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7 **Diversification of clearwing butterflies with the rise of the Andes**

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27 **Short running head:** Diversification of clearwing butterflies

28

29 **ABSTRACT**

30 **Aim**

31 Despite the greatest butterfly diversity on Earth occurring in the Neotropical Andes and
32 Amazonia, there is still keen debate about the origins of this exceptional biota. A
33 densely sampled calibrated phylogeny for a widespread butterfly subtribe, Oleriina
34 (Ithomiini: Nymphalidae) was used to estimate the origin, colonization history and
35 diversification of this species-rich group.

36 **Location**

37 Neotropics

38 **Methods**

39 Ancestral elevation ranges and biogeographical range evolution were reconstructed
40 using data generated from detailed range maps and applying the dispersal-extinction-
41 cladogenesis model using stratified paleogeographic time slice matrices. The pattern of
42 diversification through time was examined by comparing constant and variable rate
43 models. We also tested the hypothesis that a change in elevation is associated with spe-
44 ciation.

45 **Results**

46 The Oleriina likely originated in the Central or Northern Occidental Andes in the Early
47 to Middle Miocene and rapidly diversified to include four genera all of which originat-
48 ed in the Andes. These clades, together with four species groups, experienced varying
49 spatial and temporal patterns of diversification. An overall early burst and decreasing
50 diversification rate is identified, and this pattern is reflected for most subclades.

51 **Main conclusions**

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Changes in the paleogeological landscape, particularly the prolonged uplift of the Andes, had a profound impact on the diversification of the subtribe. The Oleriina mostly remained within the Andes and vicariant speciation resulted in some instances. Dynamic dispersal occurred with the disappearance of geological barriers such as the Acre System and the subtribe exploited newly available habitats. Our results confirm the role of the Andean uplift in the evolution of Neotropical biodiversity.

59 **Keywords**

60 Andes, biogeography, diversification, ecological speciation, *Hyposcada*, Ithomiini butterflies, *Megoleria*, Neotropics, *Oleria*, *Ollantaya*.

63 **INTRODUCTION**

64 Like all other large groups of organisms, the taxonomic diversity of butterflies is highest in the Neotropical region and is estimated at 7700 species (Lamas, 2004). The majority of these species are found in the tropical Andes of Colombia, Ecuador, Peru and the western Amazonian lowlands, but the origin and diversification patterns of most groups remain poorly understood. The complex geological history of the Neotropics, together with paleoclimatic changes, have created a biogeographically diverse region with a mosaic of ecosystems and habitats (Gentry, 1982; Turchetto-Zolet *et al.*, 2013). Undoubtedly, this history had a profound influence on the origin of much of the region's endemic biodiversity and shaped diversification processes (Hoorn *et al.*, 2010; Blandin & Purser, 2013; Rull, 2013).

74 Several major paleogeographic events potentially played a prominent role in the evolution of Amazonian biodiversity (Hoorn *et al.*, 2010): the discontinuous uplift of the tropical Andes, which began with sustained uplift of the Central Andes from the Late Oligocene ~26 million years ago (Ma) (Sévrier *et al.*, 1988; Ehlers & Poulsen,

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78 2009), although increasing evidence suggests more rapid growth from the Late Mio-
79 cene (12 Ma) (Kennan *et al.*, 1997; Garziona *et al.*, 2008; 2014; Whipple & Gasparini,
80 2014); the orogenesis of the Northern Colombian Andes began with the Cordillera Oc-
81 cidental and culminated with the emergence of the Cordillera Oriental (3-15 Ma) (Mo-
82 ra *et al.*, 2008); the formation of the “Pebas System”, a vast network of shallow lakes
83 and wetlands, from the Late Oligocene to the Early Miocene (11.3 to ~24 Ma) (Wes-
84 selingh *et al.*, 2002); the formation of the fluvial “Acre” System (7 to ~11.3 Ma),
85 which later became the eastward flowing paleo-Amazon (5 to ~8 Ma), after intense
86 Andean uplift created a continuous barrier and transformed Amazonian drainage pat-
87 terns (Mora *et al.*, 2010).

88 Studies of Neotropical diversification have suggested that the lowlands have been
89 an important source of biodiversity, with diversification driven by riverine barriers
90 (Ayres & Clutton-Brock, 1992; Rosser *et al.*, 2012), marine incursions (Hoorn, 2006)
91 and environmental heterogeneity (Tuomisto *et al.*, 1995). However, mounting evidence
92 suggests that the Andean orogeny and geologically dynamic areas, in general, (Hoorn
93 *et al.*, 2013) have also promoted diversification through allopatric speciation while also
94 presenting new opportunities for ecological adaptation (Gentry, 1982; Kattan *et al.*,
95 2004; Elias *et al.*, 2009; Santos *et al.*, 2009).

96 A limited number of Neotropical butterfly studies have indicated that the Andes
97 were an important source for new species. *Hypanartia* (Nymphalidae: Nymphalinae)
98 diversified entirely within the Andes with speciation occurring without significant ele-
99 vational changes (Willmott *et al.*, 2001). Similarly, Andean *Lymanopoda* (Nympha-
100 lidae: Satyrinae) diversified within elevational bands, radiating horizontally throughout
101 the Andes with occasional speciation across elevational boundaries (Casner & Pyrcz,
102 2010). The ithomiine genera, *Napeogenes* and *Ithomia*, originated at middle elevations
103 in the Andes probably through ecological adaptation, although vicariance caused by

1 104 Andean uplift was also detected (Elias *et al.*, 2009). The diversification of *Taygetis*
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3 105 (Nymphalidae: Satyrinae) in the Late Miocene to Pliocene was coincident with the
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5 106 central Andean uplift and the disappearance of geographical barriers such as Lake
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7 107 Pebas (Matos-Maravi *et al.*, 2013). The Andes also played an important role in the ra-
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9 108 diation of heliconiine butterflies (Nymphalidae: Heliconiinae) and the diversification
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11 109 of the most speciose genera is coincident with uplift of the Andes (Kozak *et al.*, 2015).
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13 110 Nevertheless, the highest community species richness of most groups is found in the
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15 111 Amazon Basin, where, for example, a large proportion of heliconiine subspecies diver-
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17 112 sity occurs (Rosser *et al.*, 2012).

