

1 **Into the Andes: multiple independent colonizations drive montane diversity in the**
2 **Neotropical clearwing butterflies Godyridina**

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4 Running title: Multiple colonizations into the Andes

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For Review Only

31 **Abstract**

32 Understanding why species richness peaks along the Andes is a fundamental question in the
33 study of Neotropical biodiversity. Several biogeographic and diversification scenarios have
34 been proposed in the literature, but there is confusion about the processes underlying each
35 scenario, and assessing their relative contribution is not straightforward. Here we propose to
36 refine these scenarios into a framework which evaluates four evolutionary mechanisms:
37 higher speciation rate in the Andes, lower extinction rates in the Andes, older colonization
38 times, and higher colonization rates of the Andes from adjacent areas. We apply this
39 framework to a species-rich subtribe of Neotropical butterflies whose diversity peaks in the
40 Andes, the Godyridina (Nymphalidae: Ithomiini). We generated a time-calibrated phylogeny
41 of the Godyridina, and fitted time-dependent diversification models. Using trait-dependent
42 diversification models and ancestral state reconstruction methods we then compared different
43 biogeographic scenarios. We found strong evidence that the rates of colonization into the
44 Andes were higher than the other way round. Those colonizations and the subsequent local
45 diversification at equal rates in the Andes and in non-Andean regions mechanically increased
46 the species richness of Andean regions compared to that of non-Andean regions (“species-
47 attractor” hypothesis). We also found support for increasing speciation rates associated with
48 Andean lineages. Our work highlights the importance of the Andean slopes in repeatedly
49 attracting non-Andean lineages, most likely as a result of the diversity of habitats and/or host-
50 plants. Applying this analytical framework to other clades will bring important insights into
51 the evolutionary mechanisms underlying the most species-rich biodiversity hotspot on the
52 planet.

53

54 Key-words: Andes, Ithomiini, Lepidoptera, Neotropics, trait-dependent diversification,
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57 **Introduction**

58 The Neotropical region, which extends from Central-America to southern Brazil, is the most
59 species-rich biogeographic region on Earth, and the origins of this rich biodiversity are keenly
60 debated. Within the Neotropics, species diversity often peaks along the tropical Andean
61 slopes across many groups, such as plants (Myers *et al.* 2000), vertebrates (Duellman 1999)
62 and arthropods (Mullen *et al.* 2011; Rosser *et al.* 2012; Chazot *et al.* 2015). Yet, the tropical
63 Andes represent a small area compared the rest of the Neotropics, and notably the Amazon
64 basin, which covers most of the region. The Andean orogeny followed a south-to-north
65 pattern of uplift, with episodic periods of intense mountain-building (Garzione *et al.* 2008;
66 Hoorn *et al.* 2010). Geological evidence shows that the Central Andes rose by 1.5–2.5 km
67 during a period of rapid uplift between 10 to 6 million years ago (Garzione *et al.* 2008; Hoorn
68 *et al.* 2010), which was followed by another period of accelerated uplift in the Northern
69 Andes between 5 and 2 million years ago (Bershaw *et al.* 2010). This rapid uplift is one of the
70 major events in the geological history of the South American continent and was likely
71 involved in the formation of the modern Amazon Basin (Hoorn *et al.* 2010). Understanding
72 the role of the Andes in generating and shaping the present-day Neotropical biota is a key
73 question that is far from being resolved.

74 In the literature, two hypotheses are often invoked to explain high species richness in
75 the tropical Andes: the so-called “species-pump” hypothesis and the “time-for-speciation”
76 hypothesis, also referred to as the “museum” hypothesis (e.g. Stebbins, 1974; Stephens &
77 Wiens 2003, Smith *et al.* 2007; Kozak & Wiens 2010; Rosser *et al.* 2012; Hutter *et al.* 2013).
78 However, there is confusion in the literature as to the mechanisms underlying each term.

79 Valentine (1967) coined the term “species-pump”, referring to the hypothesis that
80 during warm periods mollusk species ranges increased (northward) while during colder

81 periods, species went either to extinction or contracted into small, isolated populations in the
82 remaining optimal areas (“pumps”). These populations were free to evolve independently,
83 before expanding again during the following warm period and becoming sympatric “species.”
84 Later, Stebbins (1974) expanded this hypothesis to rainforest plants and Fjeldså (1994)
85 applied the “species-pump” concept to distributional patterns of tropical birds, proposing that
86 climatically buffered Andean regions acted as a “species-pump” that would “pump” species
87 generated in the Andes out to the Amazonian region. Fjeldså’s (1994) “species-pump”
88 scenario therefore involves a complex combination of extinction, range contraction,
89 speciation and colonization processes, which makes formal tests difficult to carry out.
90 Importantly, this scenario was originally proposed to explain the species diversity of the
91 Amazonian basin. These terms have later been used by other authors, but often with a
92 different meaning that corresponds to only one or a few aspects of Fjeldså’s (1994) scenario.
93 For example, Sedano & Burns (2010) interpreted a high rate of dispersal from the Andes
94 toward adjacent areas as a support for the “species-pump” hypothesis (see also e.g. Antonelli
95 & Sanmartín 2011). By contrast, Hutter *et al.* (2013) interpreted this hypothesis as a higher
96 net diversification rate in a study designed to investigate Andean diversity. Hutter *et al.*
97 (2013) therefore ignore the “pumping out” mechanism originally proposed (see also e.g.
98 Smith *et al.* 2006). In fact, the hypothesis of higher speciation rate is also referred to as the
99 “cradle” hypothesis, often used to explain large patterns of latitudinal gradient of diversity
100 (e.g. Arita & Vázquez-Domínguez 2008, Rolland *et al.* 2014).

101 A similar confusion occurs with the so-called “time-for-speciation” and “museum”
102 hypotheses. Stebbins (1974) proposed that the angiosperm “centers of diversity” are the result
103 of low disturbance and therefore low extinction rates that lead to museum-like areas with high
104 species diversity and ‘primitive’ lineages. Stephens & Wiens (2003) used the term “time-for-

105 speciation” when referring to a process where a specific region was colonized earlier than
106 other ones by a clade, therefore giving more time for diversification. Confusion arose when
107 some authors used the term “museum” to describe areas that were colonized early and had
108 more time to accumulate species (e.g. Hutter *et al.* 2013 Smith *et al.* 2006), whereas other
109 authors, such as Arita & Vázquez-Domínguez (2008), considered the tropics as a museum if
110 “origination rate is constant and extinction rate is lower in the tropics” (see also e.g. Gaston &
111 Blackburn 2000; Condamine *et al.* 2012).

112 In this paper we propose a framework of four biogeographic scenarios, which are
113 clarified in terms of mechanisms and expectations. The four scenarios rest on the four main
114 evolutionary processes proposed to explain spatial patterns of biodiversity: speciation,
115 extinction, age of colonization, and migration. These four mechanisms are not mutually
116 exclusive but each of them relies on the variation of only one of the following parameters:
117 speciation rate, extinction rate, age of first colonization and colonization rate (Figure 1). Here,
118 we apply this framework to investigate variation in diversity between Andean and non-
119 Andean regions, but this framework may be used to investigate patterns of diversity among
120 any set of regions. Our hypotheses are as follows:

121 (1) *Cradle*. Andean lineages speciate faster than non-Andean lineages, leading to a rapid
122 accumulation of species over time (Figure 1a). Indeed, the Andes offer conditions potentially
123 favorable to speciation. The uplift of the different cordilleras generated major barriers to
124 dispersal for many organisms, favoring allopatric divergence. In addition, the slopes of the
125 Andes also display a strong topological heterogeneity, with deep valleys creating further
126 opportunities for geographic divergence (Graham *et al.* 2004; Hughes & Eastwood 2006).
127 Ecological divergence is also favoured because high turnover of bioclimatic conditions
128 coupled with stratified vegetation types over small distances creates strong ecological

129 gradients. (2) *Museum*. Andean lineages have undergone lower extinction rates than non-
130 Andean lineages (Figure 1b). Here we follow Stebbins' original definition of the 'museum'
131 hypothesis (Stebbins 1974). (3) *Time-for-speciation*. The timing of colonization events of the
132 Andes might be older than the colonization of other areas and Andean lineages have thus had
133 more time to accumulate species (Figure 1c). This is the 'time-for-speciation' hypothesis
134 *sensu* Stephens & Wiens (2003). (4) *Species attractor*. The last hypothesis posits a higher
135 dispersal and colonization rate into the Andes (Figure 1d). This scenario has received less
136 attention compared to the other hypotheses (but see Beckman & Witt 2015), but with the
137 formation of the tropical Andes, the availability of newly formed ecosystems may have been
138 accompanied by many independent colonization events. Indeed, vacant ecological niches,
139 such as host-plants in the case of oligophagous herbivores, could become occupied by
140 multiple independent lineages. Under identical rates of diversification and time for speciation
141 in Andean and non-Andean regions, multiple colonizations of the Andes could increase
142 species richness in this region (Figure 1d). Under this hypothesis, the Andes play the role of
143 an "attractor" for species and colonization rates toward the Andes from adjacent areas are
144 predicted to be higher than the other way around.

145 Vertebrates, especially birds, prevail in most recent studies of patterns of Neotropical
146 diversification (Weir 2006; Brumfield & Edwards 2007; McGuire *et al.* 2007; Sedano &
147 Burns 2010; Chaves *et al.* 2011; Hutter *et al.* 2013; Castroviejo-Fisher *et al.* 2014; Fouquet *et*
148 *al.* 2014; McGuire *et al.* 2014, Beckman & Witt 2015, Lynch Alfaro *et al.* 2015, Parada *et al.*
149 2015, Dantas *et al.* 2016, Rojas *et al.* 2016). Despite their megadiversity and abundance,
150 insects are poorly known in the Neotropics compared to vertebrates. Studies of diversification
151 are often restricted to small groups or suffer from low sampling, taxonomic uncertainty or
152 scarce distribution data. Therefore, attempts to generalise the processes explaining high

153 Andean species richness described in the literature remain rare. Yet, insect clades offer the
154 opportunity to add insights into our understanding of the macroevolutionary processes that
155 shaped Andean biodiversity over time.

156 One of the best-known and most diverse groups of Neotropical insects is the butterfly
157 tribe Ithomiini (Nymphalidae: Danainae). With *ca.* 47 genera and over 390 species (Lamas
158 2004) restricted to the Neotropical region, the group has diversified during the last 35 million
159 years (Wahlberg *et al.* 2009). Ithomiini are known for their striking variety of wing patterns,
160 and many groups include species with partially or entirely transparent wings. They are a
161 major component of forest butterfly communities and interact through Müllerian mimicry
162 among themselves and with other Lepidoptera such as *Heliconius* butterflies and arctiid
163 moths (Beccaloni 1997). Three of the most diverse ithomiine genera, *Ithomia*, *Napeogenes*
164 and *Oleria*, exhibit high species richness along the Andean slopes (Jiggins *et al.* 2006, Chazot
165 *et al.* 2015). Of interest to our study, Elias *et al.* (2009) showed that the ithomiine genus
166 *Napeogenes* (25 species), which has a higher diversity in the Andes, probably originated at
167 middle elevations in the Andes and subsequently colonised the lowlands, therefore supporting
168 the “time-for-speciation” hypothesis. However, there is no indication that this pattern is
169 common to the whole tribe Ithomiini. In this study we focus on a more speciose Ithomiini
170 clade, the subtribe Godyridina. The Godyridina includes 10 genera and 77 species distributed
171 throughout the Neotropics. They also exhibit particularly high species richness in the Andes
172 (46 species) compared to other Neotropical regions (Figure 2). Here, we generated and
173 compiled DNA sequences for 206 individuals in order to infer a time-calibrated molecular
174 phylogeny that contained over 87% of species (67 out of 77 species after making taxonomic
175 changes where necessary). Combining historical biogeography, time- and trait-dependent
176 diversification analyses, we applied the above framework to test the four non-mutually

177 exclusive hypotheses proposed to explain Andean species richness: the “cradle” hypothesis
178 (higher speciation rate in the Andes), the “museum” hypothesis (lower extinction rate in the
179 Andes), the “time-for-speciation” hypothesis (older colonization time in the Andes) and the
180 “species-attractor” hypothesis (higher rates of colonization toward the Andes from adjacent
181 areas) (Figure 1).

182

183 **Material and methods**

184 *Individual-level phylogenetic tree and redefinition of species boundaries*

185 Defining species boundaries can be challenging, particularly in the case of mimetic butterflies
186 (Elias *et al.* 2007), so we included as many species and subspecies as possible to represent
187 taxonomic and geographic diversity (Supporting Information S1). We used material from our
188 own collections (Florida Museum of Natural History, Museo de Historia Natural of Lima,
189 Museu de Zoologia da Universidade of São Paulo, University College London, Muséum
190 National d’Histoire Naturel of Paris) and material kindly provided by colleagues. *De novo*
191 (75%) and published sequences (25%) for three mitochondrial (cytochrome oxidase I, tRNAL,
192 cytochrome oxidase II, 2356 base pairs (bp)) and two nuclear genes (elongation-factor alpha 1,
193 1260 bp and tektin, 734 bp) were compiled for 206 specimens (see Supporting Information S1
194 for PCR conditions and GenBank accession numbers). We could not obtain sequences for 10
195 species. We added 44 outgroups representing most genera of the subfamily Danainae
196 (Wahlberg *et al.* 2009) to our focal group sampling, for a total dataset of 250 individuals. We
197 concatenated all sequences, resulting in a total length of 4350 bp. The dataset was then
198 partitioned by gene and codon positions and the best models of substitution for optimized sets
199 of nucleotides were selected over all models implemented in MrBayes, using the ‘greedy’
200 algorithm and linked rates implemented in PartitionFinder 1.1.1 (Lanfear *et al.* 2012). We

201 performed a Bayesian inference of the phylogeny using MrBayes 3.2.2 (Ronquist *et al.* 2012),
202 allowing it to run for 10 million generations, with four Monte Carlo Markov chains that
203 sampled every 10,000 generations (resulting in 1,000 posterior trees). Although the
204 monophyly of the Ithomiini was well established by previous studies (Freitas & Brown 2004;
205 Brower *et al.* 2006; Willmott & Freitas 2006; Brower *et al.* 2014), it was not recovered in
206 preliminary runs. We therefore constrained the tribe to be monophyletic in the MrBayes runs.
207 We extracted the maximum clade credibility tree using the median of posterior distribution
208 for node ages using TreeAnnotator 1.6.2 (Drummond *et al.* 2012) and applied a 20% burn-in.
209 The resulting tree was used to investigate the established taxonomy in the light of our
210 molecular data and to define species to be included in the species-level phylogeny and in
211 subsequent analyses (Appendix 1, Supporting Information S1-S3).

212

213 *Species-level phylogeny*

214 To generate a species-level phylogeny of the Godyridina we used the consensus of
215 concatenated sequences of all individuals belonging to the same species, after redefining
216 species boundaries where applicable (e.g. Condamine *et al.* 2012, Lewis *et al.* 2015, see
217 Appendix 1). We obtained a dataset of 67 species out of 77 extant Godyridina species (after
218 our revision of species boundaries), which we combined with the sequences of the 44
219 outgroups used previously. To select the best partition scheme we used PartitionFinder
220 (Lanfear *et al.* 2012) as before, but tested only the models implemented in BEAST
221 (Drummond *et al.* 2012). First, we generated a Maximum Likelihood tree using IQ-TREE
222 1.3.11 (Nguyen *et al.* 2015). We implemented the best partition scheme previously found and
223 performed 1000 ultra-fast bootstrap iterations to get node support (Minh *et al.* 2013). The ML
224 tree is available in Supporting Information S3. Second, a time-calibrated phylogeny was

225 generated using BEAST 1.6.2 (Drummond *et al.* 2012). Following preliminary runs we
226 implemented a uniform prior for the substitution model of the mitochondrial third position.
227 We selected nine secondary calibration points based on the shared nodes with the phylogeny
228 of Nymphalidae from Wahlberg *et al.* (2009) (Supporting Information S4). We used
229 conservative uniform priors for secondary calibrations, with upper and lower bounds
230 corresponding to the 95% credibility intervals inferred in Wahlberg *et al.* (2009). We tested
231 the effect of calibrating or not the root of the tree, and of using both Yule process and birth-
232 death process as the branching process prior. This resulted in four independent runs of
233 BEAST. Each run was performed for 30 million generations, sampled every 30,000
234 generations, resulting in 1,000 trees. For each run, the maximum clade credibility tree using
235 the median of posterior distribution for node ages was extracted using TreeAnnotator
236 (Drummond *et al.* 2012), applying a 20% burn-in. Since differences in node ages between the
237 four independent runs were below two million years we only used the root-unconstrained and
238 Yule process as the branching process prior in subsequent analyses (Supporting Information
239 S5-S6).

