent results: both mPTP and bGMYC (the latter with a 0.50
271 probability threshold to define group membership) recovered *H. anachoreta* and *H. negreti* as distinct species, and
272 both methods identified 37 additional lineages in the *H. leucophrys* complex which may prove to be distinct species
273 (Figure 2, Supplementary Figure 3). Although methods did not exactly agree in how they assigned individuals to
274 presumptive species, congruence was remarkable. The only differences were that in the Cordillera de Mérida,
275 Venezuela, mPTP recognized three presumptive species while bGMYC recognized two, and that in a clade from
276 northern Peru and southeast Ecuador mPTP recognized a single presumptive species and bGMYC recognized two
277 (Figure 2). Applying more stringent probability thresholds to delimit species in bGMYC analyses resulted in the
278 inference of slightly lower numbers of presumptive species: 36 and 35 with 0.90 and 0.95 thresholds, respectively. In
279 general, presumptive species appear to have restricted ranges (Figure 4, Supplementary Figure 4); in some cases,
280 particular mountain systems harbor a single presumptive species (e.g. Sierra Madre del Sur and Trans-Mexican
281 Volcanic Belt in Mexico, Cordillera de la Costa and Sierra de San Luis in Venezuela), but more than one presumptive
282 species may also occur within a region (e.g. Sierra Madre Oriental of Mexico, Sierra Nevada de Santa Marta in

283 Colombia) and a few of them have ranges encompassing various montane areas (e.g. across cordilleras of Costa Rica
284 and Panama). The diversity of presumptive species is especially remarkable in northern South America, with 7-8
285 identified in Venezuela, 15 in Colombia, and 7-8 in Ecuador. Because our sampling was sparser in Peru and Bolivia,
286 our figures for these countries are likely underestimates of presumptive species richness.

287 Our estimates of divergence times obtained from the BEAST analysis of unique haplotypes indicate that the *H.*
288 *leucophrys* complex diverged from its sister group (i.e. the clade formed by *H. leucosticta* and *H. leucoptera*)
289 approximately 16.8 million years before present (13.0-20.5 95% highest posterior density, HPD), with the crown age of
290 extant populations dating to 10.6 m.a. (8.4-13.1 95% HPD). Over this period, the complex has diversified into
291 multiple lineages; we found it minimally consists of 10 lineages of at least 5 million years of age and of 26 lineages of
292 at least 2 million years of age (Figure 2, Supplementary Figure 3). The estimated age of the node including all South
293 American populations as well populations from Chiapas, Guatemala, and El Salvador is 6.2 m.a. (5.2-7.3 95% HPD),
294 whereas that of the node including all South American populations excluding *H. negreti* is 5.8 m.a. (4.9-6.7 95%
295 HPD).

296 Analyses of lineage accumulation over time based on presumptive species identified by bGMYP suggested that rates of
297 diversification in the *H. leucophrys* complex may have declined over time, with a significantly negative gamma
298 statistic (Figure 5). However, through much of the history of the complex, diversification appears to have been nearly
299 constant and exponential, with an apparent downturn in the last million years most likely reflecting that our species
300 delimitation analyses recognized no species younger than this age.

301 Discussion

302 *Phylogeography: bridges, barriers and the distribution of genetic variation.*

303 As evidenced by the branching pattern in the gene tree with deep splits involving populations from the north, the *H.*
304 *leucophrys* complex likely originated in the Mexican highlands ca. 8 to 13 m.a., from where it expanded south through
305 Central America, then colonizing South America. Other birds ranging broadly in montane forests also originated in
306 the northern Neotropics, including single species as well as clades which diversified in Central and South America
307 (Pérez-Emán, 2005; Cadena *et al.*, 2007; Weir *et al.*, 2008; Sánchez-González *et al.*, 2015). Molecular-based estimates
308 of when did birds colonize South America from the north vary (Bacon *et al.*, 2015; Barker *et al.*, 2015); our results
309 indicate colonization by the *H. leucophrys* complex occurred slightly earlier (ca. 7 to 5 m.a.) than a pulse of avian
310 interchange via the Isthmus of Panama 4 to 2 m.a. (Smith & Klicka, 2010). Our estimates of the age of the *H.*
311 *leucophrys* complex and of the timing of events like its colonization of South America are old relative to what one
312 would expect given published estimates of divergence times among wren genera (Barker, 2017). However, such
313 estimates were derived assuming that *Certhia* and *Troglodytes* diverged ca. 16 m.a. (Moyle *et al.*, 2016), while
314 analyses integrating more extensive fossil evidence suggest such divergence occurred much earlier, ca. 27 m.a.
315 (Claramunt & Cracraft, 2015). The time frame for wren diversification implied by the latter analysis is more
316 congruent with our estimated ages for nodes in *Henicorhina* and with previous work in other wren genera based on
317 mtDNA data (Barker, 2007).

318 Poorly supported relationships among South American clades associated with short internodes subtending long
319 branches are common to *H. leucophrys* and other birds colonizing South America from the north (e.g., Pérez-Emán,
320 2005; Cadena *et al.*, 2007). This indicates range expansions and ensuing rapid diversification of lineages in geographic
321 isolation, a pattern also documented in montane clades with South American (Chaves *et al.*, 2011) or uncertain
322 geographic origins (Gutiérrez-Pinto *et al.*, 2012). Rapid range expansions occurring in concert across birds may
323 indicate that geological changes like closure of the Isthmus of Panama and uplift of mountains increased connectivity
324 among formerly isolated regions, enabling subsequent diversification of various taxa over the vast South American
325 landscape; climatic changes driving population isolation likely facilitated such diversification (Barrantes, 2009;
326 Ramírez-Barahona & Eguiarte, 2013).

327 Genetic divergence associated with landscape features isolating montane habitats is another pattern shared by the *H.*
328 *leucophrys* complex and co-distributed clades (Weir, 2009). Such features include lowland areas in Central America
329 (Cadena *et al.*, 2007; Barber & Klicka, 2010), inter-Andean valleys like the Magdalena and Marañón (Gutiérrez-Pinto
330 *et al.*, 2012; Benham *et al.*, 2015), and alpine areas separating slopes of cordilleras (Parra *et al.*, 2009; Valderrama *et*
331 *al.*, 2014). For many Neotropical montane birds that have been studied, genetic structure across geographic barriers
332 coincides with plumage differences (Cadena *et al.*, 2011; Winger & Bates, 2015; Winger, 2017). Phenotypic differences
333 among distinct lineages of *H. leucophrys*, however, are either subtle or appear to be nonexistent (Kroodsma & Brewer,
334 2005). Reduced gene flow across barriers may have influenced vocal differentiation of wood-wrens more strongly, but
335 given their complex songs, confirming it awaits studies documenting repertoires of individuals as well as variation
336 within and among populations. Such data are relevant given uncertainty about species limits in the complex (see
337 below) because vocalizations likely play a critical role in species recognition (Caro *et al.*, 2013; but see Halfwerk *et al.*,
338 2016).

339 In sum, our study and other phylogeographic analyses point to geological and climatic dynamics of the montane
340 Neotropics as drivers of avian speciation both by (1) promoting dispersal across formerly isolated areas and (2)
341 spurring diversification linked to the origin of new habitats resulting from uplift processes and vicariance.
342 Furthermore, because wood-wrens live in rugged landscapes and disperse little, their populations may become isolated
343 and diverge even without marked geological or climatic changes (Smith *et al.*, 2014). Beyond patterns common to the
344 *H. leucophrys* complex and other tropical montane birds, two aspects appear unique to our study system. First, the
345 degree of genetic structure within a single recognized species we uncovered far exceeds that observed in other montane
346 birds. Second, our finding that distinct mtDNA lineages which likely diverged in allopatry have come into contact in
347 various regions and some coexist segregated by elevation is novel. Because the extreme genetic structure we uncovered
348 may imply that *H. leucophrys* comprises more species than traditionally thought and because secondary sympatry of
349 divergent populations is crucial to the buildup of species richness, these results have implications for understanding
350 tropical diversity and the historical and evolutionary processes generating and sustaining it.

351 ***Extreme population structure, cryptic divergence, and patterns in tropical diversity***

352 We uncovered genetic structure in the *H. leucophrys* complex across well-known geographic barriers (Hazzi *et al.*,
353 2018), but also over fine scales in ways not associated with divergence in other tropical montane birds. For example,
354 in the Cordillera Occidental and Cordillera Central of Colombia, where other birds show little to no population
355 structure (Cadena *et al.*, 2007; Gutiérrez-Pinto *et al.*, 2012; Isler *et al.*, 2012; Valderrama *et al.*, 2014), we found six
356 mtDNA lineages of at least 1 million years of age. These lineages and others have restricted ranges, and some of their
357 boundaries reflect topographic or climatic breaks (Graham *et al.*, 2010; Supplementary Figure 4). Traits affecting
358 dispersal abilities and dependence on closed understory habitats mediate divergence across putative barriers and thus
359 diversification in topographically complex landscapes (Burney & Brumfield, 2009; Smith *et al.*, 2014). Because wood-
360 wrens are small-bodied, have small and rounded wings and live in dark forest understory, they likely disperse little
361 (Moore *et al.*, 2008), and this may account in part for their exceptionally strong population structure (Claramunt *et*
362 *al.*, 2012; Salisbury *et al.*, 2012; but see Smith *et al.*, 2017). Deep phylogeographic structure also exists in other small-
363 bodied wrens (i.e. other *Henicorhina*, *Cistothorus*, *Troglodytes*; Dingle *et al.*, 2006; Campagna *et al.*, 2012; Galen &
364 Witt, 2014; Robbins & Nyári, 2014), suggesting that their biology predisposes populations to become isolated and
365 diverge.