113 In order to provide further insights into how geological events have shaped Neo-
114 tropical butterfly diversification processes, we studied the evolutionary history of the
115 diverse butterfly subtribe Oleriina (Nymphalidae: Danainae: Ithomiini). The Ithomiini
116 represent an ideal group for this purpose because they are widely distributed through-
117 out the Neotropics and are found at all elevations within the Andean mountain range up
118 to around 3000 metres. The overall diversity and distribution of the tribe is reflected in
119 the subtribe Oleriina, containing the most species-rich ithomiine genus, *Oleria* (48 spe-
120 cies), as well as three genera, *Hyposcada*, *Megoleria* and *Ollantaya* that are relatively
121 species-poor in comparison. The subtribe therefore offers a valuable system to investi-
122 gate diversification processes in ithomiine butterflies and may aid our understanding of
123 the diversification of Neotropical butterflies as a whole.

124 Using a densely sampled (86%), calibrated species-level phylogeny combined with
125 detailed biogeographic and elevation range data, we specifically address the following
126 questions: 1) When and where did the Oleriina originate? 2) What was the biogeo-
127 graphic pattern of colonization of the Neotropics and do internal clades share a similar
128 diversification history? 3) Did geological events, particularly the uplift of the Andes,
129 influence the timing and pattern of diversification of the focal group?

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131 MATERIALS & METHODS

132

133 Phylogenetic analysis of the *Oleriina* and timing of diversification

134 A dated species-level phylogeny (see Appendix S1 in Supporting Information) was
135 used for all subsequent analyses.

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137 Rates of diversification

138 To visualize the tempo of diversification, lineage-through-time (LTT) plots for 1000
139 sampled trees from the posterior distribution were generated in APE 3.0-9
140 (Paradis *et al.*, 2004) in R (R Development Core Team, 2010). In order to test whether
141 diversification rates have changed over time the gamma (γ) statistic was calculated
142 (Pybus & Harvey, 2000) for different taxonomic groups using APE 3.0-9. Positive val-
143 ues of γ indicate an increase in diversification rate and negative values of γ indicate a
144 decreasing diversification rate towards the present. The Monte Carlo constant rates test
145 (Pybus & Harvey, 2000) was used to determine if the decreasing diversification rate
146 indicated by the gamma parameter is significant given the number of missing taxa in
147 our dataset. The package LASER 2.3 (Rabosky, 2006) was used to test specific models
148 of diversification through time (see Table 1). Fit of constant and variable rate models
149 were compared using the Akaike Information Criterion (AIC) (see Table 1).

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151 Ancestral elevation range

152 To test the hypothesis that a change in elevation is associated with speciation, we used
153 BayesTraits 1.0 (Pagel *et al.*, 2004). BayesMultiState, which reconstructs the evolution
154 of a finite number of discrete states, was implemented to compare a scenario of gradual
155 evolution (where the branch scaling parameter kappa (κ) is represented by the value

1 156 one), with a scenario of punctuational evolution (κ is represented by zero), and a sce-
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3 157 nario where κ was estimated by maximum likelihood (ML). Under a model of gradual
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5 158 evolution the probability of a change in elevation is in direct proportion to the branch
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8 159 length whereas under punctuational evolution a change in elevation is associated with
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10 160 speciation.

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12 Information on the elevation range of *Oleriina* was obtained for each species (See
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14 Appendix S1). The ancestral elevation range of each species was reconstructed using
15
16 maximum parsimony (MP) in Mesquite 2.75 (Maddison & Maddison, 2011), and
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18 BayesTraits 1.0 (Pagel *et al.*, 2004) was used to reconstruct ancestral elevation states
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20 164 under a ML criterion. Each species was categorized according to its known elevation
21
22 165 range as either low (0–1000 m), mid (750–1700 m) or high (>1400 m) (see Appendix
23
24 166 S1). Some species span two elevation ranges while *Oleria quintina*, *O. padilla* and *O.*
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26 167 *phenomoe* span all three categories.

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30 169 Using BayesTraits 1.0 (Pagel *et al.*, 2004) we first tested ancestral elevation as a
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32 170 discrete trait using BayesMultiState. Ancestral states were reconstructed by fixing the
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34 171 root of each clade at low, mid and high elevation and calculating the AIC in each case
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36 172 to determine if one of the alternative states was significantly more likely. The results
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38 173 obtained for κ were used to reconstruct the ancestral elevation range. Second,
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40 174 BayesContinuous was used to test ancestral elevation as a continuous trait by examin-
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42 175 ing the minimum and maximum elevation range for each species. Random-walk versus
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44 176 directional change models of evolution were compared and the branch scaling parame-
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46 177 ters κ , delta (δ) and lambda (λ) were estimated. The δ parameter determines if the rate
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48 178 of trait evolution has accelerated or slowed over time. A δ value of less than one is a
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50 179 signature of rapid early diversification followed by slower rates of change and suggests
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52 180 adaptive radiation, whereas a δ value of greater than one indicates a signature of accel-
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54 181 erating evolution with time. The parameter λ reveals the phylogenetic signal for a giv-
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1 182 en phylogeny and trait. A lambda value of one is consistent with the Brownian motion
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3 183 or constant-variance model of evolution whereas a value of zero indicates that species
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5 184 are evolving independently. The log-likelihood was calculated in each case and the
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7 185 associated AIC determined.
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11 187 **Ancestral geographical distribution**