240

241 *Historical biogeography*

242 To infer the ancestral colonization events of the Andes we performed an ancestral
243 reconstruction of biogeographic regions on the maximum clade credibility tree. We used the
244 Dispersion-Extinction-Cladogenesis (DEC) model (Ree & Smith 2008) implemented in the R
245 package BioGeoBEARS 0.2.1 (Matzke 2014). We did not test the effect of founder-event
246 speciation because this method applies to island-dwelling clades. We defined ten
247 biogeographic regions (Figure 2) based on the main geological events that occurred in the
248 Cenozoic (Hoorn *et al.* 2010) and previous publications (Elias *et al.* 2009; Condamine *et al.*

249 2012; Lewis *et al.* 2015). We first ran a model constraining only the connectivity among
250 adjacent areas (see Supporting Information S7). Secondly, we specified unequal rates of
251 dispersal between areas and time stratification of dispersal rate in BioGeoBEARS: we defined
252 four time bins (0-5, 5-8, 8-14, 14-20 million years ago) and for each of them we specified
253 dispersal multipliers. The time bins and dispersal multipliers were designed to account for the
254 arguably major geological events such as the closure of the Panama Isthmus, the south to
255 north uplift of the Andes, the closure of the Western-Andean-Portal, the retreat of the Pebas
256 System and the creation of *terra firme* forest in the upper Amazon (Supporting Information
257 S7). Distributional data for Godyridina species were obtained from fieldwork, literature and
258 museum collections. Each species was assigned to biogeographic areas based on their current
259 known distribution combined with data on their altitudinal distribution. We allowed for up to
260 6 areas to form an ancestral geographic range.

261

262 *Trait-dependent diversification*

263 Using trait-dependent models of diversification, we tested whether (1) increased speciation
264 rates in the Andes (“cradle”), (2) lower extinction rate in the Andes (“museum”), (3) longer
265 colonization rate (“time-for-speciation”) or (4) higher rates of colonization of the Andes
266 (“species-attractor”) explain the pattern of higher species richness in the Andes (Figure 1).
267 We classified species into either Andean or non-Andean regions, based on their current
268 known distributions. We fitted Cladogenetic State dependent Speciation and Extinction
269 models (ClaSSE, Goldberg & Iqic 2012) implemented in the *diversitree* 0.9-7 R package
270 (FitzJohn 2012), which estimates speciation rates, extinction rates and transition rates of
271 multiple states of a trait (here, the Andean or non-Andean distribution). Specifically, this
272 model allows both cladogenetic (at nodes) and anagenetic (along branches) character changes.

273 For a two-state character, the model accounts for up to six speciation rates, two extinction
274 rates ($\mu_2 > \mu_1$) and two anagenetic transition rates (q_{12}, q_{21}). Two speciation rates account for
275 speciation events without character state change ($\lambda_{222}, \lambda_{111}$). Two other rates account for
276 speciation accompanied by character state change of one of two descendant species ($\lambda_{112},$
277 λ_{212}) and the last two speciation rates account for cases where speciation involved character
278 state change of the two descendant species ($\lambda_{122}, \lambda_{211}$) (cladogenetic character changes in the
279 two latter cases (Goldberg & Igc 2012; Rolland *et al.* 2014). We used the ClaSSE rather than
280 the Geographic State change Speciation and Extinction model (GeoSSE, Goldberg *et al.*
281 2011) because Andean species are typically not present outside of the Andes (and
282 reciprocally). To avoid overparametrization of the models, we imposed several constraints on
283 the models that exclude parameters that are not meaningful in terms of biogeographic events.
284 Similarly to Rolland *et al.* (2014), we constrained to zero speciation rates involving
285 simultaneous character state change in the two descendant species. We also constrained to
286 zero the anagenetic transition rates because we considered that transition from one region to
287 another was accompanied by a speciation event. Transitions between regions were therefore
288 modelled by the parameters λ_{112} and λ_{212} . We tested for all possible combinations of models,
289 constraining or not speciation, extinction and transition rates to be equal among states.
290 Therefore we ended up with 10 models, which were fitted on 300 trees randomly sampled
291 from the posterior distribution, accounting for incomplete sampling in each region (Andean:
292 88%, non-Andean: 90%). Models were compared using corrected Akaike Information
293 Criterion scores (AICc). The strength of the ClaSSE model is that it allows simultaneously
294 testing of the non-mutually exclusive “cradle”, “museum,” and “species attractor” hypotheses.
295 To test the “time-for-speciation” hypothesis, we needed to infer ancestral state for each node,
296 which is not currently implemented in ClaSSE models. Therefore we fitted the Binary State

297 Speciation and Extinction model (BiSSE, Fitzjohn 2012) equivalent to the best fitting ClaSSE
298 model on the maximum clade credibility tree, i.e. fitting anagenetic instead of cladogenetic
299 changes, and confirmed that parameter values inferred from BiSSE were consistent with those
300 inferred from ClaSSE. This allowed us to estimate the probabilities of ancestral states at each
301 node. Finally, we used this ancestral state reconstruction to represent the accumulation
302 (speciation and colonisation events through time) of Andean and non-Andean lineages.

303

304 *Time-dependent diversification*

305 Following the results of the ClaSSE analysis (see results), we further explored heterogeneity
306 in diversification rates through time and across clades. We tested whether the three richest
307 subclades within the Godyridina had significantly different time-dependent diversification
308 dynamics than the rest of the subtribe following the method presented in Morlon *et al.* (2011).
309 The genus *Hypomenitis* (see results) contains 23 species, accounting for 30% of the subtribe;
310 the genus *Godyris*, with 11 species, accounts for 14%; and the clade including the
311 polyphyletic or paraphyletic genera *Hypoleria*, *Brevioleria*, *Pachacutia* and *Mcclungia*
312 (hereafter, *Brevioleria* clade) with 15 species accounts for 20% of the diversity. In total, these
313 three subclades alone account for 64% of the subtribe's diversity. Preliminary tests and
314 ancestral state reconstructions also dictated the choice of these subclades. We investigated
315 shifts of diversification rates at the root of these three clades by comparing fits of models
316 without shifts (null model), with fits of models with one, two and three shifts (all possible
317 combinations) using AICc scores.

318

319 **Results**

320 *Phylogenetic tree and taxonomical revisions*

321 The individual-level phylogeny of Godyridina was generally well supported, except for the
322 positions of *Greta clavijoi* and for relationships within the clade containing the genera
323 *Brevioleria*, *Mcclungia*, *Pachacutia* and some *Hypoleria* species (Supporting Information S2,
324 S3, S6). Based on the relationships between individuals in this phylogeny, reassessment of
325 morphological characters in some cases and distributional data, we re-evaluated the current
326 species and genera status and propose a number of formal and informal taxonomic changes
327 (Appendix 1, Supporting Information S1-S3).

328

329 *Estimates of divergence times and historical biogeography*

330 Based on the secondary calibrations from Wahlberg *et al.* (2009), the subtribe Godyridina was
331 inferred to be 17.08 million years old (95% highest posterior density: 14.99-19.16 million
332 years) (Supporting Information S5). Based on our biogeographic reconstructions, the most
333 likely ancestral areas were the Central Andes for the *Velamysta/Veladyris* clade and the upper
334 Amazon for the remaining ingroup (Figure 3). The inference at the root was not well resolved.
335 Then diversification occurred in three main areas: Central Andes where the *Veladyris*,
336 *Velamysta* and *Godyris* diversified, the western cordillera of Northern Andes where the
337 *Hypomenitis* diversified, and the upper Amazon in which the *Brevioleria*, *Hypoleria*,
338 *Mcclungia*, *Pachacutia* and *Heterosais* diversified (Figure 3). The genera *Velamysta* and
339 *Veladyris* originated in the Central Andes and have slowly accumulated species in this region.
340 From 15 to 10 million years ago, four speciation events occurred in the upper Amazon, a
341 region partly covered during this period by the Pebas System, a complex semi-aquatic
342 ecosystem, which even occasionally transformed into marine environment (Hoorn *et al.* 2010;
343 Wesselingh *et al.* 2010; Blandin & Purser 2013, Boonstra *et al.* 2015). Since there were
344 probably emergent lowlands, especially along the eastern side of the Andes, we did not forbid

345 dispersal into this region and instead allowed a low dispersal probability. One of these early
346 lowland lineages started diversifying intensively in the upper Amazon from around 8 million
347 years ago, after the drainage of the Pebas, leading to the clade currently grouping *Hypoleria*
348 and the *Brevioleria* clade. A major colonization event of the Northern Andes occurred around
349 10 million years ago, subsequently giving birth to the entire *Hypomenitis* clade (largely
350 distributed in the Western cordillera). Around 4-5 million years ago, another colonization of
351 the Andes occurred in the genus *Godyris*, followed by local diversification. We also
352 recovered several independent colonizations of the Andes on terminal or sub-terminal
353 branches, mainly in the Northern Andes. The clade formed by *Pseudoscada* and Genus2 had a
354 much more complex spatial diversification history. Secondary colonizations of lowlands were
355 inferred in the western part of the Andes for some species and in the eastern part for others.
356 This group now occurs from Central America to the Brazilian Atlantic forest region.
357 Generally, Central America and Brazilian Atlantic forest faunas were the result of several
358 independent colonizations, with very few within-region diversification events.

359

360 *Trait-dependent diversification*

361 Two models of trait-dependent diversification were found within an interval of 2 AICc scores.
362 The model with the lowest AICc score had three parameters: a unique speciation rate for
363 Andean and non-Andean lineages ($\lambda=0.158$), and two significantly different cladogenetic
364 transition rates (Table 1. Transitions from non-Andean to Andean areas ($\lambda_{112}=0.060$) were
365 ten-fold more frequent than from the Andes to non-Andean areas ($\lambda_{212}=0.005$), as expected
366 under the “species attractor” hypothesis (Table 1). The second best fitting model involved two
367 different transition rates (values similar to those of the best model, Table 1) and also two
368 different speciation rates among the two regions. Speciation rate in the Andes ($\lambda_{222}=0.176$)

369 was slightly higher than in non-Andean regions ($\lambda_{111}=0.140$). The latter result is expected
370 under the “cradle” hypothesis. For these two best models we fitted the equivalent BiSSE
371 model on the MCC tree and estimated the probabilities of character states at each node. Both
372 reconstructions gave identical results and we only represent the reconstruction based on the
373 best model (Figure 3). The root was inferred to be non-Andean (Figure 3), rejecting the “time-
374 for-speciation” hypothesis. Major colonizations of the Andes followed by diversification
375 occurred three times, leading to the *Veladyris/Velamysta* clade, part of the genus *Godyris*, and
376 the genus *Hypomenitis*. In addition, six colonization events on terminal branches were
377 recovered, totalling nine independent colonizations of the Andes. Conversely, we only found
378 one colonization event from the Andes toward a non-Andean region (*Hypomenitis* nspC in
379 Central-America, Figure 3). The ancestral state reconstruction based on a trait-dependent
380 model of diversification was very congruent with the reconstruction based on the
381 biogeographical model. Finally, lineage accumulation through time showed that speciation of
382 non-Andean lineages slowed down around 6 million years ago (Figure 4). Almost half of non-
383 Andean speciation events (12 out of 27) occurred in a time frame of 3 million years (between
384 9 and 6 million years ago). By contrast, Andean lineages intensively accumulated in the last 7
385 million years (Figure 4) through either speciation or colonization.

386

387 *Time-dependent diversification*

388 The model with four distinct diversification dynamics (*Brevioleria* clade, *Hypomenitis*,
389 *Godyris* and the remaining backbone) was significantly better supported than the others
390 (Table 2). The mainly non-Andean *Brevioleria* clade followed a model of decreasing
391 speciation rate through time with an initial rate of speciation higher than that of the backbone
392 at the same period followed by an inflexion starting about 6 million years ago (Figure 4a).

393 The mainly Andean *Godyrus* and *Hypomenitis* genera followed a constant speciation rate
394 model, with a speciation rate higher than that of the backbone (*Godyrus*: 0.190, *Hypomenitis*:
395 0.226, backbone: 0.128). Models with extinction had a significantly worse fit than models
396 without extinction (Table 2).

397

398 Discussion

399 In this paper, we propose a revision of the systematics of the ithomiine subtribe Godyridina,
400 using a comprehensive sampling of individuals that includes new undescribed species. Based
401 on this revision, we infer the first time-calibrated species-level phylogeny of this subtribe.
402 Our time calibrations are secondary calibrations based on the time-calibrated tree of
403 Nymphalid genera (Wahlberg *et al.* 2009). Apart from *Veladyris* and *Velamysta*, which feed
404 on *Solanum* (Greeney *et al.* 2009) and *Cuatresia* (Willmott, unpubl. data), respectively, all
405 Godyridina species feed almost exclusively on *Cestrum* species (Solanaceae) (Willmott &
406 Freitas 2006), which they do not share with any other ithomiine groups. In a recent
407 phylogenetic study of the entire family Solanaceae, *Cestrum* is inferred to have diversified in
408 the last 7 million years (Särkinen *et al.* 2013), which is younger than our estimates for
409 Godyridina diversification (14.9 ±2 million years ago excluding *Veladyris* and *Velamysta*).
410 Thus, we cannot exclude the hypothesis that Godyridina are younger than inferred here using
411 secondary calibration points (Garzón-Orduña *et al.* 2015). However, the dating of the
412 Solanaceae phylogeny was limited by the quality of available fossils, forcing the authors to
413 downgrade taxonomic assignment of the fossils. This limitation, in combination with a strong
414 prior on fossil ages, incurred a bias toward younger ages, as acknowledged by the authors of
415 the study (Särkinen *et al.* 2013). The actual age of *Cestrum* is therefore likely older than the

416 estimate of Särkinen *et al.* (2013), in better agreement with Wahlberg (2009)'s and our ages
417 for the subtribe Godyridina.

418 The time-calibrated phylogeny was used to infer the geographical and temporal patterns of
419 diversification of the butterfly subtribe Godyridina, which exhibits a higher species diversity
420 in the Andes, a common ecological pattern in the Neotropics (Luebert & Weigend 2014). To
421 evaluate historical explanations for this pattern of diversity we explicitly tested four non-
422 mutually exclusive hypotheses: the “cradle” hypothesis, the “time-for-speciation” hypothesis,
423 the “museum” hypothesis, and the “species-attractor” hypothesis (Figure 1). We found a
424 strong support for the “species-attractor” hypothesis in the Godyridina, suggesting an
425 important role of multiple colonization events of the Andes. We also found moderate support
426 for a slightly higher speciation rate within the Andes, which is confirmed by the detection of a
427 shift towards higher speciation rates in two Andean genera, in agreement with the “cradle”
428 hypothesis.