366 Regardless of the ultimate causes of population structure, we discovered heretofore underappreciated diversity within a
367 taxon traditionally treated as a single species. Although our study employed only one molecular marker, some of the
368 lineages we recovered coexist as distinct phenotypic entities exhibiting behavioral barriers to hybridization (Salaman
369 *et al.*, 2003; Caro *et al.*, 2013; Burbidge *et al.*, 2015), implying that several species are involved. Genetic distances
370 (i.e., divergence times) are not appropriate surrogates for reproductive isolation (Roux *et al.*, 2016), but we note that
371 wood-wren lineages demonstrating barriers to gene flow in sympatry (i.e. *anachoreta* and *l. bangsi*; *negreti* and *l.*
372 *brunneiceps*; *negreti* and nominate *leucophrys*) last shared ancestors more recently than many other lineages in the
373 complex. It is also remarkable that the phylogeography of *H. leucophrys* resembles that of *Atlapetes* brushfinches
374 (Emberizidae), which also have a northern origin and montane distribution through the Neotropics, and which have

375 diverged into numerous lineages upon colonizing South America (Sánchez-González *et al.*, 2015; J. L. Pérez-Emán,
376 unpubl. data). In contrast to *H. leucophrys*, *Atlapetes* diversified extensively in plumage and this has arguably
377 influenced taxonomy, with researchers recognizing 28 species in the group (Remsen *et al.*, 2018). Just as lineages of
378 the *H. leucophrys* complex replace each other in space, species of *Atlapetes* are for the most part allopatric or replace
379 each other sharply along elevational or latitudinal axes in the Andes (Remsen & Graves, 1995), with their ranges often
380 matching those of lineages of *H. leucophrys* uncovered by our study. This comparison serves to illustrate what might
381 be a more general situation in which clades with roughly similar ages and genetic structure (South American *Atlapetes*
382 are actually younger than South American *H. leucophrys*) may be split to different degrees by taxonomists because of
383 differences among clades in the traits birds employ for signaling and in the lability of such traits. In other words, birds
384 like wood-wrens may be under split owing to their conserved plumage and because the role of vocalizations in species
385 recognition remains understudied (see also D'Horta *et al.*, 2013).

386 Our coalescent analyses indeed suggest that taxonomy underestimates species diversity in the *H. leucophrys* complex:
387 we consistently identified 39 presumptive species across methods. Even the 35 presumptive species identified by
388 bGMYC using a more conservative probability threshold of 0.95 represents a quite remarkable figure relative to
389 similar studies conducted in the Neotropics. In 27 clades of lowland birds ranging from Central America across the
390 Andes through much of Amazonia and even into the Atlantic Forest (Smith *et al.*, 2014), the mean number of species
391 identified using bGMYC also with a 0.95 threshold was 5.3 (range 1-18); figures were slightly higher in understory
392 birds (11 clades; mean = 6.6, range 3-11 presumptive species) but still much lower than our estimates for the *H.*
393 *leucophrys* complex. Moreover, in 173 taxonomic species of birds from the New World subject to phylogeographic
394 analyses employing mtDNA data, the largest number of presumptive species identified by bGMYC with a 0.90
395 threshold was 23 (Harvey *et al.*, 2017b; Smith *et al.*, 2017), highlighting the *H. leucophrys* complex as a distinct
396 outlier (Figure 6). This is despite our sparse sampling in the Peruvian and Bolivian Andes, where one would expect
397 more lineages exist. We do not argue that all lineages we uncovered are species given existing evidence, but several are
398 candidates for studies examining other molecular markers, morphology, voices, and behavior (Caro *et al.*, 2013;
399 Burbidge *et al.*, 2015; Halfwerk *et al.*, 2016). The allopatric ranges of most wood-wren lineages preclude tests of
400 intrinsic barriers to gene flow, but given postzygotic isolation in other phenotypically cryptic, old lineages of
401 Neotropical birds (Pulido-Santacruz *et al.*, 2018), some of them may well be reproductively isolated.

402 Even if hypothetical species our analyses flagged represent distinct lineages not yet reaching the status of “biological”
403 species (Carstens *et al.*, 2013; Sukumaran & Knowles, 2017), our work allows for conclusions about cryptic diversity
404 which should be robust to analyses involving other data. First, regardless of the species concept one follows and of the
405 criteria one uses to recognize species, there are more wood-wren species than traditionally thought. Second, the *H.*
406 *leucophrys* complex comprises multiple independently evolving populations which have diverged to different degrees
407 along the speciation continuum; if one embraces the generalized lineage concept, which views species as segments of
408 metapopulation lineages and considers all other species “concepts” as contingent –albeit not necessary– properties of
409 species one may use as criteria to recognize them (de Queiroz, 1998, 2007), then the complex is arguably a collection
410 of several kinds of species, all of which represent fundamental evolutionary units. Finally, even if one takes a
411 conservative standpoint and treats most of the lineages we uncovered as distinct populations of a single or a few
412 species (Sukumaran & Knowles, 2017), the *H. leucophrys* complex has clearly differentiated into numerous lineages
413 (especially following its colonization of South America) and such lineages have persisted over long periods.

414 Because most wood-wren lineages are not sympatric (see below), our finding that the *H. leucophrys* complex probably
415 comprises multiple species has no influence on local estimates of diversity. However, species richness and endemism at
416 regional scales might need to be revised. For example, current taxonomy recognizes only one species (and only five
417 subspecies) in the complex in Venezuela (Kroodsma & Brewer, 2005), yet we uncovered 7-8 presumptive species –each
418 endemic to a particular montane system– in the country. If lineages identified as presumptive species are elevated to
419 species status and similar patterns exist in other taxa not yet studied, then geographic variation in population
420 structure may alter knowledge of spatial patterns of diversity (e.g., differences in species richness among cordilleras
421 and slopes of cordilleras of Colombia; Kattan *et al.*, 2004; Figure 4, Supplementary Figure 4). Alternative
422 classifications also affect inferences about beta diversity; under current taxonomy, there is no species turnover along
423 thousands of kilometers and across multiple geographic barriers from Mexico to Bolivia except for the local

424 replacements involving *H. anachoreta* and *H. negreti*. At the other extreme, if distinct lineages of *H. leucophrys* are
425 species, then spatial turnover would be substantial even over relatively short distances (e.g., in Colombia), likely
426 exacerbating differences among regions in beta diversity (Gaston *et al.*, 2007; Fjelds  *et al.*, 2012) and with potential
427 conservation implications (Socolar *et al.*, 2016). Recognizing distinct lineages as species would also alter the perceived
428 role of features of montane landscapes setting range limits and thus explaining spatial turnover in assemblages
429 (Graham *et al.*, 2010).

430 In addition to affecting perceptions of patterns of diversity, our results have implications for thinking about historical
431 processes underlying such patterns. The accumulation of biological diversity via diversification within a region like the
432 montane Neotropics requires that (1) populations become isolated to initiate divergence, (2) budding population
433 isolates persist in time, (3) populations expand their ranges and come into secondary sympatry, and (4) newly
434 sympatric populations are differentiated enough that they may coexist without coalescing owing to hybridization or
435 without excluding each other via competition (Mayr, 1942; Ricklefs & Bermingham, 2007). In the following we discuss
436 our results in the context of these steps.

437 *Lineage splitting, persistence, and the origin of diversity*

438 A leading explanation for high tropical diversity involves latitudinal differences in net diversification rates (Fischer,
439 1960; Schluter & Pennell, 2017). In particular, rapid diversification may explain the high species richness and
440 concentration of narrow-ranged species of birds in tropical mountains, which cannot be accounted for by area or
441 contemporary climate (Jetz *et al.*, 2004; Fjelds  *et al.*, 2012). Although evidence that diversification rates vary with
442 latitude remains mixed in birds (Ricklefs, 2006; Martin & Tewksbury, 2008; Jetz *et al.*, 2012; Belmaker & Jetz, 2015)
443 and other taxa (e.g. Pyron & Wiens, 2013; Pyron, 2014; Rolland *et al.*, 2014; Schluter, 2016; Rabosky *et al.*, 2018),
444 tropical mountains are indeed hotbeds of rapid diversification (Madri an *et al.*, 2013). Furthermore, differences in the
445 rate at which species originate may not be as important as the rate at which they go extinct in establishing broad-
446 scale patterns in avian diversity (Hawkins *et al.*, 2006; Weir & Schluter, 2007; Pulido-Santacruz & Weir, 2016).
447 Accordingly, the high diversity and endemism of tropical montane areas may reflect low extinction rates of species
448 (Fjelds  *et al.*, 2012). In turn, higher diversification rates at higher elevations in montane areas (Quintero & Jetz,
449 2018) may reflect both high speciation and low extinction (Fjelds  & Irestedt, 2009). A complementary historical
450 explanation for diversity in tropical mountains which is less commonly addressed in the literature is high persistence of
451 budding populations, an important control of rates of speciation (Mayr, 1963; Dynesius & Jansson, 2014; Rabosky,
452 2016).

453 We found that the *H. leucophrys* complex radiated rapidly into multiple lineages, several of which have persisted for
454 periods exceeding millions of years. Also, LTT plots suggest nearly constant rates of exponential accumulation of
455 lineages over nearly 10 million years, with an apparent slowdown in diversification in the last million years. Although
456 LTT plots with such a shape and their associated negative gamma statistic are often considered evidence of ecological
457 limits to diversification (Rabosky & Hurlbert, 2015), we interpret the pattern more as an artifact of our methods
458 resulting from (1) using species based on a model specifying a divergence threshold separating population-level
459 processes (gene coalescence) from diversification dynamics (speciation and extinction) as units for analysis (Reid &
460 Carstens, 2012), and (2) potential limitations in geographic sampling leading to failure to identify additional
461 independent lineages of young age. Because the bGMYC analysis we employed to delimit presumptive species
462 established an age cutoff of ca. 1 m.a. defining the units included in the LTT analysis, we simply conclude that
463 diversification was nearly constant through much of the history of the *H. leucophrys* complex. To the extent that
464 similar diversification dynamics may characterize evolutionary history of other Neotropical montane birds, high rates
465 of lineage splitting (Harvey *et al.*, 2017b) and high persistence of such lineages over time (Smith *et al.*, 2017) have
466 likely contributed to diversification and probably account for the high diversity of tropical montane systems and, more
467 broadly, to large-scale biodiversity patterns such as latitudinal gradients in species richness.