12 188 The distribution of the Oleriina (see Appendix S2 in Supporting Information) was
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14 189 delimited on the basis of geological history, range data and previous studies (Santos *et*
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16 190 *al.*, 2009; Blandin & Purser, 2013) into ten areas (see Figs. 2 & 4). The geographic
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18 191 range evolution of the Oleriina was reconstructed using the ML dispersal-extinction-
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20 192 cladogenesis (DEC) model in Lagrange (Ree & Smith, 2008). We used the dated phy-
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22 193 logeny generated in BEAST and extant species distributional data to infer ancestral
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24 194 locations. The maximum number of ancestral areas was set to six, reflecting the maxi-
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26 195 mum number of areas occupied by extant species. Each species was coded as present
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28 196 or absent for each geographical region. Our analyses considered the main paleo-geo-
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30 197 graphical events that have occurred during the past 25 Ma (Fig.4.). This time span,
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32 198 covering the evolution of the Oleriina, was stratified into four time slices each reflect-
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34 199 ing temporal paleogeographical constraints. We followed Ree & Smith (2008) and for
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36 200 each time slice a matrix was constructed to scale the probability of dispersal between
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38 201 zero and 1 according to geographical area connectivity through time (Fig.4). Dispersals
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40 202 that involved a change in elevation were therefore multiplied by 0.01 to reflect the low
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42 203 probability of movement (Matos-Maraví *et al.*, 2013). Additional analyses tested the
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44 204 root area of the subtribe by constraining the root to be single areas and combinations of
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46 205 multiple areas. Likelihoods of models under different constraints were compared. A
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48 206 log-likelihood difference of two units was considered significant.
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208 **RESULTS**

209

210 **Oleriina phylogeny and timing of diversification**

211 Our analyses indicate that the Oleriina originated ~15.2 Ma (95% highest posterior
212 density (HPD): 13.2–25.6 Ma) and that the diversification of all extant genera followed
213 in the Middle to Late Miocene. The *Oleria* species groups, *onega* and *makrena*, diver-
214 sified mainly during the Late Miocene and Pliocene (95% HPD: 3.0–8.0 Ma), with the
215 *makrena* group diversifying further and more rapidly during the Pleistocene (95%
216 HPD: 0.5–3.0 Ma). The Pleistocene was also important in the diversification of the
217 *Oleria amalda* species group (Figs.1 & 2).

218

219 **Diversification through time**

220 Lineage-through-time (LTT) plots (Fig.3) and the gamma statistic indicate an overall
221 decreasing diversification rate for the Oleriina ($\gamma = -3.38$, $P = 0.001$ assuming 9 miss-
222 ing species). These results are reflected by the gamma statistic for *Oleria* ($\gamma = -4.22$, P
223 $= 0.001$, 6 missing species) as well as internal clades: *makrena* species group ($\gamma = -$
224 3.57 , $P = 0.001$, 3 missing species); *onega* species group ($\gamma = -2.31$, $P = 0.01$, 3 species
225 missing). In turn, a constant diversification rate could not be rejected for the *amalda*
226 species group ($\gamma = -0.19$, $P = 0.42$) or for *Hyposcada* ($\gamma = -0.27$, $P = 0.28$, 2 species
227 missing).

228 Gamma statistic results are in general supported by diversification models, in
229 which rate-variable models (DDL and/or Yule-2-rate) were preferred over rate-
230 constant models for Oleriina, *Oleria*, *makrena* and *onega* groups. Conversely, for *Hy-*
231 *poscada* and the *amalda* species group, a rate-constant pure birth model was better
232 supported (Table 1).

233

234 Evolution of elevation range

235 ML estimation of the scaling parameter κ was unable to reliably determine if evolution
236 of ancestral elevation range as a discrete trait proceeded on a punctuational basis ($\kappa =$
237 0) or on a gradual basis ($\kappa = 1$) ($\Delta\text{AIC}_{\kappa=0 \text{ vs. } \kappa=1} = 1.33$). However, when excluding the
238 species-poor basal genus, *Hyposcada*, changes in elevation were found to be associated
239 with speciation ($\Delta\text{AIC}_{\kappa=0 \text{ vs. } \kappa=1} = 2.35$). Estimating κ for the whole subtribe also con-
240 firmed this result. We therefore set κ to 0 for the ML reconstruction of elevation range.

241 Reconstruction of ancestral elevation was largely congruent between ML and MP
242 analyses at internal nodes (Fig. 1). The Oleriina originated at mid or high elevations.
243 This was followed by two radiations, one into mid/high elevations resulted in the genus
244 *Hyposcada*. The second radiation led to the origin and diversification of *Megoleria*,
245 *Ollantaya* and *Oleria*. A high elevation origin was well supported for *Megoleria* (Table
246 2). A second clade likely evolved at high elevation forming *Ollantaya* and *Oleria*. A
247 high elevation origin was strongly supported for *Ollantaya*, whereas for *Oleria* a mid
248 or high elevation origin was equally likely (Table 2). Within *Oleria*, two clades (the
249 *amalda* group and the *onega* + *aegle* groups) colonized and mostly remained at low
250 elevation with a few instances of movement to include mid elevation and one to high
251 elevation. The fourth species group, *makrena*, originated at mid-high elevations and
252 diversified rapidly in montane areas.

253 When elevation is scored as a continuous trait, estimation of the branch scaling pa-
254 rameters κ , δ and λ indicate that a random walk model is better supported than a direc-
255 tional walk model of trait evolution for both minimum and maximum elevation ranges
256 (Table 3). For minimum elevation range and the κ and λ scaling parameters, the best
257 model of evolution is a model without branch length transformation, meaning that evo-
258 lution of elevation range is gradual and Brownian-motion-like. For the δ scaling pa-
259 rameter, models $\delta = 1$ and $\delta = 0.68$ cannot be distinguished. Therefore minimum eleva-

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260 tion range either evolves at a constant rate, or at a slightly decelerating rate. For maxi-
261 mum elevation range, all values of the branch scaling parameters are equal or close to
262 one, indicating a constant, Brownian-motion-like evolution.