429 The four hypotheses jointly tested in our study have received mixed support in the
430 literature. Very few studies explicitly tested for higher speciation rate in the Andes (here
431 referred to as the “cradle” hypothesis). Hutter *et al.* (2013) used trait-dependent
432 diversification models to understand mid-altitude species richness patterns in Andean
433 glassfrogs. Because they divided the Andes into altitudinal bands, interpretations may be
434 oriented toward altitude-dependent diversification processes instead of Andean versus non-
435 Andean processes, but they found no support for a higher speciation rate in the Andes.
436 Conversely, Beckman & Witt (2015), who applied an approach similar to ours in a study of
437 New World goldfinches and siskins, found a higher speciation rate in the Andes. Plant groups
438 have shown more evidence of increased rates of speciation associated with the colonization of
439 the Andes, such as, for example, *Lupinus* (Hughes *et al.* 2006), *Astragalus* (Scherson *et al.*

440 2008), *Bromeliaceae* (Givnish *et al.* 2014), *Hedyosmum* (Antonelli & Sanmartín 2011).
441 However, the diversification of highland flora may differ from that of the fauna, with, for
442 example, an important role for long-distance dispersal and dispersal of pre-adapted temperate
443 plant lineages from the Nearctic region.

444 Our results showed evidence, although moderate, for increased speciation rates in the
445 Andes, consistent with the “cradle” hypothesis. One of the two best fitting models of trait-
446 dependent diversification inferred a slightly, but significantly higher speciation rate in the
447 Andes than in non-Andean regions. As an illustration of this, we also detected two shifts
448 toward a higher diversification rate at the root of two Andean subclades (*Hypomenitis* and
449 *Godyris*) with the time-dependent diversification models. Host-plants are known to be strong
450 drivers of diversification in phytophagous insects (Ehrlich & Raven 1964; Janz *et al.* 2006).
451 Most of the Godyridina species have specialized on different plant species belonging to the
452 highly diverse genus *Cestrum* (Willmott and Freitas 2006). In some cases, the diversity of
453 host-plants found in the Andes may have triggered ecological speciation driven by host-plant
454 shifts for Andean lineages, which may be one of the reasons for the high Andean speciation
455 rates. However, we also found a diversification rate shift in the *Brevioleria* clade, which is
456 mainly a non-Andean clade, suggesting that not only the Andes can drive high diversification.
457 This may explain why although it is significant, the difference in speciation rates among
458 regions is only about 20%. The *Brevioleria* clade is inferred to have occupied the upper
459 Amazon region since its origin, about 8 million years ago. The diversification of the
460 *Brevioleria* clade may have followed the retreat of the semi-aquatic Pebas system, when
461 forest ecosystems formed in the upper Amazon, presumably providing opportunities for
462 speciation.

463 As far as we know, the role of extinction in scenarios of Andean biogeography has
464 been poorly discussed in the literature. We defined the “museum” hypothesis as lower
465 extinction rates in the Andes than in non-Andean regions (Stebbins 1974). In the Godyridina,
466 all extinction rates were close to zero and models with different extinction rates were
467 therefore not supported, as in glassfrogs (Hutter *et al.* 2013). Antonelli & Sanmartín (2011)
468 reported lower extinction rate (combined with higher speciation rate) in the species-rich
469 Andean *Tafalla* subgenus compared to the remaining non-Andean Chloranthaceae, therefore
470 supporting the “museum” hypothesis, but Beckman & Witt (2015) found a higher extinction
471 rate in the Andes for goldfinches and siskins. It is difficult to predict what might cause
472 variations in extinction rates and in which direction. For example, landscape fragmentation
473 due to Pleistocene climatic fluctuations might have led to extinction events in the Amazonian
474 ecosystems, therefore increasing extinction rates. Conversely mountain species are generally
475 considered as being more prone to extinction during climate variations, as a result of narrow
476 distribution ranges and difficulties to track habitats during climatic fluctuations (e.g. McCain
477 & Colwell 2011; Fjelsdå *et al.* 2012). So far the role of extinction has been poorly considered
478 compared to other scenarios, but it will likely provide new insights in our comprehension of
479 the Neotropical biogeography.

480 The “time-for-speciation” hypothesis, defined as a longer presence in the Andes
481 (Stephens & Wiens 2003), has been supported in several studies (e.g. Santos *et al.* 2009). For
482 instance, Hutter *et al.* (2013) showed that glassfrogs first originated at mid-altitudes and
483 subsequently diversified at both higher and lower altitudes. An Andean origin followed by
484 subsequent colonization of the lowlands was also reported in other Ithomiini lineages, such as
485 the genera *Napeogenes* and *Ithomia* (Elias *et al.* 2009) and the subtribe Oleriina (de-Silva *et*
486 *al.* 2016). In the Godyridina the ancestral range inferred using two independent methods does

487 not support an Andean origin. From our results, the subtribe likely originated in a non-
488 Andean region, probably at the lowland interface between the Andes and the future upper
489 Amazon. In addition, the oldest Andean clade, formed by the two sister genera *Veladyris* and
490 *Velamysta*, underwent only moderate diversification (eight species when accounting for a new
491 species of *Veladyris* from Peru not included in the phylogeny) despite the longer time
492 available for speciation.

493 The “species-attractor” hypothesis, which posits that the Andes offer opportunities for
494 multiple independent colonization events, has rarely been tested explicitly but has been
495 discussed in the literature. Rates of biotic exchange between regions have been estimated in
496 some studies (e.g. Brumfield & Edwards 2007; Elias *et al.* 2009; Sedano & Burns 2010;
497 Castroviejo-Fisher *et al.* 2014, Beckman & Witt 2015). In Ithomiini, Elias *et al.* (2009) and
498 de-Silva *et al.* (2015) found higher rates of dispersal toward low altitudes, as did Beckman &
499 Witt (2015) for goldfinches and siskins. In contrast, other studies found that dispersal towards
500 the Andes is generally more frequent, with a limited number of reversals. For instance, in the
501 butterfly genus *Ithomiola* (Riodinidae: Mesosemiini), a small clade of 11 species, Hall (2005)
502 showed that diversification within the group consisted of repeated speciation events across
503 different altitudes, including several colonization events of the Andes from other areas. Hutter
504 *et al.* (2013) also reported that the inferred number of colonization events of each altitudinal
505 band by glassfrogs tends to correlate with species richness. Therefore, higher rates of
506 colonization from lowlands may also have contributed to higher species richness in the Andes,
507 but Hutter *et al.* (2013) did not explicitly test this hypothesis. In plants, Moonlight *et al.*
508 (2015) found that the Andean diversity of *Begonia* arose from multiple dispersal events into
509 the Andes, while Givnish *et al.* (2014) reported an important number of independent
510 colonization events of high elevations areas in Bromeliaceae.

511 In the Godyridina the inferred higher colonization rate of the Andes from non-Andean
512 regions (a pattern that we refer to as “species-attractor”) was almost tenfold higher than in the
513 other direction. We identified up to ten independent events of colonization of the Andes, but
514 only one for non-Andean colonization (Figure 3). From our ancestral state reconstruction, we
515 found that the accumulation of species in the Andean region accelerated during the very late
516 Miocene, and mostly occurred during Pliocene and early Pleistocene periods through either
517 colonization or speciation events, a timeframe that corresponds to the most intense orogeny
518 phase of the Andes (Hoorn *et al.* 2010). By contrast, most of the diversification of non-
519 Andean lineages appears to have occurred by the end of the Miocene. The Andes could drive
520 colonization and speciation in many ways, involving biotic factors, such as the availability of
521 new habitats, new predator communities, host-plant diversity, and abiotic factors such as
522 temperature, precipitation, environment heterogeneity and topography. It is also worth noting
523 that the Andes, extending all along the western side of South America, provide ample
524 opportunity for colonization on both sides of the cordilleras. Besides, from 20 to 10 million
525 years ago, the semi-aquatic Pebas System covered most of the upper Amazon region, with
526 even occasional marine incursions (Hoorn *et al.* 2010; Wesselingh *et al.* 2010; Blandin &
527 Purser 2013). During this period the Northern and Central Andes started to slowly increase in
528 elevation (Hoorn *et al.* 2010). Sediment deposits from the Andes towards the east
529 accompanied this uplift (Roddaz *et al.* 2010), and around 10 million years ago *terra firme*
530 forest probably started to form. The Acre System and then the Amazon River were forming,
531 and by 8 million years ago, the Amazon region was mostly emerged. This semi-aquatic Pebas
532 system probably prevented important faunal and floral exchange between the Andes and
533 Amazonia. The retreat of this system may thus have produced a broad connection between

534 these regions, thereby allowing colonizations both into (e.g., the Godyridina, this study) and
535 out of the Andes (e.g., *Napeogenes*, Elias *et al.* 2009).

536 Many Ithomiini species possess transparent wings although we observe a large
537 variation in the degree of wing transparency among species. Transparency appears to
538 dominate Ithomiini communities at high altitudes, which may indicate that transparency is a
539 potential adaptive response to the biotic and abiotic conditions found in those habitats (e.g.,
540 light, Papageorgis 1975). Multiple colonizations into the Andes may have been facilitated by
541 wing transparency because the Godyridina are among the most transparent Ithomiini,
542 reaching some extreme cases of almost complete transparency over the entire wing.

543 The role of the Andes in the diversification of the biota of the Neotropical region has
544 long been debated in the literature, and several biogeographic scenarios have been tested. In
545 this study we propose a framework to evaluate the support for four evolutionary scenarios
546 which may contribute to high Andean biodiversity, by analysing variation in speciation rates,
547 extinction rates, colonization times and colonization rates. Models testing the joint
548 contribution of two or more mechanisms can also be estimated and compared. Here, we
549 applied this framework to a species-rich group of Neotropical butterflies and found a strong
550 support for multiple independent colonization events, which led us to formulate the “species-
551 attractor” hypothesis but we also found moderate support for the “cradle” hypothesis (higher
552 speciation rate within the Andes). Using this framework to analyse the diversification of
553 many different groups of organisms will clarify the causes of the exceptional richness of the
554 Andean region, and will provide insights into the role played by the Andes in the
555 biogeography of the Neotropical region.

556

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573

574 **Authors Contributions**

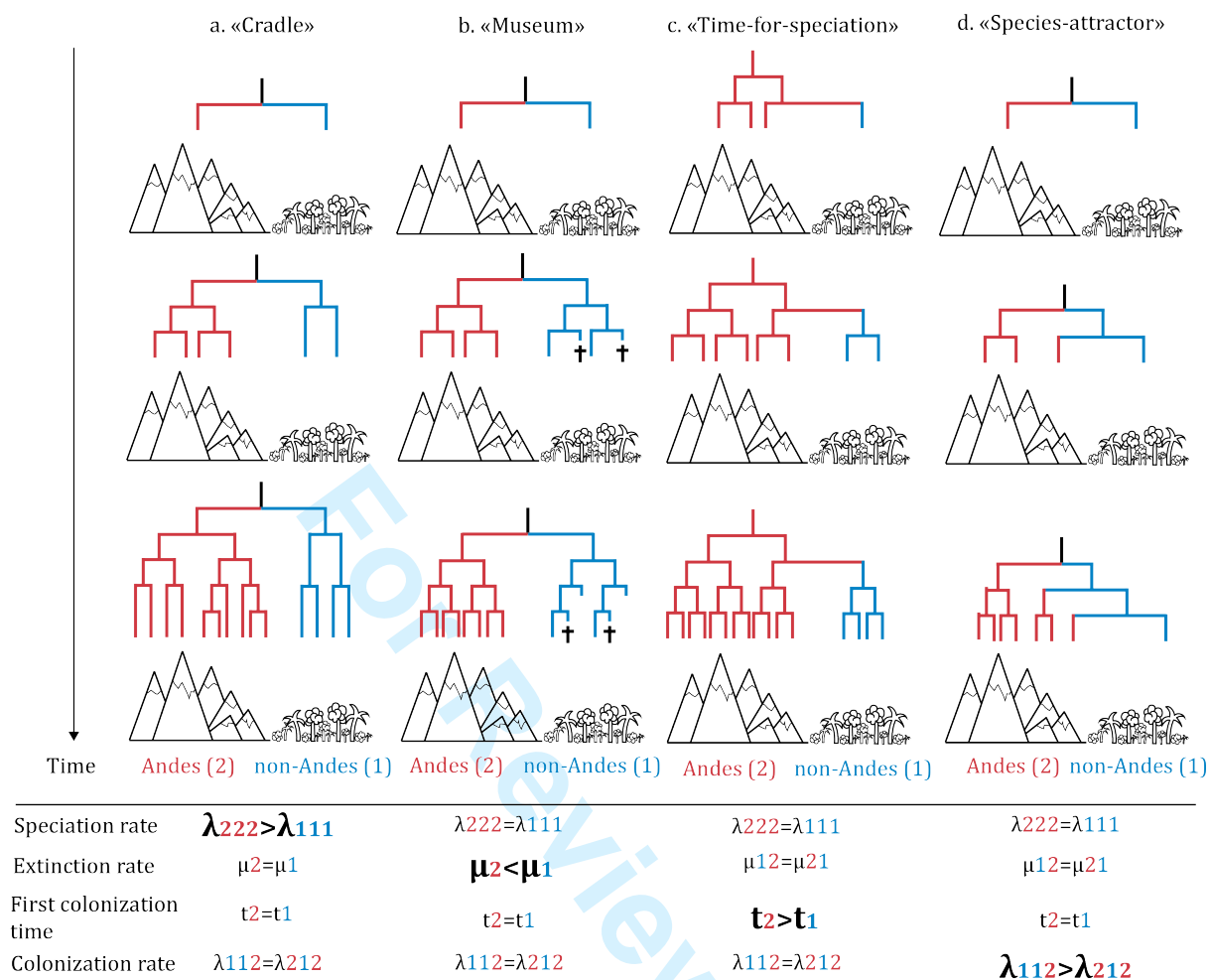
575 NC and ME designed the study. NC, ME, DdS, AVLF and KRW generated sequences. KRW,
576 ME, GL, MJ, JM, AVLF, CEGS, SU, NC and CDJ collected and provided specimens and
577 data. NC, FLC, ME and HM conducted the analyses. The manuscript was written by NC with
578 contributions from all co-authors.

579

580 **Data Accessibility**

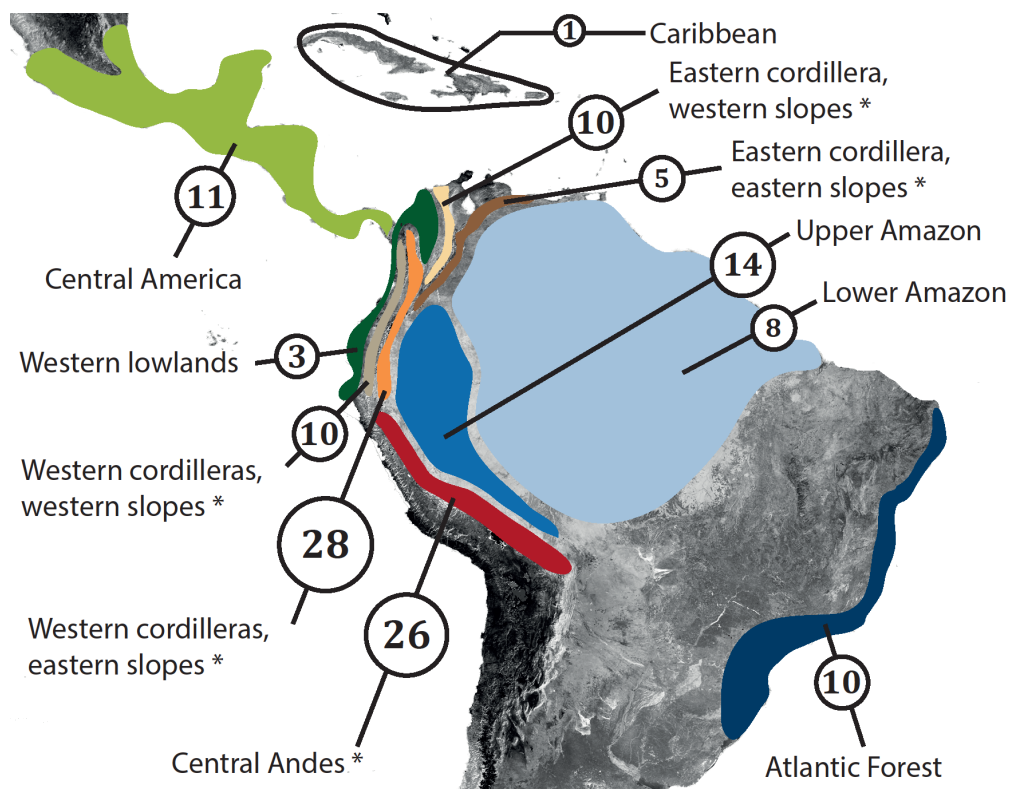
581 All sequences used this study are accessible on Genbank and accession numbers can be found
582 in Supporting Information.