468 *Range dynamics, secondary sympatry and the regional buildup of diversity*

469 Our data revealed that mtDNA lineages in the *H. leucophrys*, which likely diverged in geographic isolation, have come
470 into secondary sympatry. This is most evident where divergent mtDNA lineages not sister to each other segregate
471 with elevation. In addition to previously documented cases of elevational replacements of lineages involving distinct
472 taxa (i.e. different species or subspecies in the Sierra Nevada de Santa Marta, in western Colombia, and in western
473 Ecuador), we discovered a novel elevational replacement of distinct lineages in the Mérida Cordillera of Venezuela
474 where no phenotypic differences had been noted. Likewise, previous work in other wood-wrens revealed that although
475 *H. leucoptera* is nested within *H. leucosticta*, the lineage of *H. leucosticta* replaced by *H. leucoptera* at higher
476 elevations in the Cordillera del Cóndor east of the Andes is distantly related to it, whereas its closest relative
477 seemingly occurs in the Chocó region west of the Andes (Dingle *et al.*, 2006). The consistent pattern of elevational
478 replacements involving fairly distant relatives as opposed to sister lineages fits the hypothesis that evolutionary
479 divergence in tropical montane birds occurs largely in allopatry and not in parapatry along mountain slopes (Patton &
480 Smith, 1992; García-Moreno & Fjeldså, 2000; Caro *et al.*, 2013).

481 In addition to documenting elevational replacements, we found evidence of regional co-occurrence of lineages replacing
482 each other with latitude (e.g. along the cordilleras of Colombia and Ecuador). More fine-scaled sampling is required to
483 determine whether geographic gaps separate the ranges of such lineages or if they come into close contact. Part of the
484 observed genetic differentiation along the latitudinal axis may reflect the propensity of the linear distributions of
485 tropical montane birds to become fragmented (Graves, 1988). However, some lineages replacing each other with
486 latitude in a region are not sisters and may even be distantly related, which suggests range expansions and secondary
487 contact rather than primary divergence along cordilleras.

488 Other intriguing phylogeographic patterns aside from secondary contact of lineages in elevational or latitudinal
489 parapatry speak to the dynamism of geographic ranges over broad scales. For example, we found that populations of
490 *H. leucophrys* from southern Mexico (Chiapas), Guatemala and El Salvador are not closely related to other Middle
491 American populations; within a large, otherwise South American clade, these specimens appeared closest to *H. negreti*,
492 a species endemic to western Colombia whose northernmost records are ca. 1700 km south of montane El Salvador.
493 Likewise, the only sequence analyzed from Bolivia is a long branch more closely allied to lineages from northern South
494 America (Colombia and Venezuela) than to geographically much closer lineages from Peru. Because closest relatives
495 may occur in distant areas, spatial patterns of genetic variation are not easily accounted for by geography (e.g. by
496 isolation-by-distance; Seeholzer & Brumfield, 2018). Given that such patterns are unlikely evidence of long-distance
497 dispersal and are not unique to wood-wrens in the region (Cadena *et al.*, 2007), considering dynamics of expansion and
498 contraction of geographic ranges involving localized extinctions is crucial to understand biogeographic and
499 demographic processes underlying the distribution of genetic and species diversity in Neotropical birds.

500 Shifting climatic conditions affecting habitat connectivity drive changes in species ranges, thereby influencing
501 phylogeographic patterns and the buildup of montane diversity (Ramírez-Barahona & Eguiarte, 2013; Flantua &
502 Hooghiemstra, 2018). Species ranges may also experience phases of expansion and contraction linked to shifts in
503 ecological specialization and interactions with natural enemies (i.e. the taxon cycle; Wilson, 1959; Ricklefs &
504 Bermingham, 2002). Although taxon cycles are more evident in insular settings with discrete populations and areas
505 (e.g., Ricklefs & Bermingham, 1999; Jönsson *et al.*, 2014), they may also take place in continents (Graves, 1982). In
506 fact, lineages experiencing the taxon cycle may account for what one might call continental great speciators like
507 *Henicorhina* wood-wrens, which occur widely in space -revealing an ability to expand their ranges- yet split into
508 isolated populations at a fast rate due to cessation of gene flow (cf. Diamond *et al.*, 1976). Wood-wrens disperse little
509 at present because of their morphology and ecology, which arguably explain their remarkable patterns of genetic
510 structure reflecting long-term population isolation. However, our findings that wood-wrens dispersed throughout much
511 of the montane Neotropics from a northern area of origin and that several lineages achieved secondary sympatry
512 indicate that episodes of range expansion interspersed with periods of divergence occurred at various moments,
513 possibly in sync with morphological or behavioral changes influencing their abilities to disperse (Pigot & Tobias, 2015;
514 Hosner *et al.*, 2017). Furthermore, gaps separating the ranges of closely related lineages of wood-wrens arguably reflect
515 extinctions of intervening populations of formerly widespread lineages, which left vacant spaces that could, in turn,
516 become occupied by other expanding lineages.

517 Phylogeographers will often not detect range dynamics embodied in the taxon cycle because incomplete reproductive
518 isolation between young lineages can result in homogenization of gene pools upon secondary contact (Kearns *et al.*,
519 2018). Furthermore, niche similarities between incipient species achieving contact may preclude long-term sympatry
520 owing to interspecific competition (Pigot & Tobias, 2013). Irrespective of whether the patterns we observed resulted
521 from the taxon cycle, we identified aspects making the *H. leucophrys* complex well suited for further work on the
522 origins of tropical diversity and its accumulation over time and space. Our results and other work on the complex
523 reveal that the completion of reproductive isolation between lineages meeting in secondary sympatry seemingly
524 exhibits a continuum ranging from neutral divergence with no obvious phenotypic differences (forms in montane
525 Venezuela), to phenotypic and behavioral divergence with persistent interbreeding (*hilaris* and nominate *leucophrys* in
526 Ecuador), to completed speciation with little to no hybridization (anachoreta and negreti vs. various forms of
527 leucophrys in Colombia; Salaman *et al.*, 2003; Dingle *et al.*, 2008; Dingle *et al.*, 2010; Caro *et al.*, 2013; Burbidge *et*
528 *al.*, 2015; Halfwerk *et al.*, 2016). Furthermore, divergence in elevational ranges occurring during periods of isolation
529 (Cadena, 2007; Tobias *et al.*, 2014) or arising in secondary sympatry (Diamond, 1973; Freeman, 2015) has enabled
530 coexistence of lineages at the landscape scale in various regions. Given that range boundaries may be maintained –and
531 possibly reinforced– evolutionarily by phenotypic and behavioral barriers to interbreeding and ecologically by
532 competition (Jankowski *et al.*, 2010), our study has uniquely captured wood-wren populations in the act of building up
533 diversity via divergence and persistence in allopatry, achievement of secondary sympatry, and coexistence mediated by
534 ecological and evolutionary divergence. Comparative work on the structure and dynamics of contact zones between
535 lineages should provide rich insights into the origin and maintenance of high diversity in tropical mountains.