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264 **Ancestral geographical range**

265 The ML DEC analyses recovered the Central Andes (G) ($\log L - 236.6$), the Northern
266 Occidental Andes (F) ($\log L - 238.6$) or both areas ($\log L - 237.2$) as the most likely
267 ancestral areas of the Oleriina (Fig.2). Alternative root areas were not supported (more
268 than 2 log-likelihood units difference). Enforcing the root to include multiple areas
269 recovered all combinations of two, three, four or five areas containing F and/or G as
270 statistically supported (within 2 log-likelihood units difference). Our analyses recov-
271 ered a similar pattern when the root area was not enforced (Fig.2).

272 Our results indicate that the Oleriina most likely diverged in situ forming all four
273 genera (Figs. 2 & 4). *Hyposcada* dispersed widely with the exception of the Venezue-
274 lan Highlands and Atlantic region. The high elevation genera *Megoleria* and *Ollantaya*
275 both remained in the Central and Northern Occidental Andes but only *Megoleria*
276 reached the Northern Oriental Andes. The *Oleria onega* and *aegle* groups diverged in
277 western Amazonia, while, conversely, the *amalda* and *makrena* species groups are
278 suggested to have evolved within the Central or Northern Occidental Andes. Within
279 the *amalda* group there are two allopatric sub-clades, the first is restricted to the east-
280 ern slopes of the Central and Northern Andes and western Amazonia while the second
281 is found on the western coast and slopes of the Northern Andes and in Central Ameri-
282 ca. The *makrena* group mostly remained within the Andean region. Notably, within
283 this clade there are six instances of geographically allopatric or partially sympatric sis-
284 ter species (Fig. 2, see Appendix S1). In general, high numbers of sister species pairs

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285 are found in the same biogeographic region. The ML DEC analyses support a high rate
286 of dispersal (0.31 per million years) and low extinction rate (0.04 per million years).

287

288 **DISCUSSION**

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290 **Pattern and tempo of diversification**

291 Overall, the Oleriina show a rapid early burst in diversification followed by a marked
292 decreasing diversification rate during their history, which is also reflected in the genus
293 *Oleria*, and the *makrena* and *onega* subclades. Decreasing diversification rates, par-
294 ticularly density-dependent rates, have been interpreted as a signature of adaptive radi-
295 ation (e.g. Rabosky & Lovette, 2008, Etienne *et al.*, 2012) but see Pennell *et al.*, 2012).
296 A switch to the larval hostplant, Solanaceae, was likely a key event in the diversifica-
297 tion of the ithomiine tribe as a whole, coupled with further specialization by mostly
298 subtribal clades (Willmott & Freitas, 2006).

299 Oleriina, like all ithomiines, are chemically-defended and co-occurring species
300 share warning wing colour patterns (Müllerian mimicry (Müller, 1879)). Most ithomi-
301 ine genera are diverse in wing pattern and mimicry is suggested as a driver of diversifi-
302 cation in some clades (Jiggins *et al.*, 2006; Elias *et al.*, 2008). In *Heliconius* butterflies,
303 sister species almost always differ in mimetic pattern indicating a correlation between
304 colour pattern and species diversity (Merrill *et al.*, 2012; Kozak *et al.*, 2015). In con-
305 trast to other subtribes, the Oleriina are probably the least diverse in wing pattern
306 (Willmott & Mallet, 2004; Chazot *et al.*, 2014) and, within individual communities,
307 *Oleria* are often found to mimic one another (De-Silva *et al.*, 2010). Mimetic shifts are
308 therefore unlikely to have enhanced diversification in the subtribe.

309 The rise of the Andes could also have driven adaptive radiation across the available
310 elevational gradient, as suggested in the riodinid butterfly genus *Ithomiola* (Hall,

1 311 2005). However, in the case of Oleriina, tests of adaptive radiation linked to altitude
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4 312 were inconclusive (Table 3).

5
6 313 In contrast to other Oleriina clades, lineage accumulation in the *amalda* species
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8 314 group and *Hyposcada* is suggested to have proceeded at a near constant rate, although
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10 315 both clades contain a small number of species, potentially limiting the power to inves-
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12 316 tigate diversification. The case of *Hyposcada* is particularly intriguing, because it is an
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14 317 old clade that underwent a change in dietary repertoire with a switch to a new plant
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16 318 family, Gesneriaceae (Willmott & Freitas, 2006). Older clade age and increased eco-
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18 319 logical opportunities should both favour diversification, through time-for-speciation
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20 320 (Hutter *et al.*, 2013) and adaptive radiation (Schulter, 2000; Kozak *et al.*, 2015), yet
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22 321 this clade is particularly depauperate. Although no significant extinction was recovered
23
24 322 at the subtribe level (again, perhaps because of a lack of power in small clades), the
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26 323 long branches leading to *H. illinissa* and *H. taliata*, and to the clade containing the re-
27
28 324 maining *Hyposcada*, may suggest past extinction in this genus.
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35 326 **Rise of the Andes and biogeographic history of the Oleriina**

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37 327 Our analyses suggest that the ancestral Oleriina diverged from the rest of the Ithomiini
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39 328 during the Early to Middle Miocene between low and high elevations in the Central or
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41 329 Northern Occidental Andes. The subtribe separated into four lineages, which, with the
42
43 330 exception of *Megoleria*, all diverged during the Middle to Late Miocene with further
44
45 331 diversification during the Pliocene. Diversification within the subtribe is largely con-
46
47 332 sistent with key geological changes in the Neotropical landscape (Garziona *et al.*,
48
49 333 2008) particularly from the Late Oligocene to Pliocene (~3-26 Ma) (Hoorn & Wes-
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51 334 seling, 2010).