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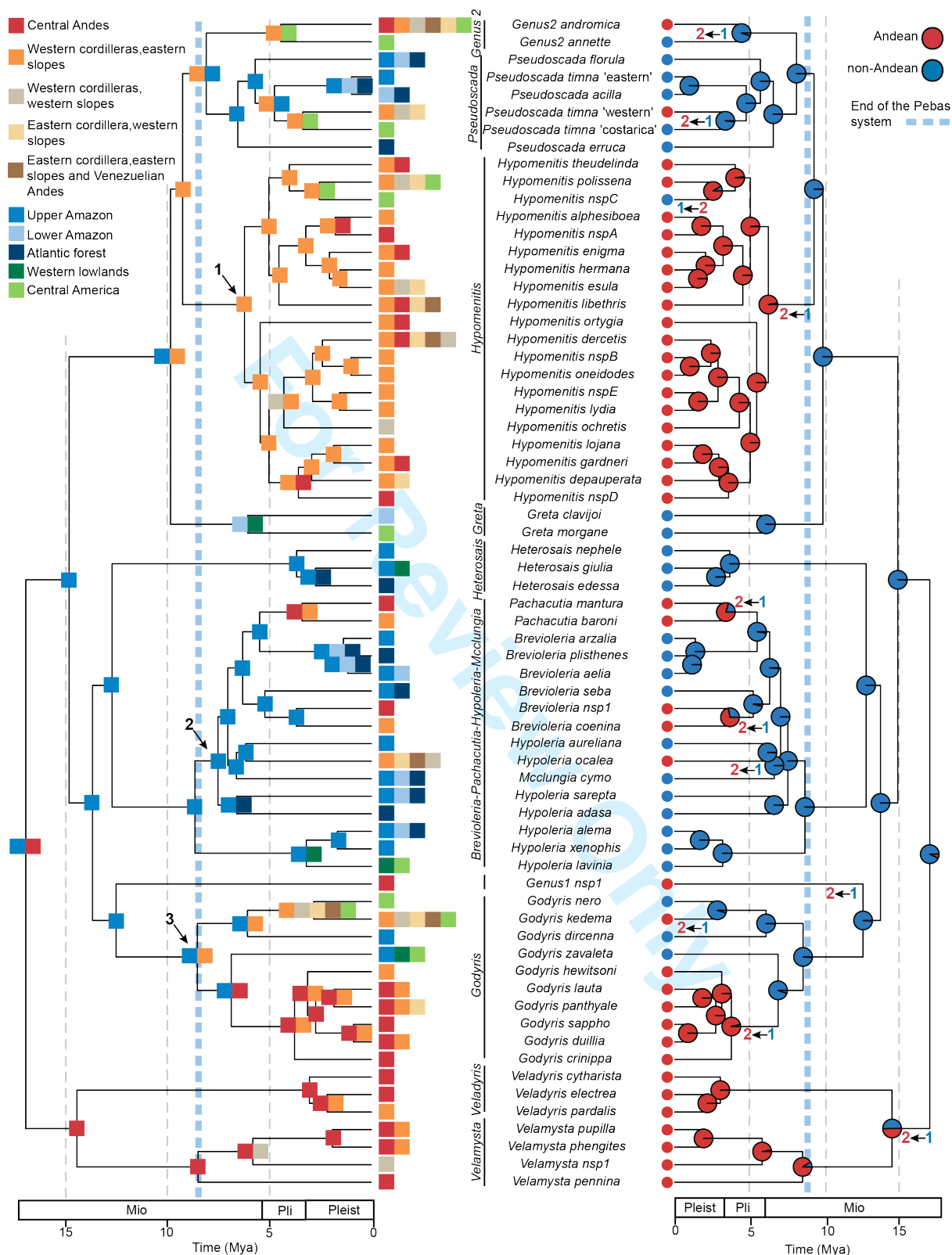
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584 Figure 1. Schematic representation of the four-hypothesis framework used to investigate the
 585 role of the Andes in diversification, and the parameters expected to vary in each hypothesis.
 586 Here we present simple cases where only one parameter varies at a time, but all combinations
 587 of varying parameters can also be tested. a. The “cradle” hypothesis posits that speciation rate
 588 of Andean lineages exceeds that of non-Andean lineages ($\lambda_{222} > \lambda_{111}$). b. The “museum”
 589 hypothesis posits that extinction rates of the Andean lineages are lower than the non-Andean
 590 lineages ($\mu_2 > \mu_1$). c. The “time-for-speciation” hypothesis states that the Andes were colonised
 591 earlier than non-Andean regions ($t_2 > t_1$), resulting in a longer time for diversification.
 592 The “species-attractor” hypothesis states that the rate of colonization from non-Andean regions to
 593 the Andean regions is higher than *vice versa* ($\lambda_{112} > \lambda_{212}$).



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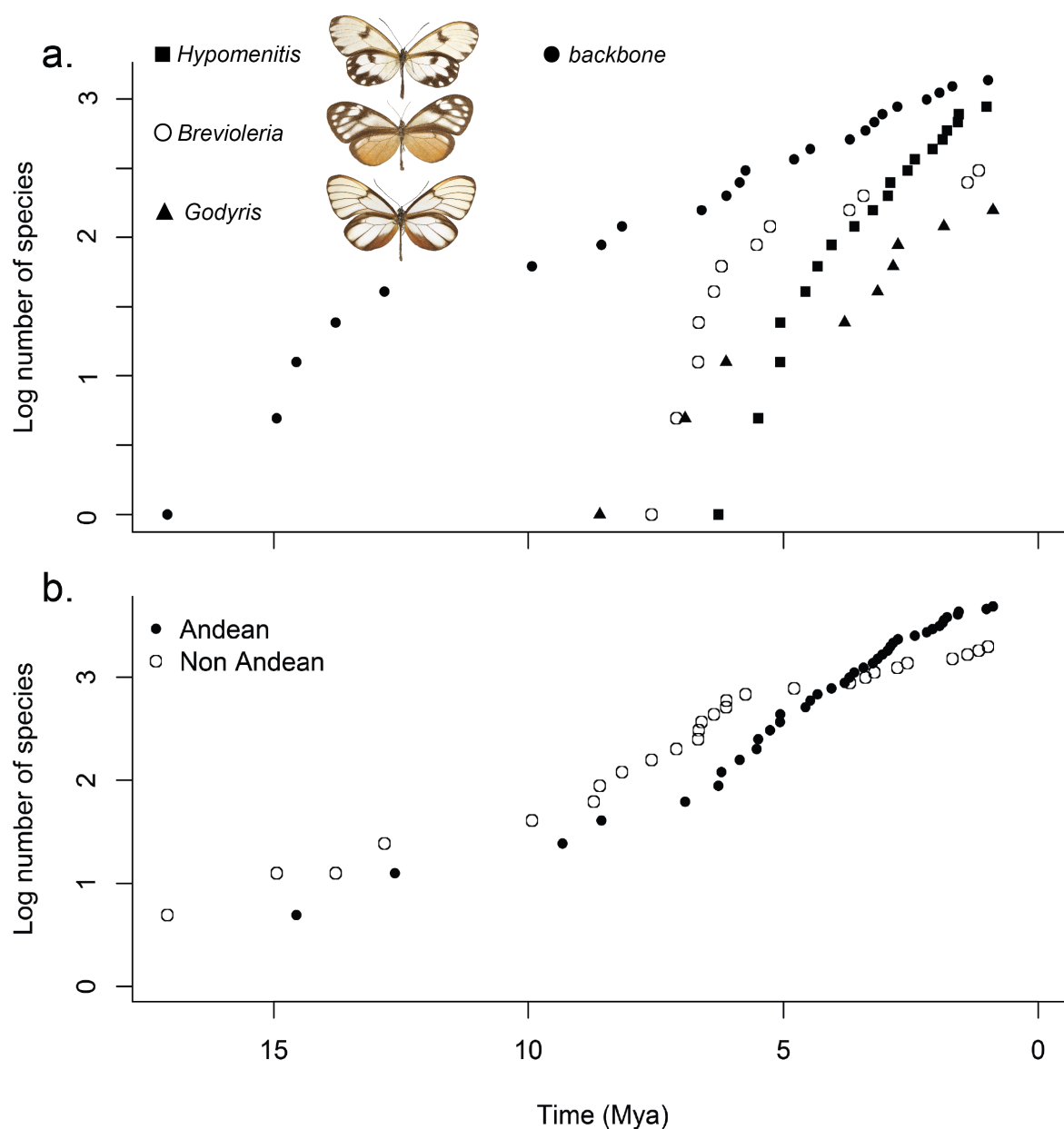
Figure 2. Map showing the delimitation of biogeographic areas used in the DEC model for ancestral reconstruction and the number of species recorded in each biogeographic region. Stars (*) indicate the Andean areas. The western and eastern cordilleras (eastern and western slopes) constitute the Northern Andes.



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603 Figure 3. Time-calibrated tree of the Godyridina. On the left, the most likely ancestral areas
604 inferred using the DEC model implemented in BioGeoBEARS are represented. On the right,
605 the probabilities for each node of being Andean (red) or non-Andean (blue) are represented.
606 This ancestral reconstruction was obtained from the best fitting model of character state-
607 dependent diversification (ClaSSE analysis, see text). Numbers on the left panel indicate the
608 three subclades for which we tested a shift in diversification rate: 1-*Hypomenitis*, 2-
609 *Brevioleria*, *Hypoleria*, *Mcclungia*, *Pachacutia*, 3-*Godyris*. On the right panel, colonization
610 events are represented (2←1: non-Andean toward Andean area, 1←2: Andean toward non-
611 Andean region). *Pleist*=Pleistocene, *Pli*=Pliocene, *Mio*=Miocene.
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 614 Figure 4. a. Lineage-through-time plots of the three subclades with diversification rate shifts
 615 (*Hypomenitis*, *Godyrus* and *Brevioleria* clade) and for the remaining backbone. b. Lineage
 616 through time plots of non-Andean and Andean lineages based on the ancestral reconstruction
 617 of trait-dependent diversification model.
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Table 1. Models and results of the ClaSSE analysis run over 300 trees randomly sampled from the posterior distribution (mean values are given), ordered by increasing AICc. Constraints of each model are indicated in the four first columns. 1=non-Andean, 2=Andean, $\lambda_{111}/\lambda_{111}$ = within region speciation rates, $\lambda_{112}/\lambda_{212}$ = cladogenetic transition rates, μ = extinction rates, df = degree of freedom (number of parameters), logL=log-likelihood, AICc= Akaike information criterion score corrected for sample size, Δ AICc = difference between the model and the best fitting model. Anagenetic transition rates and cladogenetic transition rates involving a character state change in both descendent lineages were constrained to 0 and are therefore not included in the table. The two first models are retained (models with Δ AICc < 2).

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$\lambda_{111}/\lambda_{222}$	$\lambda_{112}/\lambda_{212}$	μ	df	logL	AICc	ΔAIC	λ_{111}	λ_{222}	λ_{112}	λ_{212}	μ_1	μ_2
$\lambda_{111}=\lambda_{222} \neq$	$\lambda_{112}\neq\lambda_{212}$	$\mu_1=\mu_2$	4	-209.175	426.996	0	0.158	0.158	0.061	0.005	2.7E-06	2.7E-06
$\lambda_{111}\neq\lambda_{222} \neq$	$\lambda_{112}\neq\lambda_{212}$	$\mu_1=\mu_2$	5	-208.813	428.610	1.614	0.141	0.176	0.060	0.005	6.8E-07	6.8E-07
$\lambda_{111}=\lambda_{222} \neq$	$\lambda_{112}\neq\lambda_{212}$	$\mu_1\neq\mu_2$	5	-209.142	429.268	2.272	0.162	0.162	0.058	0.005	0.013	4.6E-07
$\lambda_{111}=\lambda_{222} \neq$	$\lambda_{112}=\lambda_{212}$	$\mu_1=\mu_2$	3	-212.167	430.715	3.720	0.155	0.155	0.035	0.035	5.3E-07	5.3E-07
$\lambda_{111}\neq\lambda_{222} \neq$	$\lambda_{112}\neq\lambda_{212}$	$\mu_1\neq\mu_2$	6	-208.813	431.026	4.030	0.141	0.176	0.060	0.005	1.6E-05	2.6E-06
$\lambda_{111}\neq\lambda_{222} \neq$	$\lambda_{112}=\lambda_{212}$	$\mu_1=\mu_2$	4	-211.647	431.939	4.944	0.132	0.175	0.036	0.036	7.5E-07	7.5E-07
$\lambda_{111}=\lambda_{222} \neq$	$\lambda_{112}=\lambda_{212}$	$\mu_1\neq\mu_2$	4	-212.039	432.723	5.727	0.165	0.035	0.165	0.035	0.032	6.7E-07
$\lambda_{111}\neq\lambda_{222} \neq$	$\lambda_{112}=\lambda_{212}$	$\mu_1\neq\mu_2$	5	-211.647	434.279	7.283	0.132	0.175	0.036	0.036	6.4E-06	4.1E-06
$\lambda_{111}=\lambda_{222} =$	$\lambda_{112}=\lambda_{212}$	$\mu_1=\mu_2$	2	-223.265	450.717	23.721	0.095	0.095	0.095	0.095	1.0E-06	1.0E-06
$\lambda_{111}=\lambda_{222} =$	$\lambda_{112}=\lambda_{212}$	$\mu_1\neq\mu_2$	3	-223.255	452.892	25.896	0.141	0.141	0.141	0.141	1.6E-05	2.6E-06

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640 Table 2. Results of time dependent diversification model comparisons (Morlon et al. 2011).
 641 We tested models with 0, 1, 2, and 3 shifts. We tested 6 models of diversification for each
 642 subclade and for the remaining backbone: constant speciation, varying speciation, constant
 643 speciation/constant extinction, varying speciation/constant extinction, constant
 644 speciation/varying extinction, varying speciation/varying extinction. Here we only report the
 645 best fitting models for each subclade. The model with three shifts was significantly better
 646 supported than the others, which was confirms using likelihood ratio tests. BCST=constant
 647 speciation, BVAR=time variable speciation, logL=log-likelihood, p(LRT)=*p*-value of the
 648 likelihood ratio test (best model against the others), λ is the speciation rate parameter and α is
 649 the rate of variation of λ through time.