536

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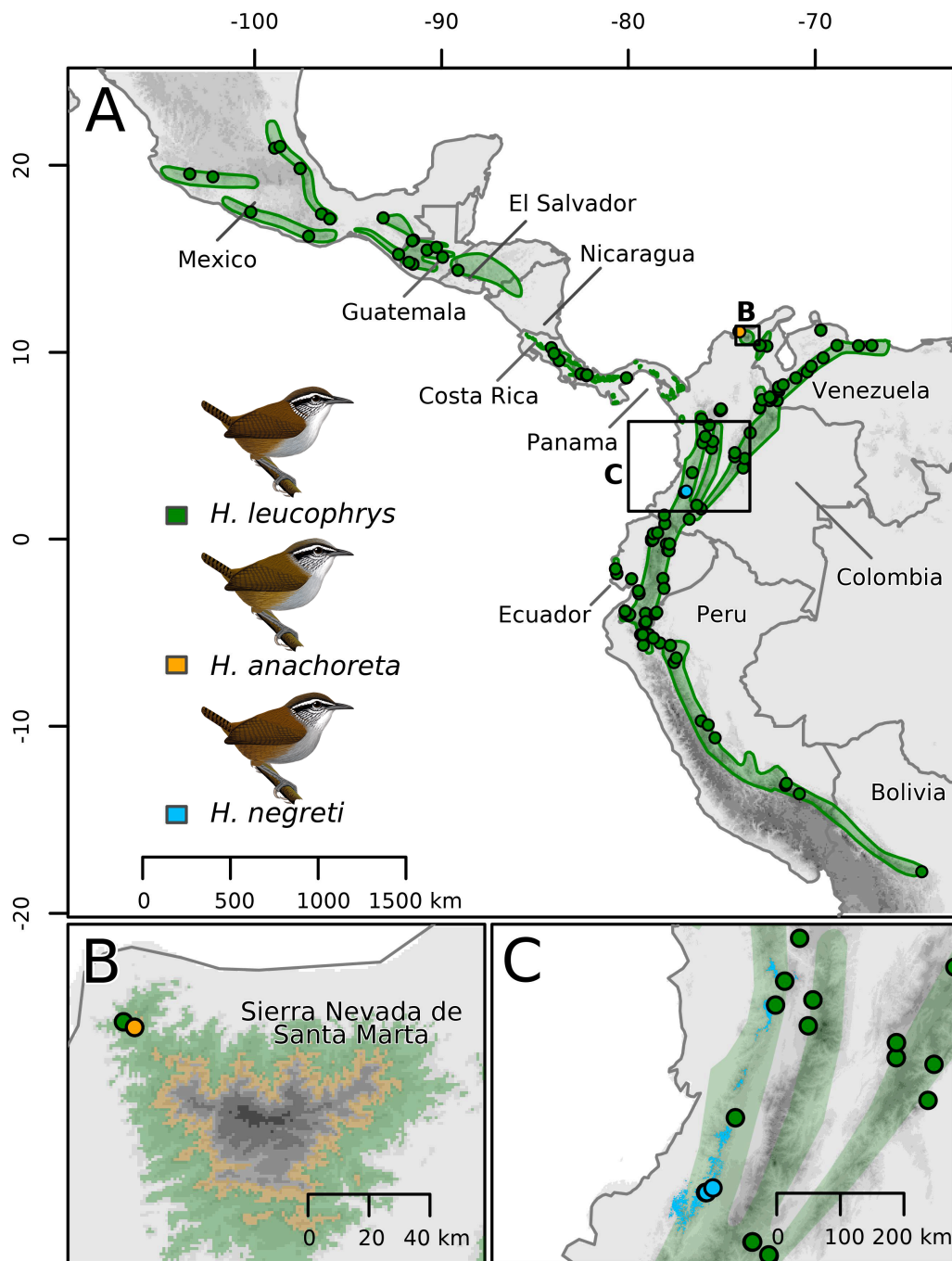
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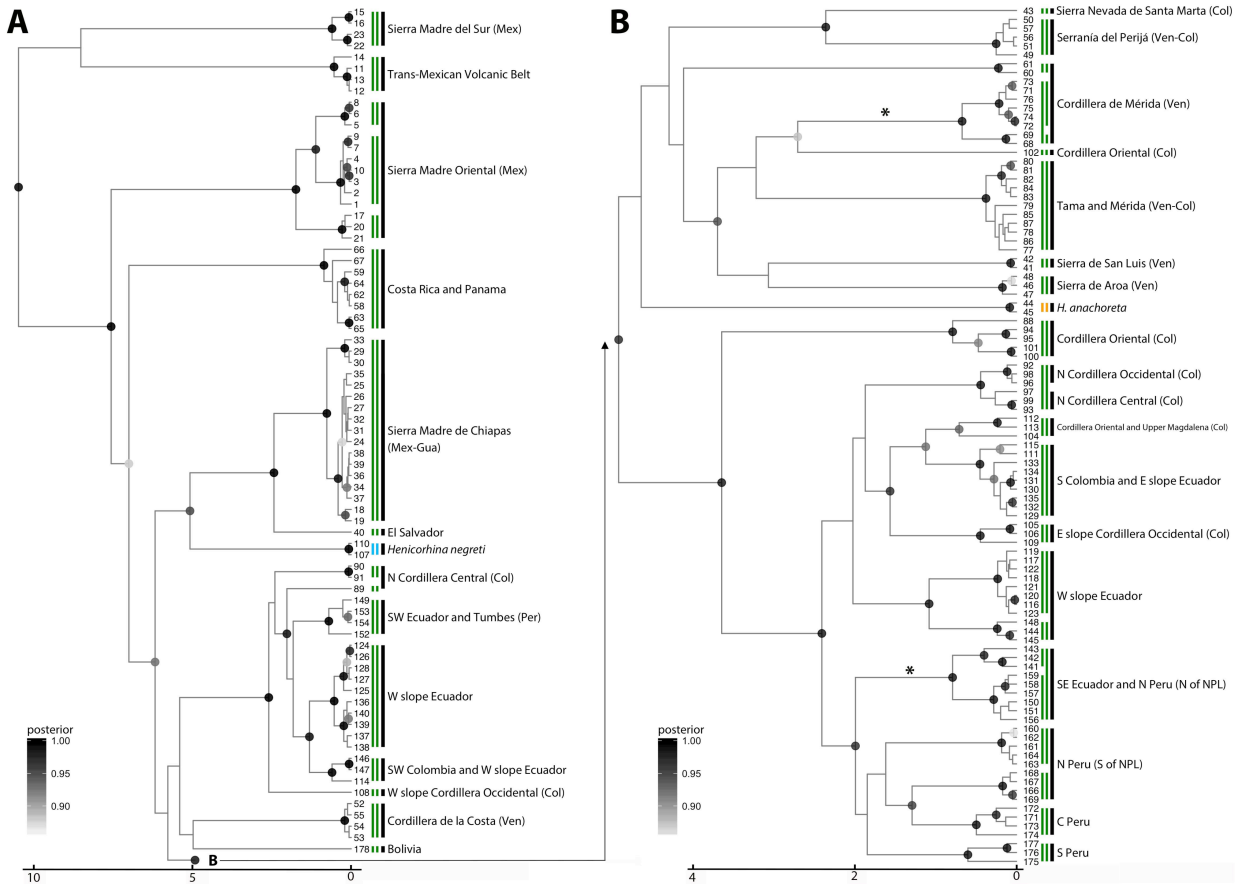
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907 **Figure 1.** Geographic distribution of wood-wrens in the *Henicorhina leucophrys* complex in the Neotropical montane
908 region and localities where specimens were sampled for our phylogeographic analyses. The complex currently
909 comprises three species: the widely distributed *H. leucophrys* ranging from Mexico to Bolivia and two narrow endemics
910 from Colombia (*H. anachoreta* in the Sierra Nevada de Santa Marta and *H. negreti* on the western slope of the
911 Cordillera Occidental). Distribution maps were obtained from BirdLife International (*H. leucophrys*) and Velásquez-
912 Tibatá et al. (2013; *H. negreti*), or generated for this study based on information on elevational range (*H. anachoreta*;
913 Cadena et al., 2016). Illustrations by F. Ayerbe.

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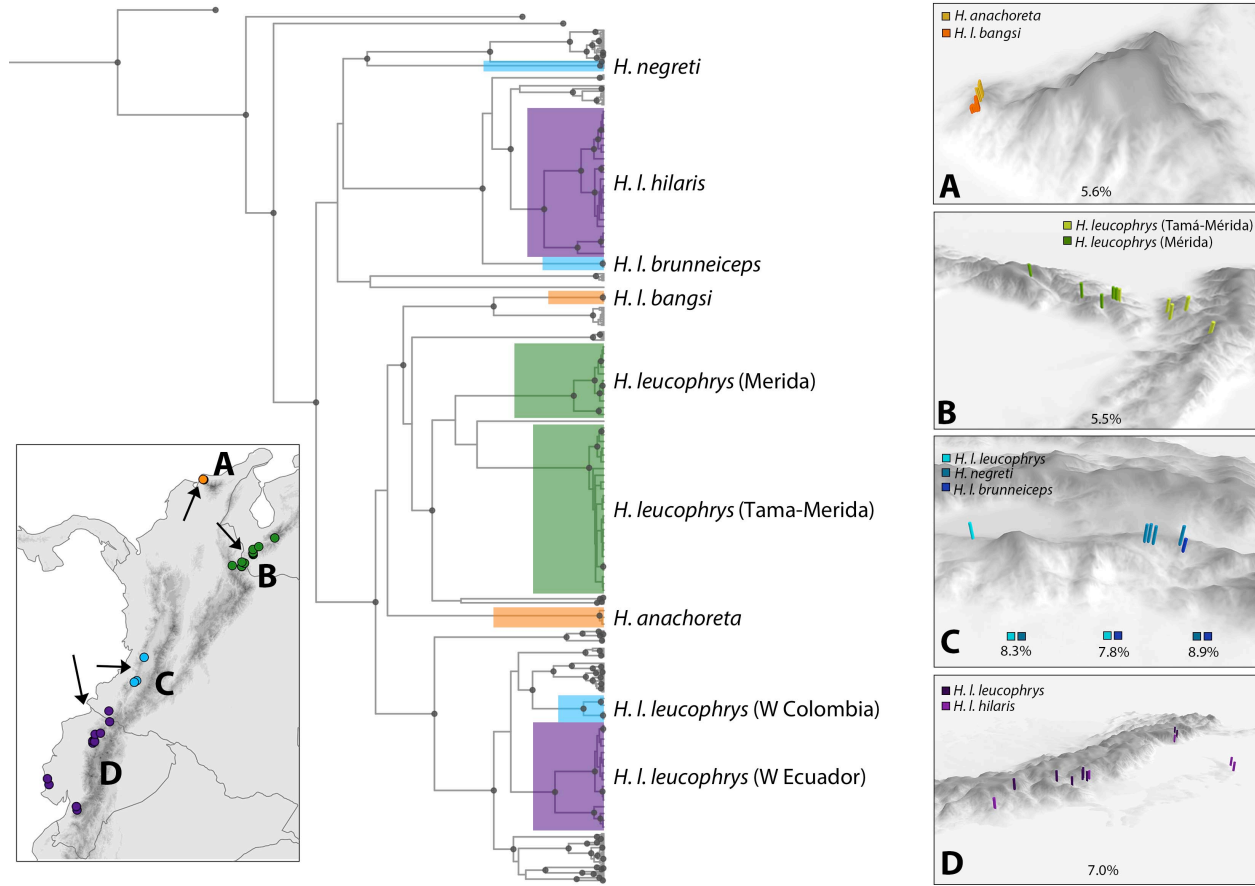


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917 **Figure 2.** Phylogenetic relationships and divergence times among unique mtDNA haplotypes in the *H. leucophrys*
 918 complex inferred using BEAST suggest (1) paraphyly of *H. leucophrys* with respect to *H. anachoreta* and *H. negreti*,
 919 (2) a northern origin for the complex with subsequent colonization of South America, and (3) marked population
 920 genetic structure partly attributable to geographic isolation mediated by physical barriers. Color shading on nodes
 921 corresponds to posterior probabilities ≥ 0.85 . Black vertical lines indicate geographic regions; note that all deep
 922 branches correspond to clades from mountain regions in Mexico and Central America and that South American
 923 populations are also strongly structured. Green vertical lines signal presumptive species identified using multi-rate
 924 Poisson Tree Processes (mPTP, left) and the Bayesian General Mixed Yule Coalescent Model (bGMYC, right); results
 925 of these analyses were almost identical, with only minor discrepancies in two clades marked with asterisks. Haplotypes
 926 are numbered at the tips of the tree; information on specimens having each haplotype is provided in Supplementary
 927 Table 1.