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55 335 *Hyposcada* diversified between low and high elevations on the slopes of the Cen-
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57 336 tral or Northern Occidental Andes. The most basal members of this clade, *H. illinissa*
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1 337 and *H. taliata*, have much older histories than the rest of the clade, having diverged
2
3 338 well within the Miocene. However, these species have contrasting histories, with *H.*
4
5 339 *illinissa* thriving at low and mid altitudes, colonizing cis- and trans-Andean habitats
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7
8 340 and western and eastern Amazonia, while *H. taliata* colonized higher elevation cis-
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10 341 Andean habitats along the eastern slopes of central Peru and Ecuador. A further diver-
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12 342 gence led to the relatively rapid radiation and formation of two subclades at low alti-
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15 343 tudes during the Late Pliocene ~3.5 Ma, in which constituent species have a broad bio-
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17 344 geographic distribution. The first clade contains the cis-Andean species, *H. kena*,
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19 345 which is commonly found in the east Andean foothills. A further divergence at ~2.5
20
21 346 Ma led to the widely distributed trans-Andean, low-mid elevation, *H. virginiana* and
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23 347 rarer, low elevation, *H. schausi*, which indicates that their ancestor may have crossed
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26 348 the Andes at the 'Western Andean Portal' (WAP). This lowland corridor separated the
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28 349 Northern and Central Andes in northern Peru and southern Ecuador until the Middle
29
30 350 Miocene (11-13 Ma) forming a biogeographic barrier to the dispersal of many montane
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32 351 species (Antonelli *et al.*, 2009). The WAP may not have attained altitudes of 1500-
33
34 352 2000m before 2-5 Ma (Blandin & Purser, 2013) allowing the dispersal of some low
35
36 353 altitude species. Furthermore, evolution of the host plant family Gesneriaceae, in par-
37
38 354 ticular, the genera, *Drymonia* and *Columnea*, which are known host plants for *H. vir-*
39
40 355 *giniana* and other *Hyposcada* species, coincided with intense Northern Andean uplift
41
42 356 in the last 10 Ma (Perret *et al.*, 2013). These plants diversified extensively, particularly
43
44 357 at mid-elevation in the Northern Andes and Central America. A second clade contains
45
46 358 two geographically allopatric species, *H. anchiala* and *H. zarepha*, with the former
47
48 359 found in the Andes and western Amazonia and the latter in the Guianas and eastern
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50 360 Amazonia. Their distribution is in accordance with that of Gesneriaceae, which are
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53 361 poorly represented in the Amazon Basin as a whole (Perret *et al.*, 2013).
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362 In contrast to *Hyposcada*, *Megoleria* originated and remained at high elevation,
363 within the Central or Northern Occidental Andes, while *Ollantaya* originated within
364 the Central Andes and subsequently dispersed into the north. *Megoleria* diverged from
365 *Oleria* + *Ollantaya* at around 14.0 Ma (95% HPD: 9.4-18.7), but split into only two
366 partially sympatric species relatively recently at 2.2 Ma (95% HPD: 0.5-4.9). *Mego-*
367 *leria*, similar to *Hyposcada*, feeds on the plant family, Gesneriaceae (Willmott &
368 Freitas, 2006), whose high species richness in the mountain forests of the Northern
369 Andes should provide ample opportunity for ecological speciation driven by adaptation
370 to alternative host plants. Yet, similar to *Hyposcada*, *Megoleria* does not seem to have
371 taken advantage of the switch.

372 *Ollantaya* diversified in the Central Andes, forming *O. canilla*, and *O. olerioides*
373 and *O. aegineta*, which separated ~8.7 Ma (95% HPD: 5.7-12.2). It is plausible that the
374 Central Andean endemic *O. canilla* was unable to cross the WAP because of its associ-
375 ation with plants restricted to the Central Andes. The subsequent diversification of the
376 genus following the closure of the WAP corridor led to the dispersal of *O. olerioides*
377 and *O. aegineta* throughout the high elevation Andes possibly due to the availability of
378 potential host plants.

379 *Oleria* originated between low and high elevation and our findings show that four
380 distinct clades diverged almost simultaneously within a preferred altitudinal range (De-
381 Silva *et al.*, 2010). The most species-rich clade, *makrena*, diverged from its sister
382 clade, the *amalda* group at ~7.3 Ma (95% HPD: 5.2-10.8) within the Central Andes.
383 The *makrena* group radiated rapidly at mid to high elevation (>750m) during the Plio-
384 cene between 3 and 7 Ma and separated into two clades. Within the first *makrena*
385 clade, the sister species, *O. boyeri* and *O. deronda* have a disjunct distribution with the
386 former endemic to the Guiana Shield and the latter occurring along the eastern slopes
387 of the Central Andes (see Appendix S2), a pattern also observed in other butterfly spe-

1 388 cies (Blandin & Purser, 2013). It is plausible that the demise of the Acre System from
2
3 389 5-7 Ma (Mora *et al.*, 2010), the filling of the deltaic proto-Orinoco Basin (Hoorn *et al.*,
4
5 390 1995) and the establishment of rainforests linking western Amazonia and the Guiana
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7 391 Shield facilitated this eastward dispersal (Gomez *et al.*, 2005). The Vaupés Arch, a
8
9 392 paleoarch formed by uplift of the Eastern Cordillera of the Northern Andes, may also
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11 393 have promoted dispersal between these regions (Hoorn *et al.*, 1995).
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14 394 Relationships within the second *makrena* clade were generally poorly resolved,
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16 395 possibly due to rapid diversification (De-Silva *et al.*, 2010), but the Northern Occi-
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18 396 dental Andes was likely to have been important in their diversification and several dis-
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20 397 tinct distribution patterns emerge. There are several examples of geographically allo-
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22 398 patric sister species, for example, *O. vicina* and *O. quadrata* diverged ~5.4 Ma (95%
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24 399 HPD: 3.7-8.0) with the former restricted to Central America while the latter is found
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26 400 within the Northern Andes and along its western slopes. Although the importance of
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28 401 the supposed recent closure of the Panamanian Isthmus ~3Ma (Coates *et al.*, 2003) in
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30 402 the diversification of some groups (Webb, 2006) is controversial (Baker *et al.*, 2014),
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32 403 the landmasses were in close proximity from the Miocene and dispersal may have oc-
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34 404 curred via the Atrato Seaway (Kirby *et al.*, 2008; Mullen *et al.*, 2011). *O. santineza* and
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36 405 *O. fumata* separated ~1.8 Ma (95% HPD: 0.9-2.8) and are confined to the east and west
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38 406 slopes of the Northern Oriental/Occidental Andes respectively. Their divergence is
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40 407 coincident with the final uplift of the Cordillera Oriental ~2-5 Ma, which was previous-
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42 408 ly isolated from the proto-Northern Andes by the Magdalena Valley (Mora *et al.*,
43
44 409 2010). *Oleria padilla* is restricted to the eastern slopes of the Central Andes and cross-
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46 410 es onto the western slopes of the Northern Andes in the vicinity of the WAP, while *O.*
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48 411 *makrena* dispersed along the eastern slopes of the Northern Andes.
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51 412 Ecological adaptation, such as diversification on new host plants, may have been
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53 413 key to the diversification of some sympatric sister species, including
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1 414 *O.athalina/O.fasciata* and *O.attalia/O.cyrene*. *Oleria victorine* has a disjunct distribu-
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3 415 tion and, unlike other *Oleria*, has colonized large swathes of the Neotropics from the
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5 416 Venezuelan Cordilleras to the Atlantic Forest. Causes for this unusually wide distribu-
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7 417 tion are unknown, but expansion in larval diet breadth could have provided opportuni-
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9 418 ties for colonization of new habitats.