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Shifts	Subtree	Model	Param	logL	p(LRT)	λ	α
BEST MODEL: <i>Brevioleria</i> + <i>Hypomenitis</i> + <i>Godyrus</i>	backbone	BCST	1	-46.307		0.128	
	<i>Brevioleria</i>	BVAR	2	-28.135		0.044	0.350
	<i>Hypomenitis</i>	BCST	1	-72.027		0.226	
	<i>Godyrus</i>	BCST	1	-21.945		0.190	
	total		5	-168.415			
<i>Brevioleria</i> + <i>Hypomenitis</i>	backbone	BCST	1	-70.484		0.150	
	<i>Brevioleria</i>	BVAR	2	-28.135		0.044	0.350
	<i>Hypomenitis</i>	BCST	1	-72.027		0.226	
	total		4	-170.647	0.0346		
<i>Brevioleria</i> + <i>Godyrus</i>	backbone	BCST	1	-120.654		0.187	
	<i>Brevioleria</i>	BVAR	2	-28.135		0.044	0.350
	<i>Godyrus</i>	BCST	1	-21.945		0.190	
	total		4	-170.734	0.0313		
<i>Brevioleria</i>	backbone	BCST	1	-144.247		0.190	
	<i>Brevioleria</i>	BVAR	2	-28.135		0.044	0.350
	total		3	-172.382	0.0189		
Whole tree		BCST	1	-175.429	0.0072	0.188	
<i>Hypomenitis</i> + <i>Godyrus</i>	backbone	BCST	1	-79.473		0.151	
	<i>Hypomenitis</i>	BCST	1	-72.027		0.226	
	<i>Godyrus</i>	BCST	1	-21.945		0.190	
	total		3	-173.445	0.0065		
<i>Hypomenitis</i>	backbone	BCST	1	-103.383		0.162	
	<i>Hypomenitis</i>	BCST	1	-72.027		0.226	
	total		2	-175.411	0.0029		
<i>Godyrus</i>	backbone	BCST	1	-153.325		0.188	
	<i>Godyrus</i>	BCST	1	-21.945		0.190	
	total		2	-175.270	0.0033		

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880 Appendix 1. Cases where the taxonomy adopted in this paper differ from the previous
 881 published taxonomic arrangement, particularly Lamas (2004). Some changes were made
 882 because they seem best supported by current evidence but still require further research,
 883 whereas other formal changes were made where additional morphological and/or
 884 biogeographic data were consistent with a revised classification.
 885

Classification in this paper	Lamas (2004) classification	Resulting formal classification	Explanation
<i>Brevioleria plisthenes</i>	<i>Brevioleria aelia plisthenes</i>	<i>Brevioleria aelia plisthenes</i> (d'Almeida, 1958)	We treat <i>Brevioleria plisthenes</i> as a distinct species in this paper, based on its quite isolated distribution from other <i>B. aelia</i> (Hewitson, 1852) taxa (where it was placed by Lamas, 2004) and its stable and distinctive wing pattern. Nevertheless, <i>Brevioleria</i> remains taxonomically highly complex and a thorough revision of the genus is required, so we do not make any formal changes here.
<i>Godyris hewitsoni</i>	<i>Godyris nepos hewitsoni</i>	<i>Godyris hewitsoni</i> (Haensch, 1903) rev. stat.	We treat <i>Godyris hewitsoni</i> as a species distinct from <i>Godyris nepos</i> (Weymer, 1875), since it differs in wing venation, having the base of vein M3 nearer the wing base than the base of vein M1 on both wings (the opposite is true in <i>nepos</i>). Since similar differences in venation separate three sympatric <i>Godyris</i> species in Ecuador (<i>G. duillia</i> (Hewitson, 1854), <i>G. hewitsoni</i> and <i>G. panthyle</i> (C. & R. Felder, 1862)), we regard such differences as likely to be significant at the species level. In addition, <i>G. nepos</i> has a distinctive wing pattern, with reddish HW markings that are more similar to those of <i>G. duillia</i> than other <i>Godyris</i> . Finally, no even slightly intermediate forms or subspecies are known between <i>G. hewitsoni</i> and <i>G. nepos</i> , and we have not found any characters that suggest that these are sister taxa.
Genus1 nsp1	<i>Greta</i> n. sp.	<i>Greta</i> n. sp.	An undescribed species from Peru included by Lamas (2004) in the genus <i>Greta</i> , here is hypothesized to be sister to <i>Godyris</i> . Its generic status requires confirmation with detailed morphological study, but there is no reason to suspect that the current DNA-based topology is incorrect.
Genus2 <i>andromica</i>	<i>Greta andromica</i>	<i>Greta andromica</i> (Hewitson, [1855])	The molecular data place <i>andromica+annette</i> as a clade sister to <i>Pseudoscada</i> , a topology consistent with morphological data (Willmott & Freitas, 2006), and they are here treated as a distinct genus, given the differences in size and habitat elevation in comparison with <i>Pseudoscada</i> . However, detailed morphological study is needed to determine whether this clade has any morphological synapomorphies and what its relationships are to other <i>Greta</i> not included in the current paper, to decide on the most appropriate taxonomic treatment.
Genus2 <i>annette</i>	<i>Greta annette</i>	<i>Greta annette</i> (Guérin-Ménéville, [1844])	See above under <i>Greta andromica</i> .
<i>Greta</i> is restricted to <i>G. clavijoi</i> , <i>G. morgane</i>		<i>Greta clavijoi</i> Neild, 2008, <i>Greta morgane</i> (Geyer, 1837)	Based on morphology (Willmott & Freitas, 2006), the type species of <i>Greta</i> Hemming, 1934, <i>G. diaphanus</i> (Drury, 1773), is sister to <i>G. morgane</i> (<i>G. clavijoi</i> was not included in Willmott & Freitas, 2006). We thus apply the name <i>Greta</i> in this paper to the clade <i>G. morgane+G. clavijoi</i> .
<i>Heterosais nephele</i>	<i>Heterosais giulia nephele</i>	<i>Heterosais nephele</i> (Bates, 1862) rev. stat. , <i>H. nephele geder</i> (Hewitson, 1869) rev. stat.	Molecular data show that transandean and Amazonian <i>Heterosais</i> are strongly distinct, and possibly not even sister taxa, consistent with differences in male androconial scales between taxa from the two regions. Transandean taxa (<i>H. g. giulia</i> (Hewitson, [1855]), <i>H. g. pallidula</i> Haensch, 1903, <i>H. g. cadra</i> (Godman & Salvin, 1878)) have a much smaller distal patch of hair-like androconial scales on the dorsal hindwing, not extending basally past the base of vein Cu1, whereas in Amazonian taxa (<i>H. n.</i>

			<i>nephele</i> , <i>H. n. geder</i>) the scale patch extends about halfway between the bases of veins Cu2 and Cu1.
<i>Hypoleria alema</i>	<i>Hypoleria lavinia</i> ssp. (east of Andes)	<i>Hypoleria lavinia</i> (Hewitson, [1855]) is restricted to taxa occurring west of the Andes, and <i>Hypoleria alema</i> (Hewitson, [1857]) becomes the oldest name for the Amazonian taxa formerly included in <i>H. alema</i> and <i>H. lavinia</i> . In addition to <i>Hypoleria alema ina</i> (Hewitson, [1859]), <i>Hypoleria alema</i> thus includes the following as subspecies, all n. stat. : <i>H. alema asellia</i> (Hopffer, 1874), <i>H. a. cajona</i> Haensch, 1905, <i>H. a. chrysodonia</i> (Bates, 1862), <i>H. a. consimilis</i> Talbot, 1928, <i>H. a. garleppi</i> Haensch, 1905, <i>H. a. indecora</i> Haensch, 1905, <i>H. a. karschi</i> Haensch, 1903, <i>H. a. meridana</i> Fox, 1948, <i>H. a. oreas</i> Weymer, 1899, <i>H. a. proxima</i> Weymer, 1899.	Molecular data indicate that the taxa east and west of the Andes that were included within <i>Hypoleria lavinia</i> in Lamas (2004) are strongly divergent. In addition, the east Ecuadorian Andes foothill taxon <i>ina</i> , hitherto regarded as conspecific with Colombian <i>H. alema</i> , was not differentiated from Amazonian <i>H. lavinia chrysodonia</i> . The data suggest that <i>H. lavinia</i> should be split into distinct species east and west of the Andes, and that <i>ina</i> (and presumably <i>alema</i>) should be regarded as subspecies of the eastern species. Morphological data are consistent with this hypothesis. The male genitalic valva is more elongated with a less strongly produced dorso-posterior projection in <i>H. lavinia</i> specimens dissected from Ecuador and southeastern Peru and in <i>H. alema ina</i> and <i>H. alema alema</i> , in comparison with examined <i>H. lavinia</i> specimens from western Ecuador, Panama and Mexico. A long series of highly variable specimens phenotypically intermediate between <i>H. lavinia chrysodonia</i> and east Ecuadorian <i>H. alema</i> , collected by P. Boyer (pers. comm.) at an elevational contact zone, supports the conspecificity of these taxa.
<i>Hypoleria lavinia</i>	<i>Hypoleria lavinia</i> ssp. (west of Andes)	<i>H. lavinia lavinia</i> , <i>H. l. cassotis</i> (Bates, 1864), <i>H. l. libera</i> Godman & Salvin, 1879, <i>H. l. rhene</i> (Godman & Salvin, 1878), <i>H. l. riffarthi</i> Haensch, 1905, <i>H. l. vanilia</i> (Herrich-Schäffer, 1865), <i>H. l. vaniliana</i> Kaye, 1919.	See discussion above.
<i>Hypoleria mulviana</i>	<i>Hypoleria lavinia mulviana</i>	<i>Hypoleria mulviana</i> d'Almeida, 1958 rev. stat.	<i>Hypoleria mulviana</i> was treated as a subspecies of <i>H. lavinia</i> by Lamas (2004). However, there is limited evidence (potentially unreliably labeled specimens) to suggest sympatry in the central Amazon, and the male genitalia are quite distinct from other <i>H. lavinia</i> and <i>H. alema</i> (see above); the ventral posterior projection on the valva is narrow and posteriorly (rather than inwardly) directed, the aedeagus is approximately twice as long and the tegumen is raised up higher above the valvae.
<i>Pseudoscada timna</i> 'costarica'	<i>Pseudoscada timna</i>	<i>Pseudoscada timna pusio</i> (Godman & Salvin, 1877)	The molecular data showed that divergence between <i>P. timna</i> from Costa Rica, western Ecuador and the Amazon is similar to that between other species in this genus, and that Amazonian <i>P. timna</i> are sister to Brazilian <i>P. acilla</i> . We treat these three clades of <i>P. timna</i> as three species in the analysis here, but further molecular and morphological research is required. In particular, the relationships of northwest South American <i>P. timna</i> taxa (<i>P. t. saturata</i> (Staudinger, 1885) and <i>P. t. troetschi</i> (Staudinger, [1884])) to Costa Rican <i>P. t. pusio</i> and the undescribed west Ecuadorian taxon need to be determined before the classification can be revised.
<i>Pseudoscada timna</i> 'eastern'	<i>Pseudoscada timna</i>	<i>Pseudoscada timna timna</i> (Hewitson, [1855])	See above.
<i>Pseudoscada timna</i> 'western'	<i>Pseudoscada timna</i>	<i>Pseudoscada timna</i> (Hewitson, [1855]) n. ssp.	See above.
<i>Veladyris cytharista</i>	<i>Veladyris pardalis cytharista</i>	<i>Veladyris cytharista</i> (Salvin, 1869) rev. stat.	The Ecuadorian to north Peruvian taxa <i>Veladyris pardalis aurea</i> Lamas, 1980, <i>V. p. pardalis</i> (Hewitson, [1855]) and <i>V. p. totumbra</i> (Kaye, 1919) formed a clade distinct from the Peruvian <i>V. p. cytharista</i> , which clustered with

			<i>Veladyris electrea</i> (Brabant, 2004). In addition, <i>V. p. christina</i> Lamas, 1980, seems to be sympatric in north Peru (Amazonas) with an undescribed taxon which we regard as conspecific with <i>V. p. cytharista</i> ; <i>V. p. christina</i> shares a distinctive white spot on the ventral hindwing in cell Sc+R1-Rs with the Ecuadorian <i>Veladyris pardalis</i> taxa, and we thus retain all four of these taxa in <i>V. pardalis</i> , and treat <i>V. cytharista</i> rev. stat. as a distinct species. A revision of the genus is in preparation by KRW, GL and others.
<i>Velamysta</i> nsp1			This is an undescribed species recently discovered in western Ecuador by T. Kell (Kell, Willmott & Lamas, unpubl. data).
<i>Hypomenitis</i> spp.	<i>Greta</i> spp.	We reinstate <i>Hypomenitis</i> to include the following species (and their subspecies and synonyms as listed in Lamas, 2004), all rev. stat. : <i>H. alphasiboea</i> (Hewitson, 1869), <i>H. depauperata</i> (Boisduval, 1870), <i>H. dercetis</i> (Doubleday, 1847), <i>H. enigma</i> (Haensch, 1905), <i>H. esula</i> (Hewitson, 1855), <i>H. gardneri</i> (Weeks, 1901), <i>H. hermana</i> (Haensch, 1903), <i>H. libethris</i> (C. & R. Felder, 1865), <i>H. lojana</i> Vitale & Bollino, 2001, <i>H. lydia</i> (Weymer, 1899), <i>H. ochretis</i> (Haensch, 1903), <i>H. oneidodes</i> (Kaye, 1918), <i>H. ortygia</i> (Weymer, 1890), <i>H. polissena</i> (Hewitson, 1863), <i>H. theudelinda</i> (Hewitson, [1861]).	The majority of the montane species treated in <i>Greta</i> by Lamas (2004) form a well-supported clade, including <i>Ithomia theudelinda</i> Hewitson, the type species for <i>Hypomenitis</i> Fox, 1945, that is significantly separated from that containing <i>G. morgane</i> (and presumably the type species of <i>Greta</i> , <i>G. diaphanus</i> , see discussion above). Although Willmott & Freitas (2006) found no morphological synapomorphy for the two representative species of <i>Hypomenitis</i> , <i>H. ortygia</i> + <i>H. theudelinda</i> , support for the topology of this part of the tree was very weak, and the shared mid- to high elevation cloud forest habitats of all species included here in <i>Hypomenitis</i> is consistent with the monophyly indicated by the molecular data.

Supporting Information

Supporting Information S1. Primers and list of species with Genbank accession numbers.

PCR conditions followed Elias *et al.* (2009).