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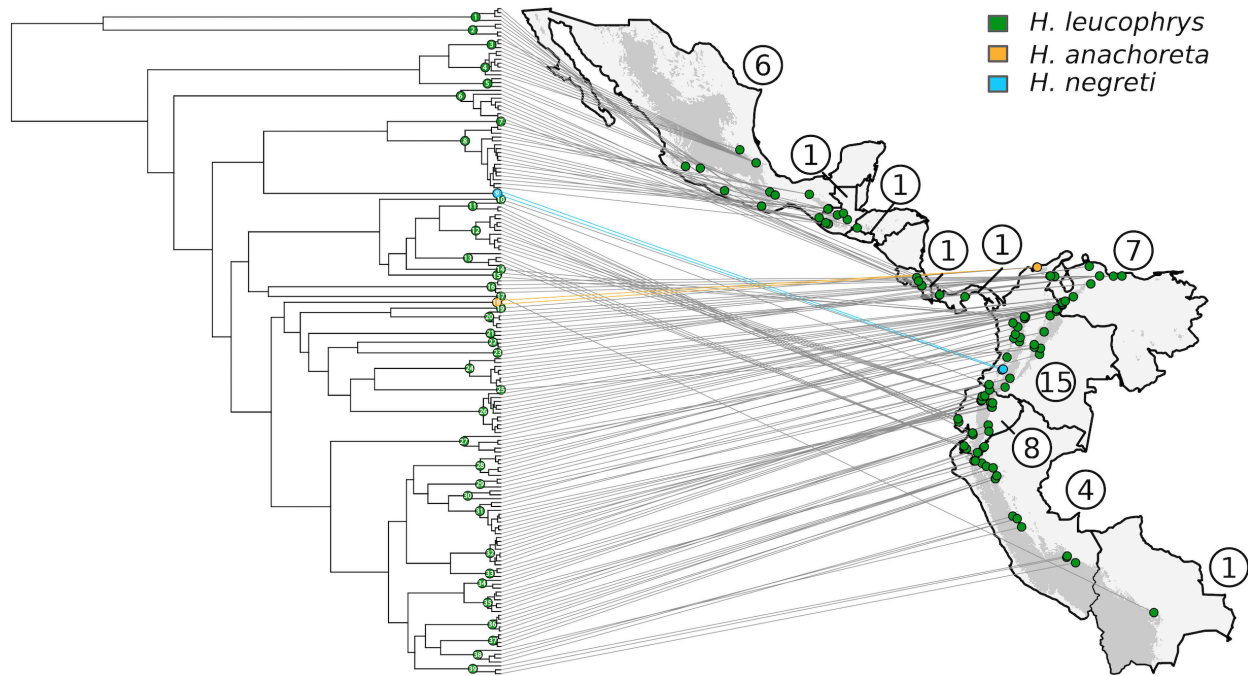


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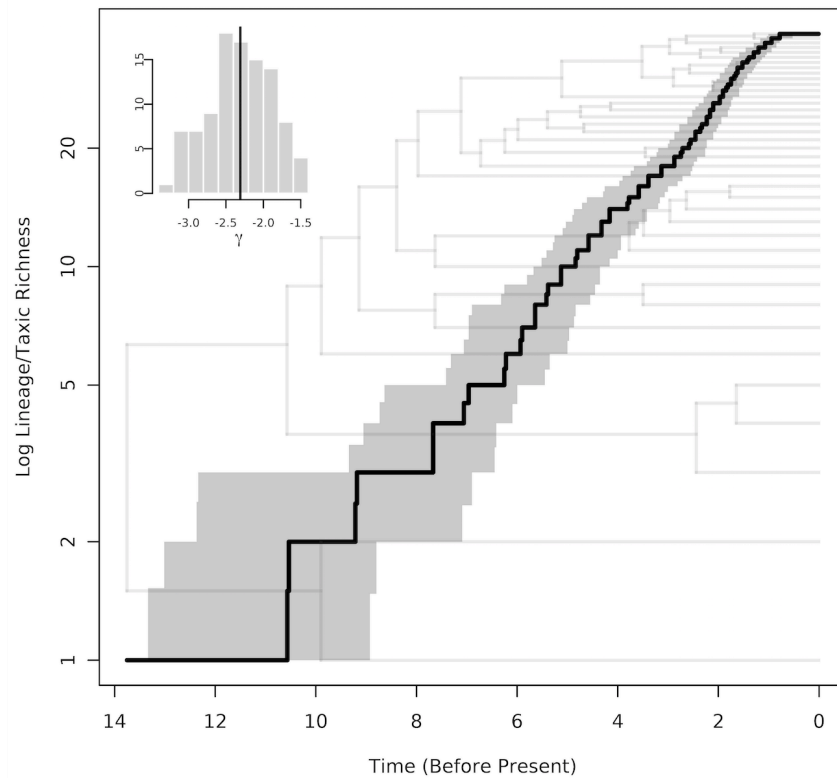
931 **Figure 3.** Elevational replacements involving distinct lineages of the *H. leucophrys* complex in montane South
 932 America. Lineages replacing each other with elevation in a region share colors in the map, the phylogeny (modified
 933 from Supplementary Figure 1, nodes indicated with grey dots have ≥ 0.85 posterior probability support), and the close-
 934 up view of mountain slopes, where different shades are used for each lineage (arrows on the map show the direction
 935 from which mountains are seen in panes A-D). In at least three regions (A,C, D), elevational replacements do not
 936 involve sister taxa with the only possible exception being the novel case of cryptic replacement of lineages in the
 937 Cordillera de Mérida, Venezuela (B), where affinities of lineages to each other and to those from other regions are not
 938 strongly supported. Lineages involved in elevational replacements are deeply divergent from each other (panes show
 939 mean uncorrected p distances in ATPase genes), occur in close proximity, and correspond to different presumptive
 940 species identified by coalescent analyses (see text).

941



944 **Figure 4.** Geographic locations where we sampled 39 presumptive species in the *H. leucophrys* complex identified by
945 coalescent analyses of mtDNA sequences. Dots and numbers on the tree (modified from Figure 2) correspond to
946 species statistically inferred by the Bayesian General Mixed Yule Coalescent Model (bGMYC) with the threshold
947 probability used to define group membership set at 0.50. Colors correspond to species epithets as per the current
948 three-species taxonomy. Encircled numbers on the map indicate the number of presumptive species occurring in each
949 country. Almost identical patterns were observed using the multi-rate Poisson Tree Processes (mPTP) method. For
950 close-up views of geographic locations where each presumptive species was sampled, see Supplementary Figure 4.

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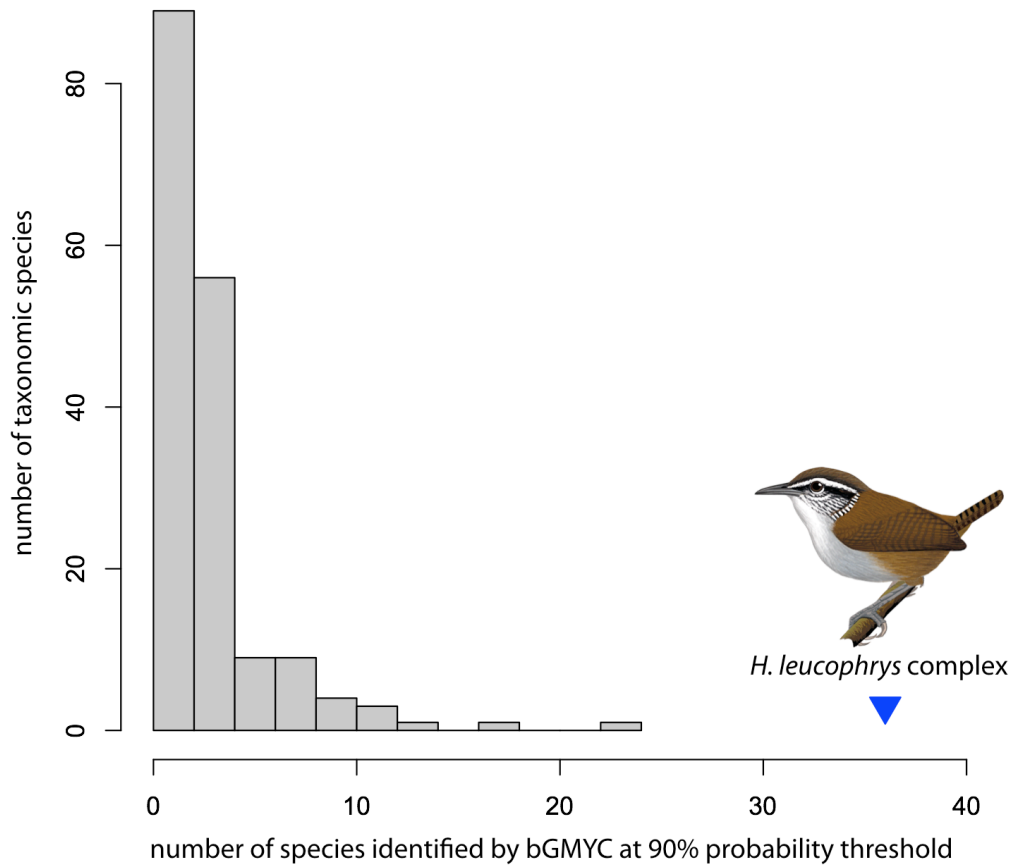


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954 **Figure 5.** Lineage-through time plot showing accumulation of lineages over time in the *H. leucophrys* complex. Black
955 lines are estimates based on the maximum clade credibility tree and grey indicates the 95% credibility interval across
956 100 trees for the plot and for estimates of the gamma statistic. The shape of the curve and the associated gamma
957 statistic suggests that rates of lineage accumulation have declined over time, but note that because this analyses used
958 results of bGMYC as input no presumptive species younger than 1 million years were considered. The pattern may
959 also reflect incomplete sampling of young lineages particularly within South America.