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12 419 The less diverse *amalda* species group diversified in the Central or Northern Occi-
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14 420 dental Andes, but, in contrast to the *makrena* group, this occurred at low elevation. The
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16 421 *amalda* group has two allopatric subclades, an Amazonian clade that colonized the
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18 422 eastern slopes of the Central and Northern Andes and Amazonia, and a trans-Andean
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20 423 clade that diversified along the western slopes of the Andes and Cordillera Occidental
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22 424 before dispersal into Central America. The distribution of these clades suggests that
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24 425 their low altitude common ancestor crossed the Andes in the region of the WAP around
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26 426 6.4 Ma (95% HPD: 4.1-8.9) before the WAP attained sufficient altitude to prevent fur-
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28 427 ther dispersal. This provided an alternative dispersal route and further opportunities for
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30 428 diversification of the group.

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33 429 The *onega* group diversified in lowland forest habitats of western Amazonia main-
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35 430 ly during the Late Miocene and Pliocene. Their diversification coincides with the dis-
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37 431 appearance of Lake Pebas and contraction of the Acre System, which are likely to have
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39 432 acted as dispersal barriers between the Andes and Amazonia (Wahlberg & Freitas,
40
41 433 2007; Antonelli *et al.*, 2009; Hoorn & Wesseling, 2010). The eastward development of
42
43 434 terra firme rainforests prompted dispersal of a relatively high number of species into
44
45 435 eastern Amazonia, the Guiana Shield and Atlantic region (see Appendix S2). However,
46
47 436 low diversity of the host plant, Solanaceae, within these regions (Knapp, 2002) may
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49 437 have precluded further diversification driven by adaptation to alternative host plants.
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51 438 Indeed, forest productivity is higher on nutrient-rich western Amazonian soils, in con-
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53 439 trast to the nutrient poor soils of the eastern Amazon (Hoorn *et al.*, 2010). Further di-
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1 440 versification within the monotypic *O. aegle* group in eastern Amazonia and the Guian-
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3 441 as may also have been limited by the availability of larval host plants as has been noted
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5 442 with other ithomiine genera in this region (Elias *et al.*, 2009). Several instances of
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7 443 sympatric *onega* group sister species within western Amazonia suggests that fine-scale
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9 444 ecological adaptation, such as specialization on different but related host plant species
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11 445 (Willmott & Mallet, 2004), might have been important in the diversification of this
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13 446 clade.
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17 447 For the Oleriina, in general, distinct Northern Andean distribution patterns have
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19 448 emerged from our analyses. A remarkable number of species exist within the Cordille-
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21 449 ra Occidental, at all elevations, whereas only a few species have colonized the Cordil-
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23 450 lera Oriental, of which only one, *Megoleria susiana*, is a strictly high elevation species;
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25 451 although there are a few instances of mid/high altitude species that have diversified
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27 452 within the last 2 Ma. Other species remain within the eastern Ecuadorian Andes or
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29 453 where the Cordillera Oriental joins the western Colombian Cordilleras. This pattern is
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31 454 consistent with the geologically recent emergence of the east Colombian Cordillera and
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33 455 the appearance of cloud forests between 3-5 Ma (Kattan *et al.*, 2004). There are only
34
35 456 three instances of dispersal as far as the Venezuelan Cordilleras, consistent with their
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37 457 emergence as recently as 3.5 Ma (Albert *et al.*, 2006). *Oleria phenomoe* is found only
38
39 458 in this region, suggesting the extinction of it or its sister species in Northern Andean
40
41 459 ancestral areas. Dispersal into the Atlantic region has occurred rarely, but may have
42
43 460 been via the Mato Grosso Arch, which linked the Central Andes to the Brazilian Shield
44
45 461 perhaps from the Late Eocene (Hoorn & Wesselingh, 2010), or via continuous forest
46
47 462 cover which previously connected eastern Amazonia and the Atlantic Forest (Costa,
48
49 463 2003, and references therein). These regions are now linked by interconnecting forest
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51 464 patches through an otherwise open landscape, which may explain the presence of *O.*
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1 465 *aquata* within the northeastern Caatinga and central Cerrado regions of the Brazilian
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3 466 Shield.

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6 467 In general, changes in elevation occurred rarely in the Oleriina, as in other butter-
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8 468 flies (Willmott *et al.*, 2001; Elias *et al.*, 2009; Chazot *et al.*, 2014). Butterflies are like-
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10 469 ly to be limited by physiological and ecological constraints, particularly among
11
12 470 ithomiines where co-occurring species often share the same microhabitat and mimetic
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14 471 pattern and jointly advertise their unpalatability (Willmott & Freitas, 2006; Chazot *et*
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16 472 *al.* 2014). However, exceptions are found in some groups, such as the riordinid butterfly
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18 473 genus *Ithomiola*, that radiated across an elevational gradient in the Andes (Hall, 2005).