Genes region	Primer	Sequence (5' to 3')
COI-tRNA-COII	LCO, F	GGTCAACAAATCATAAAGATATTGG
	Lep 3.1, R	AAATTTTAATTCCTGTTGGTACAGC
	Nancy, R	CCTGGTAAAATTAATAATAAACTTC
	Jerry, F	CAACAYTTATTTTGATTTTTTGG
	Pat, R	ATCCATTACATATAATCTGCCATA
	Geoith, F	TAGGWTTAGCWGGAATACC
	Evaith, R	GAGACCAATACTTGCTTTCAGACATCT
<i>EF1a</i>	EFrcM4, R	ACAGCVACKGTYTGYCTCATRTC
	Ef1a-257F, F internal	TATCACTATTGACATCGC
<i>Tektin</i>	Tektin A, F	ACCAGTGGRGAYATYCTWGG
	Tektin 3, R	CGCAGTTTYTGATRCTYT

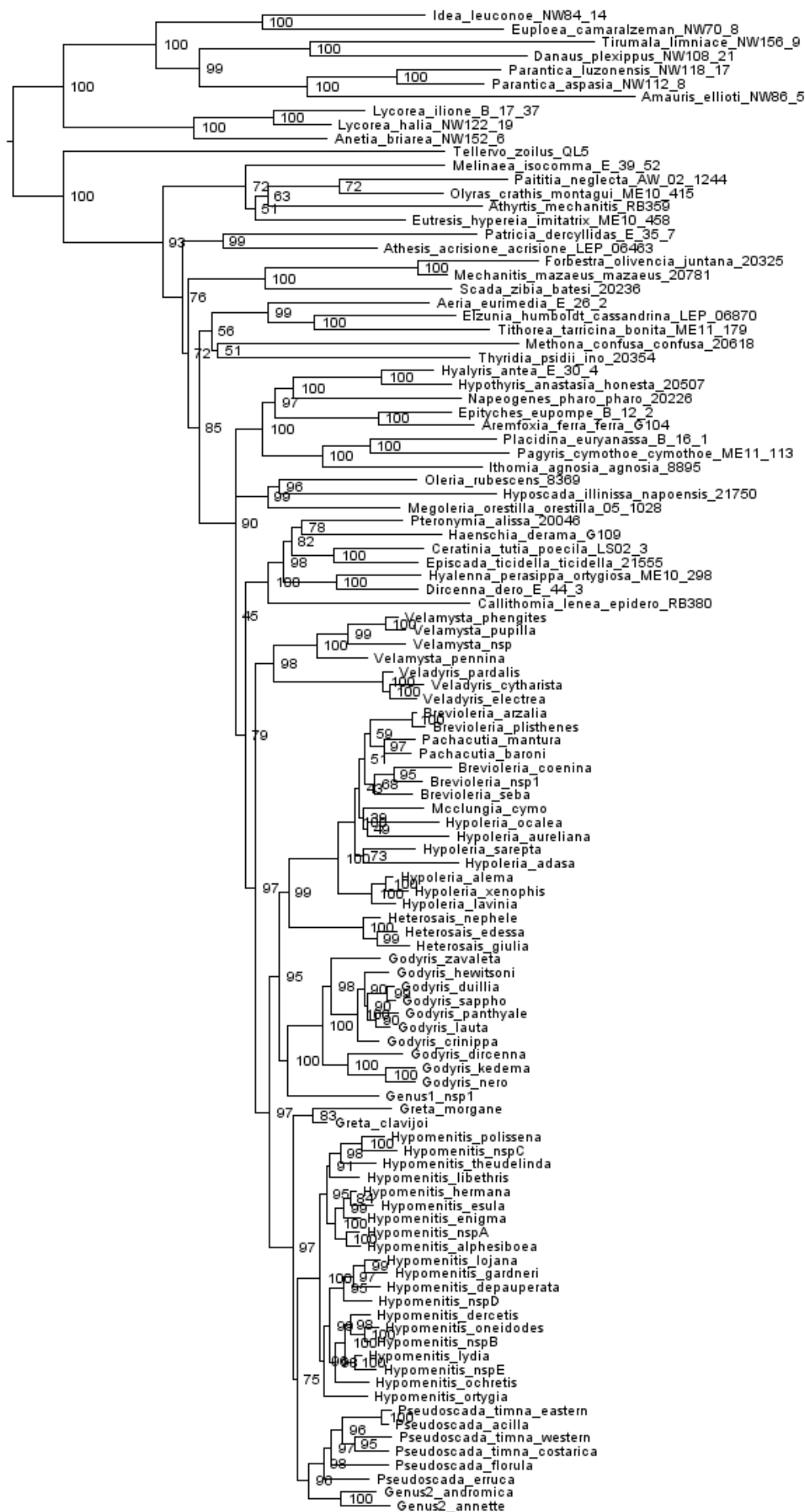
List of specimens used with Genbank accession codes.

Sequences were submitted to Genbank and codes will be added in the next version of the supporting information.

Supporting Information S2. Phylogenetic tree of 206 individuals based on the concatenation of COI-tRNA-COII-EFI-Tektin gene fragments inferred with MrBayes.

For Review Only

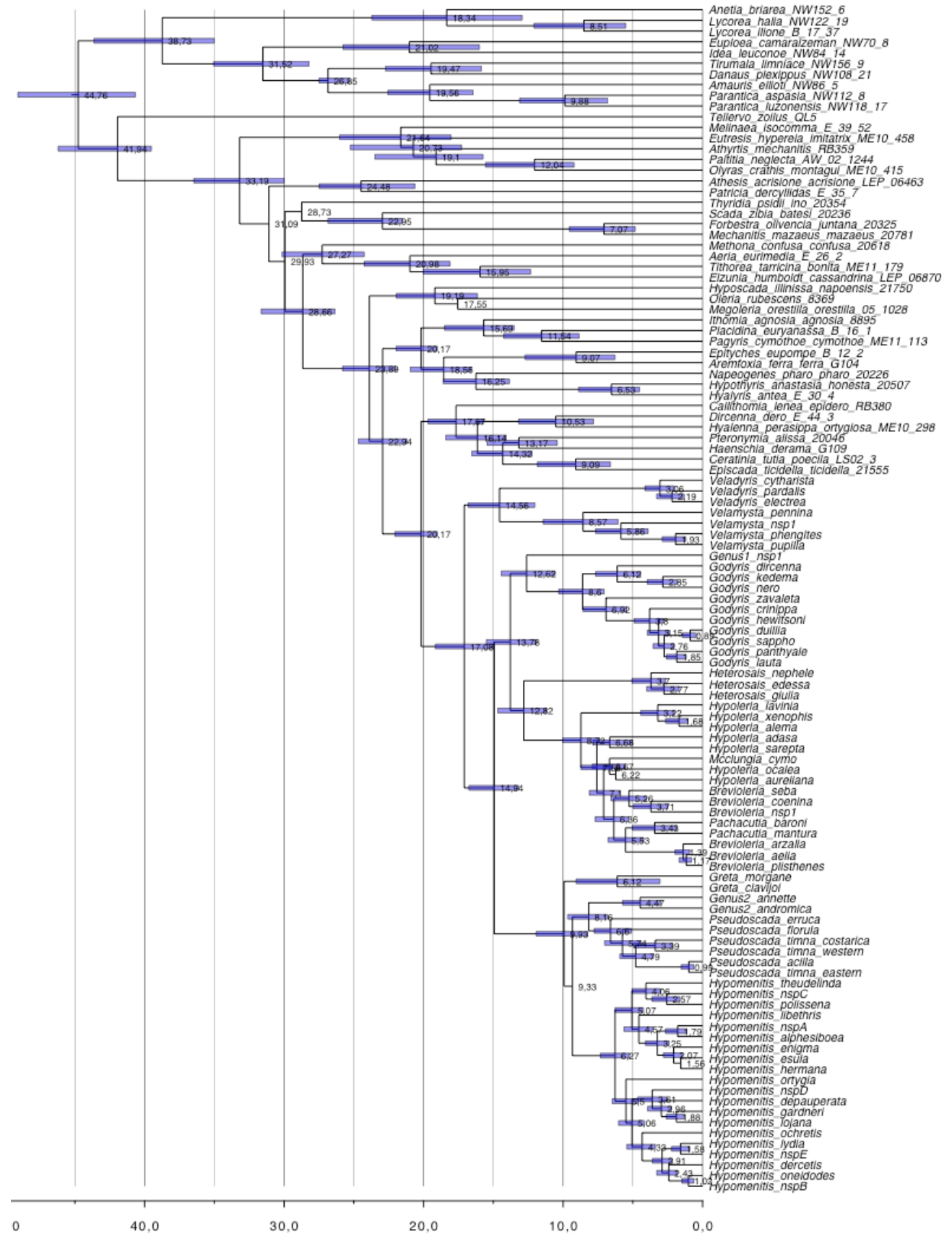
Supporting Information S3. Maximum Likelihood tree inferred using IQ-tree software. We performed 1000 ultra-fast bootstrap iterations to get node supports (Minh *et al.* 2013).



Supporting Information S4. Secondary calibration points used with uniform distribution between the lower and upper bound, corresponding to the 95% credibility interval reported in Wahlberg *et al.* (2009).

Calibrated node	Lower bound	Upper bound
(<i>Aeria</i> , (<i>Elzunia</i> , <i>Tithorea</i>))	18.0	28.0
(<i>Athesis</i> , <i>Patricia</i>)	14.0	27.5
Danaini 'crown'	35.0	48.0
(<i>Godyridina</i> , <i>Dircennina</i>)	19.0	24.0
(<i>Ithomiina</i> , <i>Napeogenina</i>)	19.0	23.5
(<i>Scada</i> , (<i>Mechanitis</i> , <i>Forbestra</i>))	21.5	29.0
Oleriina 'crown'	22.0	27.5
(<i>Tellervo</i> , <i>Ithomiini</i>)	39.5	52.0
((<i>Tirumala</i> , <i>Danaus</i>), (<i>Amauris</i> , <i>Parantica</i>))	24.5	27.5
root	44.0	58.0

Supporting Information S5. Time-calibrated maximum clade credibility tree. Median of node ages are shown at the nodes. Bars show the 95% credibility interval of node ages.



Supporting Information S6. Time-calibrated maximum clade credibility tree. Bayesian posterior probabilities are shown at the nodes.



Supporting Information S7. Matrices of dispersal probabilities for four time slices as used in the Dispersal-Extinction-Cladogenesis model of BiogeoBears.

Between 20 to 14 million years ago, the uprising Northern (Western Cordillera) and Central Andes were separated from the Gondwanan proto-continent by the Pebas System. The Pebas was a complex semi-aquatic ecosystem, probably connected northward to the Atlantic Ocean, which may have lead to occasional marine incursions. Connection may have also existed westward with the Pacific Ocean through the West Andean Portal which likely separated for a time the Northern and Central Andes.

Between 14 to 8 million years ago, the Pebas system retreated northward and eastward leading to the Acre System, which was progressively replaced by *terra firme*. The uplift of Eastern Cordilleras accelerated.

Between 8 to 5 million years ago, the Acre System disappeared, while the Amazon River was established. Uplift of the Andes, especially Eastern Cordilleras continued.

Between 5 to 0 million years ago, the Panama isthmus was closed, allowing continuous connections with Central America.

CAM: Central America

WL: Western Andean lowlands/Magdalena valley

WWco: Western cordilleras, western slopes

EWco: Western cordilleras, eastern slopes

CA: Central Andes

WEco: Eastern cordilleras, western slopes

EEco: Eastern cordilleras, eastern slopes

UA: Upper-Amazon

LA: Lower-Amazon

AF: Atlantic-Forest

0-5 Mya	CAm	WL	WWco	EWco	CA	WEco	EEco	UA	LA	AF
CAm	1	0.6	0.3	0.3	0	0.06	0	0	0	0
WL	0.6	1	0.1	0.1	0.06	0.1	0.01	0.01	0.001	0
WWco	0.3	0.1	1	0.1	0.6	0.04	0.06	0.01	0.006	0
EWco	0.3	0.1	0.1	1	0.6	0.4	0.6	0.1	0.06	0.04
CA	0	0.06	0.6	0.6	1	0.24	0.36	0.1	0.06	0.04
WEco	0.06	0.1	0.04	0.4	0.24	1	0.1	0.04	0.01	0
EEco	0	0.01	0.06	0.6	0.36	0.1	1	0.1	0.1	0.04
UA	0	0.01	0.01	0.1	0.1	0.04	0.1	1	0.6	0.4
LA	0	0.001	0.006	0.06	0.06	0.01	0.1	0.6	1	0.4
AF	0	0	0	0.04	0.04	0	0.04	0.4	0.4	1

5-8 Mya	CAm	WL	WWco	EWco	CA	WEco	EEco	UA	LA	AF
CAm	1	0.2	0.1	0.1	0	0	0	0	0	0
WL	0.2	1	0.2	0.2	0.12	0.2	0.04	0.04	0.008	0
WWco	0.1	0.2	1	0.2	0.6	0.08	0.12	0.04	0.024	0
EWco	0.1	0.2	0.2	1	0.6	0.4	0.6	0.2	0.12	0.08
CA	0	0.12	0.6	0.6	1	0.24	0.36	0.2	0.12	0.08
WEco	0	0.2	0.08	0.4	0.24	1	0.2	0.04	0.04	0
EEco	0	0.04	0.12	0.6	0.36	0.2	1	0.2	0.2	0.08
UA	0	0.04	0.04	0.2	0.2	0.04	0.2	1	0.6	0.4
LA	0	0.008	0.024	0.12	0.12	0.04	0.2	0.6	1	0.4
AF	0	0	0	0.08	0.08	0	0.08	0.4	0.4	1

8-14 Mya	CAm	WL	WWco	EWco	CA	WEco	EEco	UA	LA	AF
CAm	1	0	0	0	0	0	0	0	0	0
WL	0	1	0.4	0.4	0.24	0.4	0.16	0.16	0.2	0
WWco	0	0.4	1	0.4	0.6	0.16	0.24	0.16	0.032	0
EWco	0	0.4	0.4	1	0.6	0.4	0.6	0.4	0.08	0
CA	0	0.24	0.6	0.6	1	0.24	0.36	0.2	0.24	0.16
WEco	0	0.4	0.16	0.4	0.24	1	0.4	0.16	0.16	0
EEco	0	0.16	0.24	0.6	0.36	0.4	1	0.2	0.4	0.16
UA	0	0.16	0.16	0.4	0.2	0.16	0.2	1	0.6	0.4
LA	0	0.2	0.032	0.08	0.12	0.16	0.4	0.6	1	0.4
AF	0	0	0	0	0.08	0	0.16	0.4	0.4	1

14-20 Mya	CAm	WL	WWco	EWco	CA	WEco	EEco	UA	LA	AF
CAm	1	0	0	0	0	0	0	0	0	0
WL	0	1	0.4	0.4	0.08	0	0	0	0	0
WWco	0	0.4	1	0.4	0.2	0	0	0	0	0
EWco	0	0.4	0.4	1	0.2	0	0	0.1	0.1	0
CA	0	0.08	0.2	0.2	1	0	0	0.1	0.08	0
WEco	0	0	0	0	0	1	0	0	0	0
EEco	0	0	0	0	0	0	1	0	0	0
UA	0	0	0	0.1	0.1	0	0	1	0.4	0.4
LA	0	0	0	0.1	0.04	0	0	0.4	1	0.4
AF	0	0	0	0	0	0	0	0.4	0.4	1

GENUS	SPECIES	subspecies	specimen number	comments	COI	COII	EFla
Velamysta	peninna	ssp	G115		KX362073		
Velamysta	peninna	peninna	G116		KX362055		
Velamysta	phengites		E-39-32		DQ157548	DQ157548	DQ177994
Velamysta	pupilla	greeneyi	424		KX362082		KX362004
Velamysta	pupilla	greeneyi	ME10-351		KX362095		
Velamysta	pupilla		E-43-3		DQ071864	DQ071864	DQ073021
Velamysta	nsp1		LEP-04368		KX362126		KX361968
Godyris	crinippa	nubilosa	G118		KX362066		
Godyris	dircenna	dircenna	05-1321		JX573763		JX573692
Godyris	dircenna	dircenna	05-1369		KX362093		KX361957
Godyris	dircenna		G119		KX362043		
Godyris	duillia		E-37-1		DQ157495	DQ157495	DQ177941
Godyris	duillia		ME10-130		KX362074		
Godyris	hewitsoni	ssp	21050		JX573764	JX573764	JX573693
Godyris	hewitsoni	ssp	21067		KX362107		
Godyris	kedema		BMC-1705		KX362044		KX362002
Godyris	lauta	lauta	LEP-11125		KX362088		
Godyris	lauta	lauta	9242		KX362010		
Godyris	nero		99-SRNP-12088		GU333959		
Godyris	nero		06-SRNP-4980		JQ548288		KX361997
Godyris	nero		99-SRNP-5672		GU333957		
Godyris	nero		99-SRNP-5379		GU333958		
Godyris	nero		99-SRNP-5677		GU333956		
Godyris	panthyale	panthyale	21186		JX573765	JX573765	JX573694
Godyris	panthyale	panthyale	21180		KX362108		
Godyris	sappho	ssp	05-1155		KX362024		KX361990
Godyris	sappho		ME10-402		KX362026		
Godyris	sappho		G120		KX362045		
Godyris	zavaleta		E-44-1		DQ069235	DQ069235	DQ073027
Godyris	zavaleta	matronalis	20219		EU068785		KX361967