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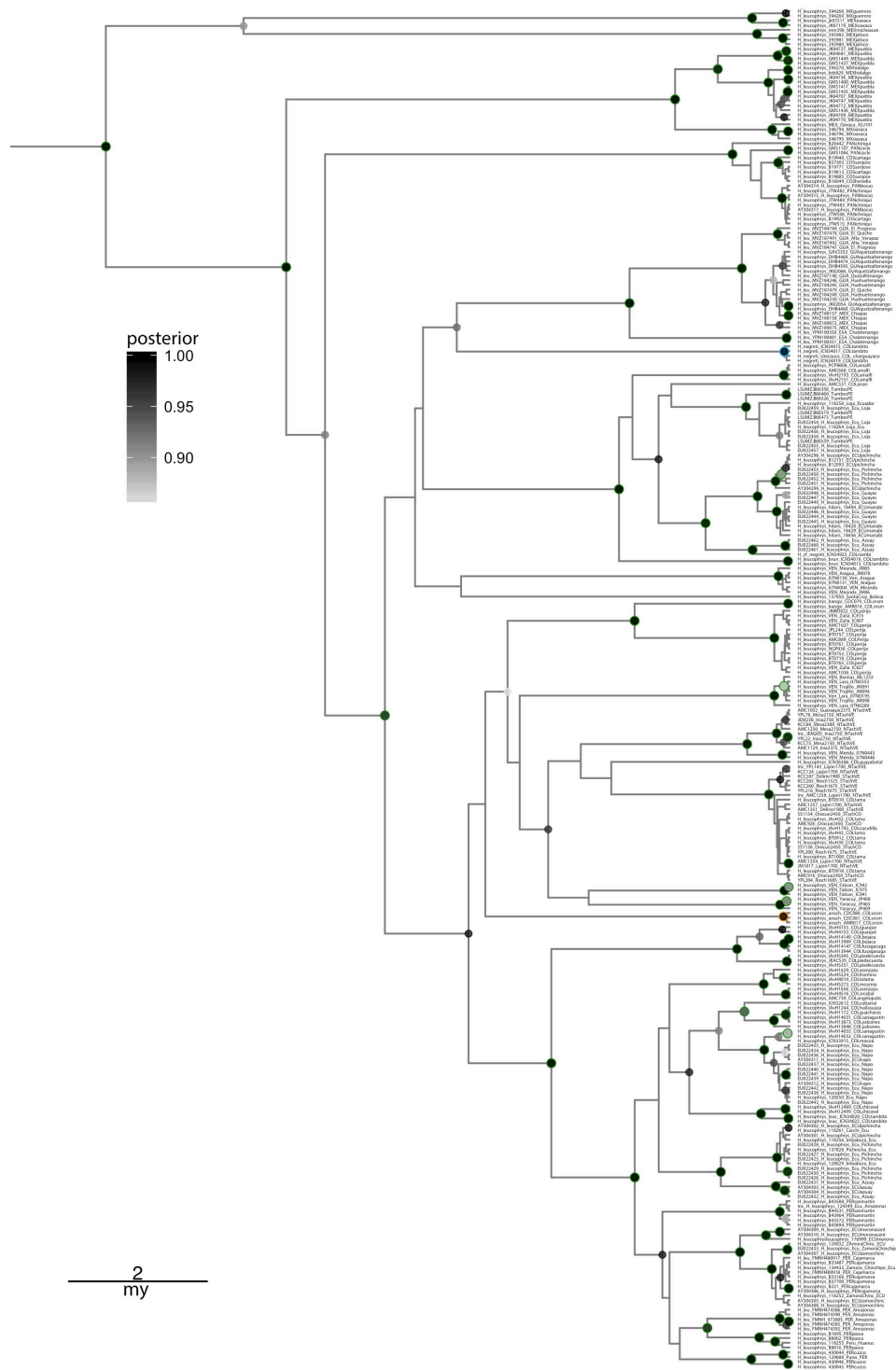
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963 **Figure 6.** Relative to the frequency distribution of the number of presumptive species identified by coalescent analyses
964 of mtDNA sequence data within 173 taxonomic species of New World birds (data from Harvey et al. 2017, Smith et
965 al. 2017), our result for the *H. leucophrys* complex is a distant outlier. Even if many lineages cannot be shown to be
966 reproductively isolated from others, the data reveal a remarkable and previously undocumented degree of population
967 genetic structuring. Illustration by F. Ayerbe.

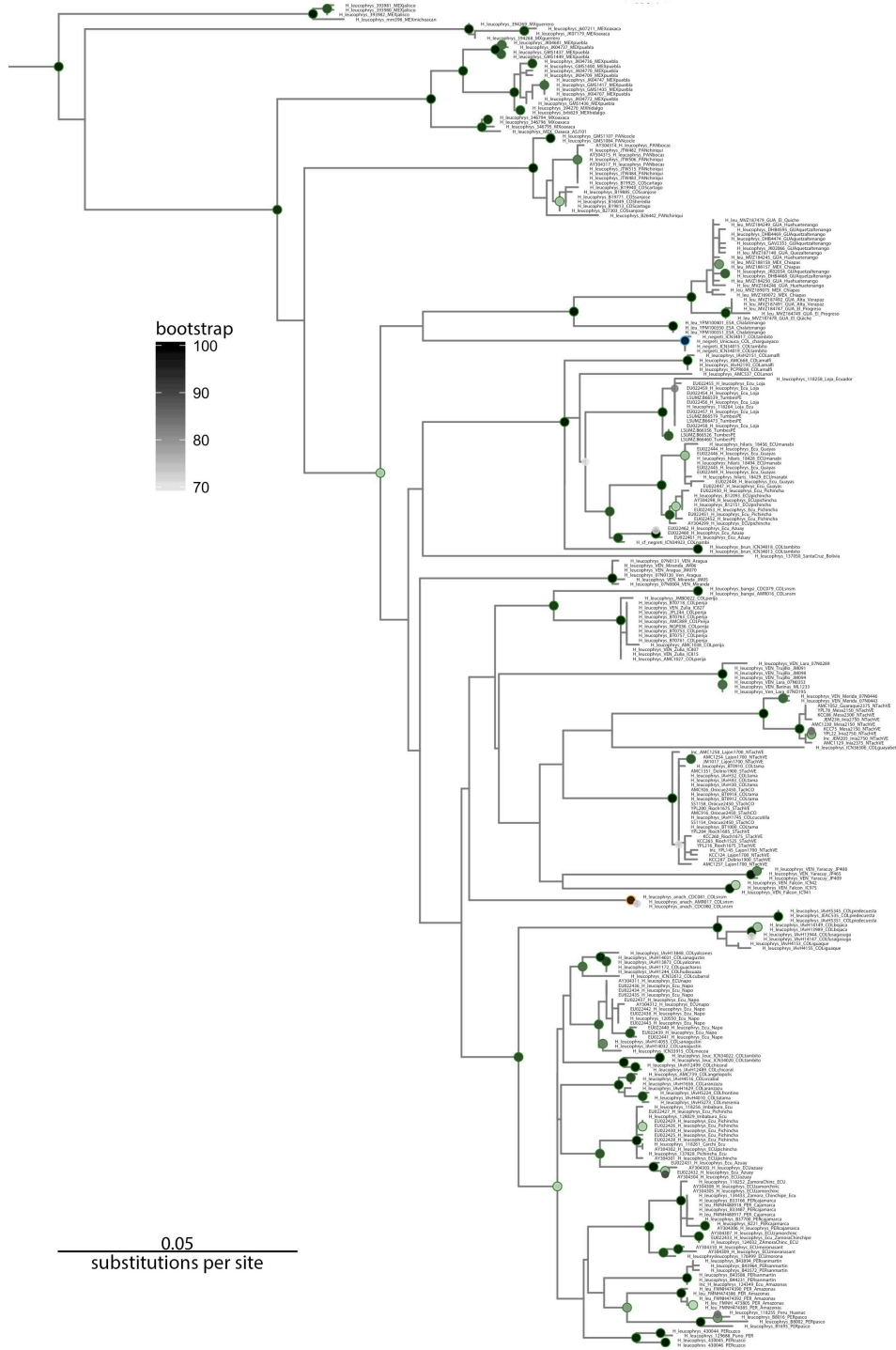
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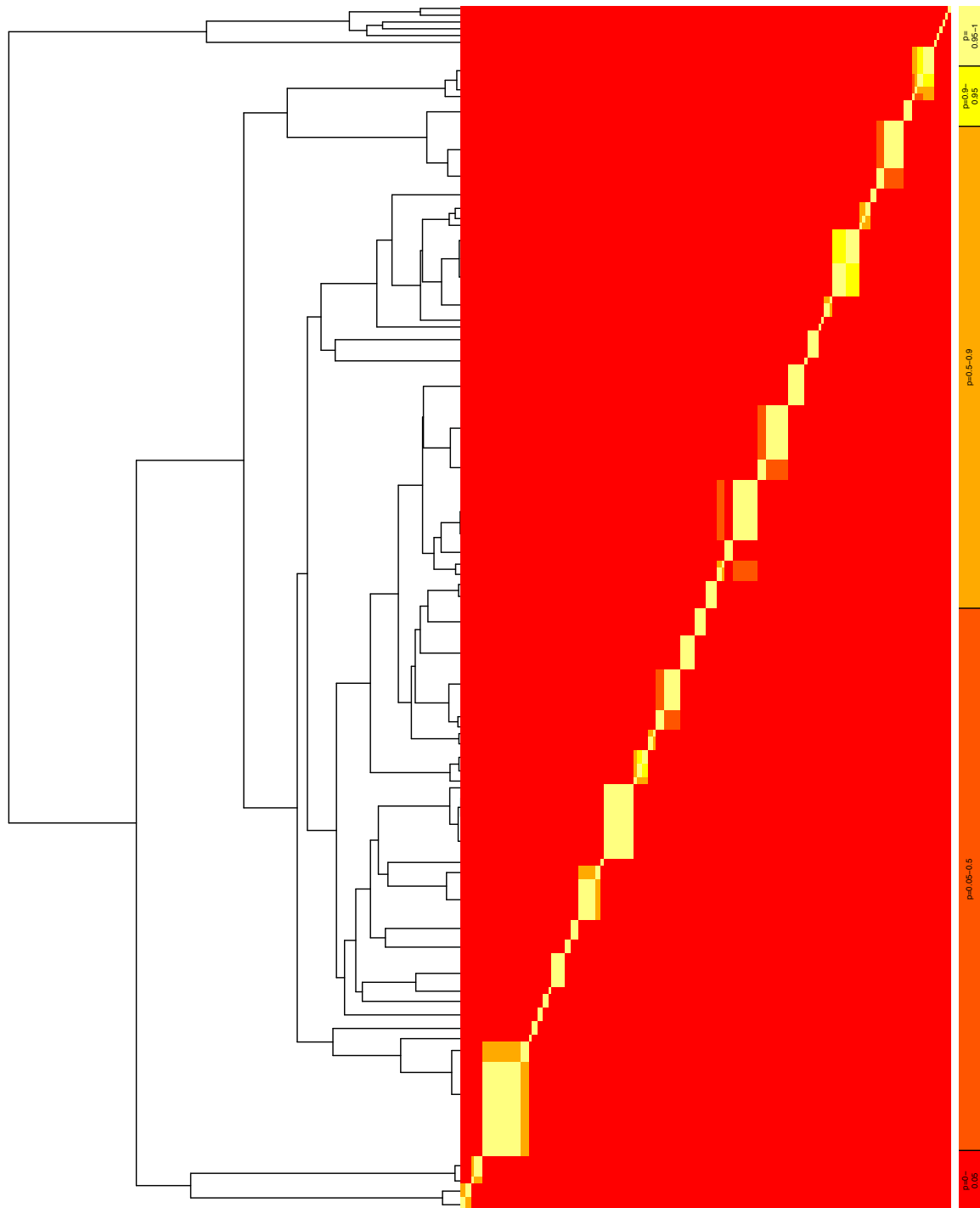
971 **Supplementary Figure 1.** Phylogenetic relationships among individuals in the *H. leucophrys* complex inferred using
972 Bayesian analysis of sequences of the ATPase 6&8 mitochondrial genes. The phylogeny is the maximum clade
973 credibility tree obtained in BEAST. Nodal support (i.e., posterior probabilities ≥ 0.85) is shown using a grey scale.
974 Nodes with a colored outline (green = *H. leucophrys*, blue = *H. negreti*, orange = *H. anachoreta*) were also recovered
975 with strong support ($\geq 80\%$ bootstrap) in maximum-likelihood analysis (Supplementary Figure 2).