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21 474 In summary, our results reveal that the Andean orogeny instigated and had a pro-
22
23 475 found influence on the diversification of the Oleriina, in agreement with the ithomiine
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25 476 genera *Napeogenes* and *Ithomia* (Elias *et al.*, 2009), and other butterfly groups such as
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27 477 *Morpho* (Blandin & Purser, 2013), *Taygetis* (Matos-Maraví *et al.*, 2013) and
28
29 478 *Lymanopoda* (Casner & Pyrcz, 2010). Oleriina apparently dispersed throughout the
30
31 479 Andes and into newly available cis- and trans-Andean habitats when dispersal barriers
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33 480 such as the Acre System retreated and with the closure of the WAP. The mountains
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35 481 formed a barrier causing vicariant speciation in some instances and the geologically
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37 482 recent uplift of the Colombian Cordillera Oriental helped to foster the rapid radiation
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39 483 of the *Oleria makrena* species group. Much of the Oleriina diversity remained within
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41 484 the Andes, but our findings suggest the Andes also acted as a source for lowland line-
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503

504 REFERENCES

505

- 506 Albert, J.S., Lovejoy, N.R. & Crampton, W.G.R. (2006) Miocene tectonism and the
507 separation of the cis- and trans-Andean river basins: evidence from Neotropical fishes.
508 *Journal of South American Earth Sciences*, **21**, 14-27.
- 509 Antonelli, A., Nylander, J.A.A., Persson, C. & Sanmartin, I. (2009) Tracing the impact
510 of the Andean uplift on Neotropical plant evolution. *Proceedings of the National*
511 *Academy of Sciences*, **106(24)**, 9749-9754.
- 512 Ayres, J.M. & Clutton-Brock, T.H. (1992) River boundaries and species range size in
513 Amazonian primates. *American Naturalist*, **140**, 531-537.

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- 514 Baker, P.A., Fritz, S.C., Dick, C.W., Eckert, A.J., Horton, B.K., Manzoni, S., Ribas,
515 C.C. Garziane, C.N. & Battisti D.S. (2014) The emerging field of geogenomics: Con-
516 straining geological problems with genetic data. *Earth-Science Reviews*. **135**, 38-47.
- 517 Blandin, P. & Purser, B. (2013) Evolution and diversification of Neotropical
518 butterflies: insights from the biogeography and phylogeny of the genus *Morpho* Fab-
519 ricius, 1807 (Nymphalidae: Morphinae), with a review of the geodynamics of South
520 America. *Tropical Lepidoptera Research*. **23(2)**, 62-85.
- 521 Casner, K.L. & Pyrcz T.W. (2010) Patterns and timing of diversification in a tropical
522 montane butterfly genus, *Lymanopoda* (Nymphalidae, Satyrinae). *Ecography* **33**, 251-
523 259.
- 524 Chazot, N., Willmott, K., Santacruz Endera, P. G., Toporov, A., Hill, R. I., Jiggins, C.
525 D. & Elias, M. (2014). Filtering by elevation and mutualistic mimicry shape the
526 structure of Andean butterfly communities. *American Naturalist*, **183**, 26-39.
- 527 Coates, A.G., Aubry, M.P., Berggren, W.A., Collins, L.S. & Kunk, M. (2003) Early
528 Neogene history of the Central American arc from Bocas del Toro, western Panama.
529 *Bulletin of the Geological Society of America*, **115**, 271-287.
- 530 Condamine, F.L., Toussaint, E.F.A., Cotton, A.M., Genson, G.S., Sperling, F.A.H. &
531 Kergoat, G.J. (2013) Fine-scale biogeographical and temporal diversification processes
532 of peacock swallowtails (*Papilio* subgenus *Achillides*) in the Indo-Australian
533 Archipelago. *Cladistics*. **29**, 88-111.
- 534 Costa, L.P., (2003) The historical bridge between the Amazon and the Atlantic Forest
535 of Brazil: a study of molecular phylogeography with small mammals. *Journal of*
536 *Biogeography*. **30**, 71-86.

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57
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59
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- 537 De-Silva, D.L., Day, J.J., Elias, M., Willmott, K., Whinnett, A. & Mallet, J. (2010)
538 Molecular phylogenetics of the neotropical butterfly subtribe Oleriina (Nymphalidae:
539 Danainae: Ithomiini). *Molecular Phylogenetics and Evolution*, **55**, 1032-1041.
- 540 Ehlers, T.A. & Poulsen, C.J. (2009) Influence of Andean uplift on climate and
541 paleoaltimetry estimates. *Earth and Planetary Science Letters*. **281**, 238-248.
- 542 Elias, M., Gompert, Z., Jiggins, C. & Willmott, K. (2008) Mutualistic interactions
543 drive ecological niche convergence in a diverse butterfly community. *PLoS Biology*. **6**,
544 e300.
- 545 Elias, M., Joron, M., Willmott, K., Silva-Brandao, K.L., Kaiser, V., Arias, C.F.,
546 Pinerez, L.M.G., Uribe, S., Brower, A.V.Z., Freitas, A.V.L. & Jiggins, C.D. (2009) Out
547 of the Andes: patterns of diversification in clearwing butterflies. *Molecular Ecology*,
548 **18**, 1716-1729.
- 549 Etienne, R.S., Haegeman, B., Stadler, T., Aze, T., Pearson, P.N., Purvis, A. &
550 Phillimore, A.B. (2012) Diversity-dependence brings molecular phylogenies closer to
551 agreement with the fossil record. *Proceedings of the Royal Society B*. **279**, 1300-1309.
- 552 Garzzone, C.N., Hoke, G.D., Libarkin, J.C., Withers, S., MacFadden, B., Eiler, J.,
553 Ghosh, P. & Mulch, A. (2008) Rise of the Andes. *Science*. **320**, 1304-1307.
- 554 Garzzone, C.N., Auerbach, D.J., Jin-Sook Smith, J., Rosario, J.J., Passey, B.H., Jordan,
555 T.E. & Eiler, J.M. (2014) Clumped isotope evidence for diachronous surface cooling of
556 the Altiplano and pulsed surface uplift of the Central Andes. *Earth and Planetary
557 Science Letters*, **393**, 173-181.