Godyris	zavaleta	matronalis	20207	EU069042		EU069146
Godyris	zavaleta	ssp1	02-324	EU068788		
Godyris	zavaleta	matronalis	20480	EU068786		
Godyris	zavaleta	matronalis	20606	EU068787		
Godyris	zavaleta	matronalis	ME10-482	KX362033		
Godyris	zavaleta	srnkai	02_92	KX362078		KX361998
Godyris	zavaleta	ssp	02-1041	EU068789		KX361999
Godyris	zavaleta	ssp 4	04-309	KX362046		KX362000
Godyris	zavaleta	huallaga	05-1395	KX362067		
Godyris	zavaleta	ssp 4	04-328	KX362086		KX362008
Godyris	zavaleta	sosunga	KW13-6a	KX362014		
Godyris	zavaleta	sosunga	KW13-6b	KX362015		
Godyris	zavaleta	zygia	KW13-7	KX362016		
Veladyris	pardalis		E-45-1	DQ157547	DQ157547	DQ177993
Veladyris	pardalis	aurea	ME10-38	KX362030		KX361955
Veladyris	pardalis	totumbra	21504	JX573827		JX573754
Veladyris	cytharista		05-1038	KX362081		KX361991
Veladyris	electrea	nssp	G124	KX362025		
Pachacutia	baroni		LEP-11127	KX362089		
Pachacutia	mantura	joroni	MC11-63	KX362127		
Hypoleria	alema	alema	ME10-517	JX573785		
Hypoleria	alema	chrysodonia	ME10-215	KX362109		
Hypoleria	alema		05-844	KX362058		KX361954
Hypoleria	alema	chrysodonia	20657	EU069045		EU069151
Hypoleria	alema	chrysodonia	20673	EU068798		
Hypoleria	alema	chrysodonia	20220	EU068796		
Hypoleria	alema	chrysodonia	LS02-98	EU068985		EU069152
Hypoleria	alema		B-16-8	DQ157504	DQ157504	DQ177949
Hypoleria	alema		BAKU-44	KX362047		KX361953
Hypoleria	alema	ssp	BAKU-52	KX362059		
Hypoleria	alema	ssp	BAKU-53	KX362060		
Hypoleria	lavinia	lavinia	LEP-00092	KX362120		
Hypoleria	lavinia	lavinia	LEP-00093	KX362121		
Hypoleria	lavinia	cassotis	08-SRNP-72597	JQ538543		
Hypoleria	lavinia	cassotis	08-SRNP-65239	JQ538447		
Hypoleria	lavinia	cassotis	05-SRNP-33790	JQ548234		
Hypoleria	lavinia	cassotis	KW13-30	KX362049		

Hypoleria	lavinia		YB-BCI8137		HM416537		
Hypoleria	lavinia		YB-BCI2749		HM416503		
Hypoleria	lavinia	vanilia	LEP-11339		KX362069		
Hypoleria	xenophis		05-624		KX362050		KX361952
Hypoleria	xenophis		G127		KX362061		
Hypoleria	adasa		BAKU-27		KX362075		
Hypoleria	aureliana		02-679		KX362048		
Hypoleria	aureliana		MJ07-265		KF268431		KX361956
Hypoleria	aureliana		MJ07-264		KX362092		
Hypoleria	ocalea		BMC-1631		KX362070		
Hypoleria	ocalea	gephira	LEP-11332		KX362124		
Hypoleria	sarepta	famina	21693		KX362021		EU069245
Brevioleria	aelia	pachiteae	05-418		KX362076		KX361995
Brevioleria	aelia	pachiteae	05-112		KX362056		
Brevioleria	aelia	plisthenes	BAKU-45		KX362028	KX362028	KX361945
Brevioleria	arzialia		E-44-4	ganbank id : aelia	DQ157477	DQ157477	DQ177924
Brevioleria	arzialia	ssp2	ME-2007 LS02-14		EU068977	EU068977	EU069119
Brevioleria	arzialia	ssp1	ME10-205		KX362012		
Brevioleria	arzialia	ssp1	ME10-206		KX362040		
Brevioleria	arzialia	ssp1	05-874		KX362039		KX361963
Brevioleria	arzialia	arzialia	02_3431		KX362083		KX362001
Brevioleria	arzialia		264		KX362077		KX361948
Brevioleria	coenina		ME10-359		JX573755		JX573684
Brevioleria	seba	oculata	20458		EU069025	EU069025	EU069120
Brevioleria	seba	oculata	ME10-212		KX362087	KX362087	
Brevioleria	seba	ssp1	02_3237		KX362057		KX361996
Brevioleria	seba		02_3477		KX362065		KX362005
Brevioleria	nsp1		G128		KX362023		
Mcclungia	cymo		B-19-3		DQ157512	DQ157512	DQ177958
Mcclungia	cymo	subtilis	06-205		KX362063		
Mcclungia	cymo	subtilis	ME11-159		JX573792		JX573720
Mcclungia	cymo		BAKU-42		KX362035	KX362035	KX361947

Mclungia	cymo		03_74		KX362085		
Genus1	nsp1		MJ07-701		KX362128		KX361949
Genus2	andromica		E-39-29		DQ157496	DQ157496	DQ177942
Genus2	andromica		22		KX362100	KX362100	KX361970
Genus2	andromica		02-1694		KX362098	KX362098	KX361969
Genus2	andromica	andania	05-1026		KX362099	KX362099	KX361989
Genus2	andromica	andania	21054		JX573767	JX573767	JX573696
Genus2	andromica	andania	21055		KX362101	KX362101	KX361971
Genus2	andromica	andania	21627		KX362106	KX362106	KX361972
Genus2	andromica	andania	05-1037				KX361992
Genus2	andromica	andromica	LEP-11338		KX362041		
Genus2	andromica	lyra	KW13-12		KX362013		
Genus2	annette		CR-1-5		DQ157497	DQ157497.1	DQ177943
Genus2	annette	championi	05-SRNP-35673		KX362119		KX362006
Genus2	annette	championi	09-SRNP-35381		KX362042		KX362007
Greta	clavijoi		LEP-01286		submitted		
Greta	morgane	oto	NW70_9		AY090206		AY090172
Greta	morgane	oto	05_SRNP_59557		JQ548125		
Greta	morgane	oto	03_SRNP_8669		GU333965		
Greta	morgane	oto	05_SRNP_23112		GU157182		
Greta	morgane	oto	04_SRNP_49510		GU157174		
Greta	morgane	oto	05_SRNP_22989		GU157181		
Hypomenitis	alphesiboea		259		KX362125	KX362125	KX361973
Hypomenitis	alphesiboea		05-1012		JX573766	JX573766	JX573695
Hypomenitis	nspA		21006		JX573768	JX573768	JX573697
Hypomenitis	nspA		21361		KX362114	KX362114	KX361981
Hypomenitis	nspA		MJ07-704		KX362032		KX361950
Hypomenitis	depauperata	umbrosa	LEP-06790		KX362062		KX361993
Hypomenitis	dercetis	dercetis	21040		JX573769	JX573769	JX573698
Hypomenitis	dercetis		02_2144		KX362102	KX362102	KX361974
Hypomenitis	enigma	ssp	21074		JX573770	JX573770	JX573699
Hypomenitis	enigma	ssp	21270		KX362103	KX362103	KX361976
Hypomenitis	enigma	ssp	21292		KX362112	KX362112	KX361977
Hypomenitis	enigma	ssp	21293		KX362110	KX362110	KX361978

Hypomenitis	enigma	ssp	21070		KX362022		KX361975
Hypomenitis	nspB		21002		JX573771	JX573771	JX573700
Hypomenitis	nspB	ssp	MJ07-706		KX362011		KX361951
Hypomenitis	esula		KW-120728-13		KX362017		
Hypomenitis	nspC		KW13-13b		KX362034		
Hypomenitis	gardneri	devriesi	21121		JX573772	JX573772	JX573701
Hypomenitis	gardneri	devriesi	21282		KX362113	KX362113	KX361979
Hypomenitis	hermana		E-39-46		DQ069236	DQ069236	DQ073028
Hypomenitis	hermana	joiceyi	400		KX362105		
Hypomenitis	hermana	ssp	21145		JX573773		JX573702
Hypomenitis	hermana	ssp	21341		KX362117		KX361958
Hypomenitis	hermana	ssp	21493		KX362096		KX361964
Hypomenitis	libethris	libethris	21160		JX573774	JX573774	JX573703
Hypomenitis	libethris	libethris	21579		KX362116	KX362116	KX361959
Hypomenitis	lojana		21181		JX573775	JX573775	JX573704
Hypomenitis	lojana		21291		KX362111	KX362111	KX361980
Hypomenitis	lojana		21468		KX362071	KX362071	KX361960
Hypomenitis	lydia		21122		JX573776	JX573776	JX573705
Hypomenitis	lydia		21272		KX362079	KX362079	KX361962
Hypomenitis	ochretis	ochretis	LEP-08656		submitted		
Hypomenitis	ochretis	ochretis	MJ07_697		KX362019		
Hypomenitis	oneidodes	ssp	21476		JX573777	JX573777	JX573706
Hypomenitis	oneidodes	ssp	21535		KX362052	KX362052	KX361982
Hypomenitis	ortygia	ortygia	21203		JX573778	JX573778	JX573707
Hypomenitis	ortygia	ortygia	21233		KX362097	KX362097	
Hypomenitis	ortygia	pyrczi	02-1693		KX362027	KX362027	KX361983
Hypomenitis	nspD		MJ07_693		KX362018		
Hypomenitis	nspD		MJ07_694		KX362020		
Hypomenitis	polissena		E-17-9		DQ157498	DQ157498	DQ177944
Hypomenitis	polissena		21		KX362104	KX362104	KX361984

Hypomenitis	theudelinda		E-28-4		DQ157499	DQ157499	DQ177945
Hypomenitis	theudelinda	zalmunna	21000		JX573779	JX573779	JX573708
Hypomenitis	theudelinda	zalmunna	21147		KX362053	KX362053	KX361985
Hypomenitis	nspE		BMC-1704		KX362072		KX362009
Hypomenitis	nspE		BMC-1711		KX362051		
Heterosais	edessa		BAKU-43		KX362031	KX362031	KX361946
Heterosais	edessa		BAKU-72		KX362068		
Heterosais	giulia	giulia	LEP-11343		KX362129		
Heterosais	nephele	nephele	PE-19-1	ID genbank:Heterosais guilia nephele	DQ157500	DQ157500	DQ177946
Heterosais	nephele	nephele	LS03-169		EU068984	EU068984	EU069149
Heterosais	nephele	nephele	20667		EU069043	EU069043	EU069148
Pseudoscada	acilla		BAKU-73		KX362037		
Pseudoscada	acilla		BAKU-25		KX362029		
Pseudoscada	acilla		BLU342		KX362090		
Pseudoscada	acilla	quadrifasciata	B-20-3	id genbank: P.timna	DQ157535	DQ157535	DQ177980
Pseudoscada	acilla		03-111	id UCL: P.timna	KX362094		KX362003
Pseudoscada	erruca		B-13-3		DQ157534	DQ157534	DQ177979
Pseudoscada	erruca		BAKU-20		KX362084		KX361994
Pseudoscada	florula	aureola	LS02-16		EU069101	EU069101	EU069247
Pseudoscada	florula	gracilis	04-111		KX362036	KX362036	KX361961
Pseudoscada	florula	gracilis	05-854		KX362054	KX362054	KX361986
Pseudoscada	florula	gracilis	02_1914		KX362130	KX362130	
Pseudoscada	florula	aureola	20214		EU068971		EU069246
Pseudoscada	florula	aureola	02_2086		DQ078319	DQ078319	
Pseudoscada	florula	gracilis	02-423		DQ078313	DQ078313	
Pseudoscada	florula	genetyllis	BLU435		KX362091		
Pseudoscada	timna		93		KX362118	KX362118	KX361966
Pseudoscada	timna		E-17-4		DQ157536	DQ157536	DQ177981
Pseudoscada	timna		LEP-08654		KX362115		
Pseudoscada	timna		LEP-00091		KX362123		
Pseudoscada	timna		LEP_06796		KX362122		
Pseudoscada	timna	utilla	20678		EU068941	EU068941	
Pseudoscada	timna	utilla	LS02-32		EU069015	EU069015	EU069249
Pseudoscada	timna		05-607		KX362080		KX361987
Pseudoscada	timna	ssp	02-1355		KX362064		KX361965

Pseudoscada	timna	timna	02-762	KX362038	KX361988
Pseudoscada	timna	pusio	06_SRNP_65072	JQ544063	
Pseudoscada	timna	pusio	06_SRNP_9283	JQ548418	
Pseudoscada	timna	pusio	06_SRNP_31461	JQ548293	
Pseudoscada	timna	pusio	05_SRNP_33463	JQ548236	
Pseudoscada	timna	pusio	06_SRNP_9374	JQ548511	
Pseudoscada	timna	pusio	01_SRNP_176	GU334301	

SPECIES NOT INCLUDED (no sequence)

Godyris	nepos
Veladyris	nsp
Pachacutia	cleomella
Pachacutia	germaini
Hypoleria	mulviana
Hypomenitis	cubana
Hypomenitis	nspD
Hypomenitis	gabiglooris
Hypomenitis	nsp
Greta	diaphanus

OUTGROUPS

Ceratinia_tutia_poecila_LS02_3
 Callithomia_lenea_epidero_RB380
 Dircenna_dero_E_44_3
 Hyalenna_perasippa_ortygiosa_ME10_298
 Episcada_ticidella_ticidella_21555
 Haenschia_derama_G109
 Pteronymia_alissa_20046
 Placidina_euryanassa_B_16_1
 Pagyris_cymothoe_cymothoe_ME11_113
 Ithomia_agnosia_agnosia_8895
 Methona_confusa_confusa_20618
 Thyridia_psidii_ino_20354
 Scada_zibia_batesi_20236
 Forbestra_olivencia_juntana_20325
 Mechanitis_mazaeus_mazaeus_20781
 Athesis_acrisione_acrisione_LEP_06463

Eutresis_hypereia_imitatrix_ME10_458
Athyrta_mechanitis_RB359
Paititia_neglecta_AW_02_1244
Olyras_crathis_montagui_ME10_415
Patricia_dercyllidas_E_35_7
Melinaea_isocomma_E_39_52
Aremfoxia_ferra_ferra_G104
Epityches_eupompe_B_12_2
Hyaliris_antea_E_30_4
Napeogenes_pharo_pharo_20226
Hypoathyris_anastasia_honesta_20507
Megoleria_orestilla_orestilla_05_1028
Hyposcada_illinissa_napoensis_21750
Oleria_rubescens_8369
Elzunia_humboldt_cassandrina_LEP_06870
Tithorea_tarricina_bonita_ME11_179
Aeria_eurimedia_E_26_2
Tellervo_zoilus_QL5
Parantica_luzonensis_NW118_17
Parantica_aspasia_NW112_8
Amauris_elliotti_NW86_5
Danaus_plexippus_NW108_21
Tirumala_limniace_NW156_9
Idea_leuconoe_NW84_14
Euploea_camaralzeman_NW70_8
Lycorea_ilione_B_17_37
Lycorea_halia_NW122_19
Anetia_briarea_NW152_6