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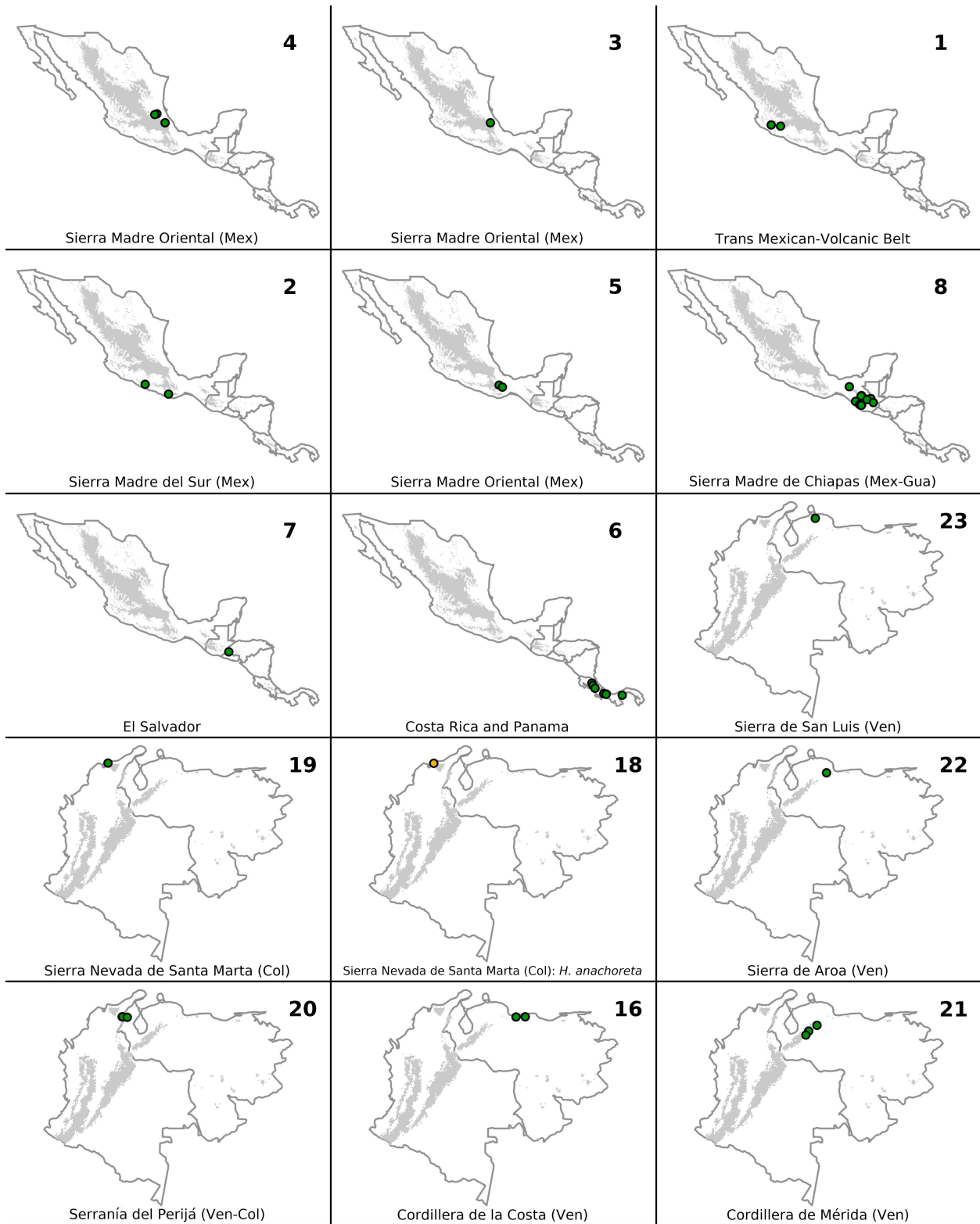
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978 **Supplementary Figure 2.** Phylogenetic relationships among individuals in the *H. leucophrys* complex inferred using
979 maximum-likelihood analysis of sequences of the ATPase 6&8 mitochondrial genes. The phylogeny is the maximum-
980 likelihood tree obtained in RAxML. Nodal support (i.e., bootstrap values $\geq 80\%$) is shown using a grey scale. Nodes
981 with a colored outline (green = *H. leucophrys*, blue = *H. negreti*, orange = *H. anachoreta*) were also recovered with
982 strong support (≥ 0.90 posterior probability) in Bayesian analysis (Supplementary Figure 1).



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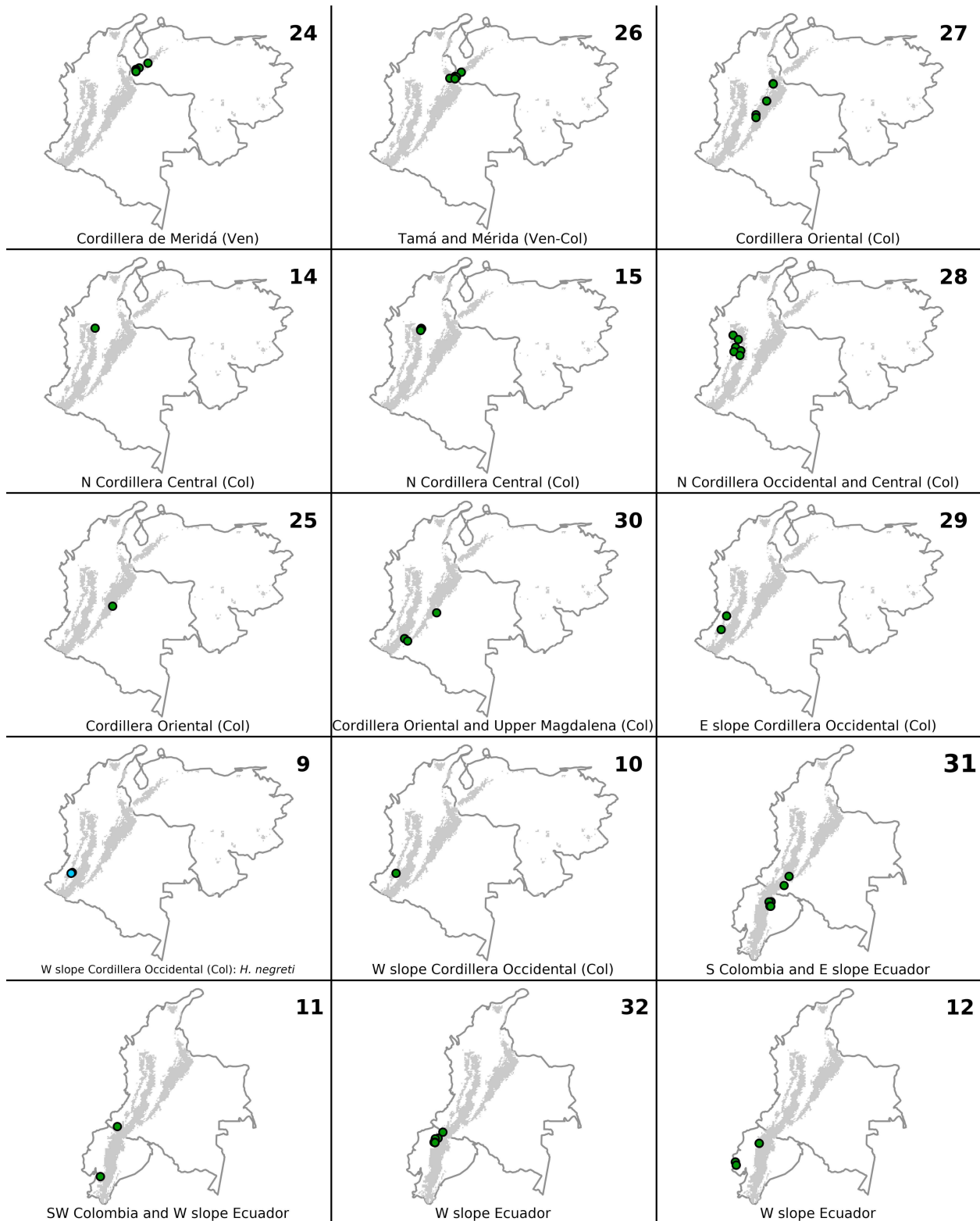
984 **Supplementary Figure 3.** Results of species delimitation analysis in the *H. leucophrys* complex employing the Bayesian
985 General Mixed Yule Coalescent Model (bGMYC). The phylogeny showing relationships among haplotypes is the
986 maximum clade credibility obtained using BEAST and the table to the right is a sequence-by-sequence matrix in
987 which cells are color-coded to indicate the posterior probability that each pair of sequences is conspecific.



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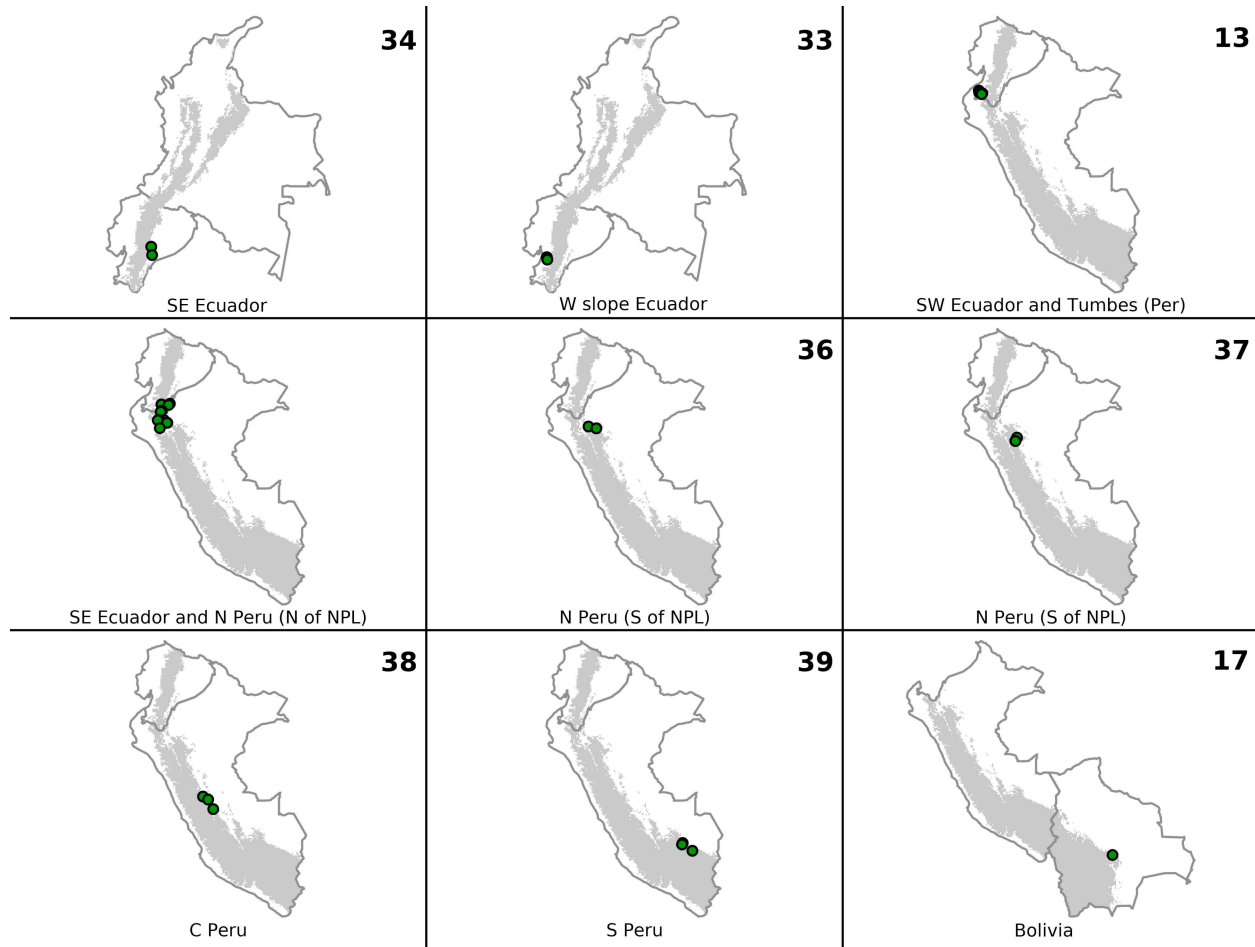
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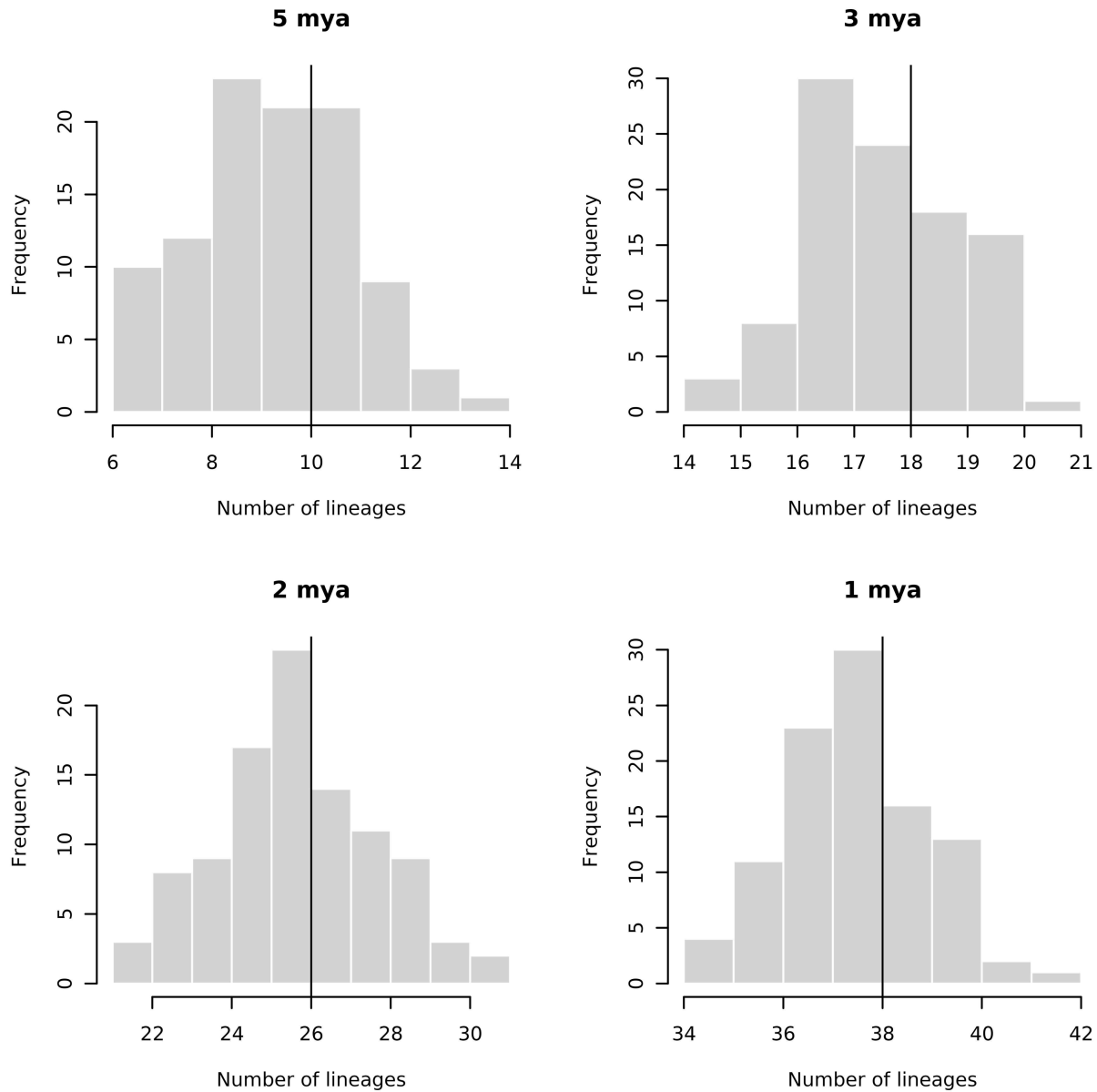
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996 **Supplementary Figure 4.** Close-up views of geographic locations where presumptive species in the *H. leucophrys*
997 complex identified by coalescent analyses of mtDNA sequences were sampled. Maps showing known locations of each
998 presumptive species are ordered roughly from North to South, and are numbered according to numbers on nodes in
999 the tree in Figure 4; points on maps are colored based on the current three-species taxonomy recognizing *H.*
1000 *leucophrys*, *H. negreti*, and *H. anachoreta*. Some presumptive species have relatively large ranges (e.g. no. 6 across
1001 Costa Rica and Panama) whereas others appear to be much more restricted, in some cases found at single localities so
1002 far (e.g. no. 14 and 15 in the northern extreme of the Cordillera Central in Antioquia, Colombia).

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1005

1006 **Supplementary Figure 5.** Number of mtDNA lineages in the *H. leucophrys* complex of various ages (from 5 to 1 million
1007 years ago [m.a.]). Vertical black lines correspond to the median number of lineages dating to at least each of the four
1008 ages (i.e. splitting from their common ancestor with other lineages before each age) observed in a sample of 100 trees
1009 in the posterior distribution obtained using BEAST; gray bars are the frequency distributions of number of lineages
1010 per age across all trees.

1011

1012 **Supplementary Table 1.** (Provided as a separate .xlsx file). Information on specimens considered in phylogeographic
1013 analyses including museum catalogue numbers, locality data, and GenBank accession numbers when available (those
1014 for sequences generated for this study are pending). For each specimen, we also indicate the name used to refer to it in
1015 Supplementary Figures 1 and 2, the ATPase 6/8 haplotype as shown in Figure 2, and the ID of the presumptive
1016 species identified using bGMYC to which it belongs (Figure 3, Supplementary Figure 4).