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Tektin	Publication	Locality	Latitude
		Bolivia: La Paz, Sandillani	1612
		Peru: CU, Est. Biol. Wayquecha	1311
KX362222		Ecuador: Sucumbios, La Bonita	
KX362234		Ecuador: Napo, Yanayacu, nr Cosanga	0.6S
	Whinnett 2005	Ecuador: Napo, Yanayacu	0.6S
		Ecuador: Sucumbios, La Bonita, Tulcan Rd	
		Ecuador: Pichincha, Reserva Las Gralarias	
		Peru: Amazonas, San José de Molinopampa	617
KX362182	Chazot et al 2014	Peru: San Martin, Tarapoto, Río Shilcayo	6° 27' 07 S
KX362195		Peru: San Martin, Tarapoto, Río Shilcayo	550
		Peru: San Martin, Morroyacu	
	Brower 2006	Ecuador: Zamora-Loja, Highway, km 40	
KX362232		Ecuador: Napo, Hollin	0.69S
KX362244	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362196		Colombia: Antioquia, Amagá, Vereda La Mina	6°2'23.42" N
		Ecuador: Tungurahua, Río Ulba, nr. Baños	-1.441666667
KX362203		Ecuador	
KX362205	Janzen unpub	Costa Rica: Alajuela, Area de Conservacion Guanacaste, Sector San Cristobal, Quebrada Sucia	
KX362204	Janzen unpub	Costa Rica: Area de Conservacion Guanacaste, Sector San Cristobal, Estacion San Cristobal	
	Janzen unpub	Costa Rica: Alajuela, Area de Conservacion Guanacaste, Sector San Cristobal, Quebrada Cementerio	
	Janzen unpub	Costa Rica: Alajuela, Area de Conservacion Guanacaste, Sector San Cristobal, Vado Rio Cucaracho	
	Janzen unpub	Costa Rica: Alajuela, Area de Conservacion Guanacaste, Sector San Cristobal, Quebrada Cementerio	
KX362248	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362131		Peru: San Martín, Venceremos + 4 km (Segundo Baden)	5° 40' 142 S
KX362143		Ecuador: Napo, Cocodrilo	0° 39' 0 S
KX362198		Peru: Cuzco, El Mirador	1304
AY848717	Whinnett 2005	Ecuador: Sucumbios, El Recodo	
KX362201	Elias 2007	Ecuador: Orellana, Río Anangu	

	Elias 2007	Ecuador: Orellana, Rio Anangu	
	Elias 2007	Peru: San Martín, Pongo	
	Elias 2007	Ecuador: Orellana, Rio Anangu	
		Ecuador: Orellana, Rio Anangu	
KX362233		Ecuador: Napo, Mariposa	0° 54' 36 S
KX362183		Peru: San Martín, Km 30, Tarapoto - Yurimaguas	6° 24' 809 S
KX362226	Elias 2007	Peru: San Martín, Km 8, Tarapoto - Yurimaguas	6° 27' 43" S
KX362139		Peru: San Martín, Km 7.2, Pongo - Barranquita	06°17'12.3" S
KX362192		Peru: San Martín, Km 30, Tarapoto - Yurimaguas	6° 24' 588 S
		Peru: San Martín, Km 7.2, Pongo - Barranquita	06°17'12.3" S
KX362237		Guatemala: El Peten, Tikal	17°13'16"N
KX362238		Guatemala: El Peten, Tikal	17°13'16"N
KX362239		Costa Rica: Guanacaste, Santa Rosa	10°50'19"N
	Brower 2006	Ecuador: Sucumbios, La Bonita - Tulcan Road	
KX362141		Ecuador: Napo, Yanayacu	0° 36' 0 S
	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
KX362224		Peru: San Martín, Venceremos + 4 km (Segundo Baden)	5° 40' 142 S
		Peru: Amazonas, San José de Molinopampa	617
		Ecuador: Morona-Santiago, km 19 Macas-Nueve de Octubre rd. Río Abanico	-2.255
KX362197		Peru: SM, Sauce, Limoncocha	
KX362200	Chazot et al 2014	Ecuador: Napo, Hollin	0.69S
		Ecuador: Napo, Mariposa	0° 54' 36 S
KX362227		Peru: San Martín, Camp 2 on trail from Quebrada Yanayacu to Laguna del Mundo Perdido, PNCAZ	6°46'42.06S
	Elias 2007	Ecuador: Orellana, Rio Anangu	
	Elias 2007	Ecuador: Orellana, Rio Anangu	
	Elias 2007	Ecuador: Orellana, Rio Anangu	
	Elias 2007	Ecuador: Sucumbios, Garza Cocha	
	Brower 2006	Brazil: São Paulo, Jundiá	
KX362134		Brazil: São Paulo, Monte Alegre Dosul	
KX362241		Brazil: Alagoas, Frag. Coimbra Usina Serra Grande	9°0'1"S
KX362213		Brazil: Alagoas, Frag. Coimbra Usina Serra Grande	9°0'1"S
		Ecuador: Manabí, Cerro Prieto, S Santa Lucía, km 20 Jipijapa-Guayaquil rd.	
		Ecuador: Pichincha, Río Silanche	
	BOLD	Costa Rica: Area de Conservacion Guanacaste, Sector Pitilla, Manguera	
	BOLD	Costa Rica: Area de Conservacion Guanacaste, Brasilia, Moga	
	BOLD	Costa Rica: Area de Conservacion Guanacaste, Sector Pitilla, Pasmompa	
KX362243	BOLD	Panama: Panama	

	BOLD	Panama: Panama	
	BOLD	Panama: Panama	
KX362214		Colombia: Antioquia	
KX362215		Peru: San Martín, Robashca, Puesto de Control 11, PNCAZ	6° 42' 38 S
KX362216		Peru: San Martín, Yacusisa	646
KX362217		Brazil: São Paulo, Boracéia	
KX362230		Peru: San Martín, Biodiversidad USM, Km 19, Tarapoto - Yurimaguas	06°27'42.6" S
KX362189		Peru: SM, Shapaja-Chazuta Km5	
KX362140		Peru: SM, Shapaja-Chazuta Km5	
KX362218		Colombia: Antioquia, Gomez Plata, Porce	6°46'34" N
KX362242		Colombia: Antioquia	
KX362190		Ecuador: Luis Garcia, Panayaku	
KX362191		Peru: Loreto, Cerro de Mira Culo, PNCAZ	7° 27' 12 S
		Peru: San Martín, Puente Serranoyacu	05°40'31.6" S
KX362132		Brazil: São Paulo, Monte Alegre Dosul	
	Brower 2006	Ecuador: Sucumbios, El Recodo	
	Elias 2007	Ecuador: Sucumbios, Garza Cocha	
KX362229		Ecuador: Napo, Mariposa	0° 54' 36 S
		Ecuador: Napo, Mariposa	0° 54' 36 S
KX362138		Peru: San Martín, Caño Negro, Río Biabo, PNCAZ	7° 45' 10.15" S
KX362228		Peru: Cuzco, De Pilcopata a Santa Rosa de Huacaria	
KX362137		Ecuador: Azuay, Comunidad Shuar Mirador, 70 km E of Macas (Macas to Puyo road)	
	Chazot et al 2014	Ecuador: Napo, Cocodrilo	0° 39' 0 S
KX362142	Elias 2007	Ecuador: Orellana, Rio Anangu	
KX362202		Ecuador: Napo, Mariposa	0° 54' 36 S
KX362194		Peru: Cuzco, Palma Real (otro lado del Río)	12°37'18.06"S
KX362193		Peru: Cuzco, Pilcopata	
		Peru: Cuzco, Quebrada Quitacalzón	1301
		Brazil: Sao Paulo, Campinas	
KX362136	Chazot et al 2014	Peru: San Martín, Achinamiza, Bajo Río Huallaga	6° 28' 952 S
KX362135		Ecuador: Zamora-Chinchiipe, Quebrada Chorillos	
		Brazil: São Paulo, Monte Alegre Dosul	

KX362176		Brazil: São Paulo, Campinas	22° 49' 34 S
KX362245		Peru: Junín, 1Km S of Mina Pichita	1105
KX362145	Brower 2006	Brazil: Sao Paulo, Campinas	0° 1' 60 S
KX362144		Ecuador: Pichincha, Mindo, Yellow House Trail, Hacienda de San Vicente	5° 41' 5.99" S
KX362146		Peru: San Martín, Río Nieva	5° 39' 830 S
KX362147	Chazot et al 2014	Peru: Amazonas San Martín, Km 387, Limite San Martín, Amazonas border	
KX362148		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362149		Ecuador: Zamora-Chinchiipe, San Francisco	
KX362235		Peru: San Pedro	4°6.80'S
KX362249		Ecuador: Zamora-Chinchiipe, Podocarpus National Reserve	
		Colombia: Antioquia	
		Costa Rica: Puntarenas, Las Alturas	8.95
KX362206	Brower 2006	Costa Rica: Monte Verde	
KX362225		Venezuela	
	BOLD	Costa Rica: Area de Conservacion Guanacaste, Sector Mundo Nuevo, Vado Miramonte	
	BOLD	Costa Rica: Alajuela, Area de Conservacion Guanacaste, Sector San Cristobal, Sendero Palo Alto	
	Janzen unpub	Costa Rica: Guanacaste, Area de Conservacion Guanacaste, Sector Del Oro, Quebrada Trigal	
	Janzen unpub	Costa Rica: Guanacaste, Area de Conservacion Guanacaste, Sector Cacao, Gongora Bananal	
	Janzen unpub	Costa Rica: Guanacaste, Area de Conservacion Guanacaste, Sector Del Oro, Quebrada Trigal	
KX362223	Chazot et al 2014	Peru: Amazonas, Jorge Chávez 1	
KX362150	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362151		Ecuador: Zamora-Chinchiipe, San Francisco	1303
		Peru: Cuzco, San Pedro	
KX362207		Ecuador: Loja nr. Amaluza Centro Admin. PN Colambo-Yacuri, km 16.5 Jimbura-San Andrés rd.	-4.71166667
KX362185	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
KX362152		Peru: San Martín, La Antena, Km 16, Tarapoto - Yurimaguas	6° 27' 18 S
KX362153	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362154		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362155		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S

KX362186		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362187	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
KX362247		Peru: Junín, 2Km N of Mina San Vicente	1113
KX362246		Colombia	
KX362240		Costa Rica: Puntarenas, Las Alturas	8°57'0"N
KX362156	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
KX362157		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
AY848718	Brower 2006	Ecuador: Sucumbios, La Bonita	
KX362158		Ecuador: Napo, Yanayacu, near Cosanga	
KX362159	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
KX362160		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362161		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362162	Chazot et al 2014	Venezuela: Aragua, Rancho Grande	
KX362163		Peru: San Pedro	
KX362164	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
KX362165		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362166		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362167	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
KX362168		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362208	Chazot et al 2014	Ecuador: Carchi, Maldonado-Tulcán rd. Ecuador: Carchi, Las Juntas	00 53 19 N
KX362169	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
KX362170		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362171	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	
KX362172		Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362188		Peru: San Martín, Río Nieva	5° 41' 5.99" S
KX362250		Peru: Junín, 1Km S of Mina Pichita Peru: Junín, 1Km S of Mina Pichita	1105 1105
KX362173s	Brower 2006	Ecuador: Carchi, Lita Ecuador: Pichincha, Mindo, Yellow House Trail, Hacienda de San Vicente	0° 1' 60 S

KX362174	Brower 2006	Ecuador: Loja, San Pedro de Vilcabamba	
KX362175	Chazot et al 2014	Ecuador: Zamora-Chinchiipe, San Francisco	4.69 S
KX362199		Colombia: Antioquia, La Estrella, Romeral	6°8'16.46"N
KX362209		Colombia: Antioquia, La Estrella, Romeral	6°8'16.46"N
KX362133		Brazil: São Paulo, Monte Alegre Dosul	
KX362210			
KX362211		Colombia: Antioquia	
KX362212	Brower 2006 Elias 2007 Elias 2007	Peru: Huanuco, Tingo Maria Ecuador: Sucumbios, Garza Cocha Ecuador: Orellana, Rio Anangu	
KX362219		Brazil: São Paulo, Boracéia	
KX362177	Brower 2006	Brazil: Sao Paulo, M. Guacu Brazil: Bahia, Serra Bonita	15°25'17.68"S
KX362220	Brower 2006	Brazil: São Paulo, Campos do Jordao Brazil: Minas Gerais, Alto Caparaó, Parque Nacional de Caparaó Base alto Caparaó'	20°25'S
KX362221	Elias 2007	Ecuador: Sucumbios, Garza Cocha	9° 06' 13 S
KX362178		Peru: Ucayali, Río Previsto suspension bridge, 8 km W of El Boquerón del Padre Abad	6° 45' 4.54 S
HM052165	Elias 2007/Dasmahapatra2010	Peru: San Martín, Laguna del Mundo Perdido, PNCAZ	6° 24' 30 S
	Whinnett 2005	Peru: San Martín, Km 28, Tarapoto - Yurimaguas	
	Whinnett 2005	Ecuador: Orellana, Rio Anangu	5° 58' 489 S
		Peru: San Martín, Km 26, Yurimaguas - Tarapoto (now Km 24)	6° 24' 30 S
		Peru: San Martín, Km 28, Tarapoto - Yurimaguas	
KX362236	Brower 2006	Ecuador: Pichincha, Km 106.5, road along Mindo Ecuador: Carchi, Lita	
KX362181	Elias 2007 Elias 2007	Ecuador: Orellana, Rio Anangu Ecuador: Sucumbios, Garza Cocha	
KX362179		Peru: San Martín, Robashca, Puesto de Control 11, PNCAZ	6° 42' 38 S
KX362180		Peru: San Martín, Km 42, Tarapoto - Yurimaguas	6° 25' 29.4 S

KX362231

Peru: San Martín, Puente Serranoyacu

05°40'31.6" S

BOLD

Costa Rica: Area de Conservacion Guanacaste, Sector Pitilla, Sendero Memos

BOLD

Costa Rica: Area de Conservacion Guanacaste, Sector San Cristobal, Finca San Gabriel

BOLD

Costa Rica: Area de Conservacion Guanacaste, Sector Pitilla, Sendero Naciente

BOLD

Costa Rica: Area de Conservacion Guanacaste, Sector Pitilla, Sendero Mismo

BOLD

Costa Rica: Area de Conservacion Guanacaste, Sector San Cristobal, Camino Brasilia

Janzen unpub

Costa Rica: Alajuela, Area de Conservacion Guanacaste, Sector San Cristobal, Rio Blanco Abajo

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<u>Longitude</u>
6754
7135
77.88W
77.88W
7733
76° 20' 46 W
7701
77.73W
79.09 W
75°41'35.42" W
-78.39166667
79.09 W
77° 45' 136 W
77° 47' 24 W
7133

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77° 47' 24 W
76° 18' 503 W
76° 19' 23" W
76° 13'54.0" W
76° 18' 245 W
76° 13'54.0" W
89°37'29"W
89°37'29"W
85°37'8" W

77° 52' 48 W

77° 45' 136 W

7733

-78.2

77.73W
77° 47' 24 W
75°53'49.44W

35°50'25"W
35°50'25"W

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76° 02' 00 W
7649

76°17'30.8" W

75°04'20" W

75° 50' 16 W
77°40'28.7" W

77° 47' 24 W
77° 47' 24 W
76° 20' 3.86" W

77° 47' 24 W

77° 47' 24 W
72°41'24.85"W

7130

75° 54' 300 W

For Review Only

47° 4' 4 W

7525

78° 47' 60 W
77° 46' 56.37" W
77° 45' 224 W

79.09 W

78°57.90'W

-82.83333333

For Review Only

79.09 W
7133-4

-79.44

76° 17' 54 W

79.09 W
79.09 W
79.09 W

79.09 W

7524

82°50'0"W

79.09 W

79.09 W
79.09 W

79.09 W
79.09 W

79.09 W

78 04 47 W

79.09 W

79.09 W
77° 46' 56.37" W

7525
7525

78° 47' 60 W

For Review Only

79.09 W

75°39'30.15" W
75°39'30.15" W

39°30'12.25"W

41°50'W

75° 44' 28 W
75° 52' 8.29 W
76° 19' 30 W

76° 13' 856 W
76° 19' 30 W

76° 02' 00 W
76° 15' 01.6 W

For Review Only

77°40'28.7" W

For Review Only

For Review Only