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- 558 Gentry, A.H. (1982) Neotropical floristic diversity: phytogeographical connections
559 between Central and South America, Pleistocene climatic fluctuations, or an accident
560 of the Andean orogeny? *Annals of the Missouri Botanical Garden*, **69**, 557-593.
- 561 Gomez, E., Jordan, T.E., Allmendinger, R.W., Cardozo, R.W. & Cardozo, N. (2005)
562 Development of the Colombian foreland basin as a consequence of diachronous
563 exhumation of the northern Andes. *Geological Society of America Bulletin*. **117**, 1272-
564 1292.
- 565 Hall, J.P.W. (2005) Montane speciation patterns in *Ithomiola* butterflies
566 (Lepidoptera:Riodinidae): are they consistently moving up in the world? *Proceedings*
567 *of the Royal Society B: Biological Sciences*, **272**, 2457-2466.
- 568 Hoorn, C., Guerrero, J., Sarmiento, G.A. & Lorente, M.A. (1995) Andean tectonics as
569 a cause for changing drainage patterns in Miocene northern South America. *Geology*,
570 **23**, 237-240.
- 571 Hoorn, C. (2006) The birth of the mighty Amazon. *Scientific American*, **294(5)**, 52-59.
- 572 Hoorn, C., Wesseling, P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J.,
573 Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C.,
574 Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T. &
575 Antonelli, A. (2010) Amazonia through time: Andean uplift, climate change, landscape
576 evolution, and biodiversity. *Science*. **330**, 927-931.
- 577 Hoorn, C. & Wesseling, P. (eds) (2010) *Amazonia, Landscape and Species Evolution:*
578 *a look into the past*. Wiley-Blackwell, Chichester, UK.

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60
- 579 Hoorn, C., Mosbrugger, V., Mulch, A. & Antonelli, A. (2013) Biodiversity from
580 mountain building. *Nature Geoscience*. **6**, 154.
- 581 Hutter, C.R., Guayasamin, J.M. & Wiens, J.J. (2013) Explaining Andean
582 megadiversity: the evolutionary and ecological causes of glassfrog elevational richness
583 patterns. *Ecology Letters*. **16**, 1135-1144.
- 584 Jiggins, C.D., Mallarino, R., Willmott, K.R. & Bermingham, E. (2006) The
585 phylogenetic pattern of speciation and wing pattern change in Neotropical *Ithomia*
586 butterflies (Lepidoptera: Nymphalidae). *Evolution*. **60**, 1454-1466.
- 587 Kattan, G.H., Franco, P., Rojas, V. & Morales, G. (2004) Biological diversification in a
588 complex region: a spatial analysis of faunistic diversity and biogeography of the Andes
589 of Colombia. *Journal of Biogeography*, **31**, 1829-1839.
- 590 Kennan, L., Lamb, S.H. & Hoke, L. (1997) High-altitude palaeosurfaces in the
591 Bolivian Andes: evidence for late Cenozoic surface uplift. *Geological Society, London,*
592 *Special Publications*, **120**, 307-323.
- 593 Kirby, M.X., Jones, D.S. & MacFadden, B.J. (2008) Lower Miocene stratigraphy along
594 the Panama Canal and its bearing on the Central American Peninsula. *PLoS One*. **3**,
595 e2791.
- 596 Kozak, K.M., Wahlberg, N., Neild, A., Dasmahapatra, K.K., Mallet, J. & Jiggins, C.D.
597 (2015) Multilocus species trees show the recent adaptive radiation of the mimetic
598 *Heliconius* butterflies. *Systematic Biology*, in press.
- 599 Knapp, S. (2002) Assessing patterns of plant endemism in Neotropical uplands.
600 *Botanical Review*, **68**, 22-37.

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52
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54
55
56
57
58
59
60
- 601 Lamas, G. (2004) Ithomiinae. *Atlas of Neotropical Lepidoptera. Checklist: Part 4A*
602 *Hesperioidea – Papilionoidea*. (ed. by J.B. Heppner), Association of Tropical
603 Lepidoptera, Scientific Publishers, Gainesville, FL.
- 604 Maddison, W. P. and D.R. Maddison. (2011) Mesquite: a modular system for
605 evolutionary analysis, version 2.75.
- 606 Matos-Maraví, P.F., Peña, C., Willmott, K.R., Freitas, A.V.L. & Wahlberg, N. (2013)
607 Systematics and evolutionary history of butterflies in the “*Taygetis* clade”
608 (Nymphalidae: Satyrinae: Euptychiina): Towards a better understanding of Neotropical
609 biogeography. *Molecular Phylogenetics and Evolution*, **66**, 54-68.
- 610 Merrill, R.M., Wallbank, R.W.R., Bull, V., Salazar, P.C.A., Mallet, J., Stevens, M. &
611 Jiggins, C.D. (2012) Disruptive ecological selection on a mating cue. *Proceedings of*
612 *the Royal Society B*. **279**, 4907-4913.
- 613 Mora, A., Parra, M., Strecker, M.R., Sobel, E.R., Hooghiemstra, H., Torres, V.
614 & Vallejo-Jaramillo, J. (2008) Climatic forcing of asymmetric orogenic evolution in the
615 Eastern Cordillera of Colombia. *Bulletin of the Geological Society of America*. **120**,
616 930-949.
- 617 Mora, A., Baby, P., Roddaz, M., Parra, M., Brusset, S., Hermosa, W. & Espurt, N.
618 (2010) Tectonic history of the Andes and sub-Andean zones: implication for the devel-
619 opment of the Amazon drainage basin. *Amazonia, Landscape and Species Evolution: A*
620 *look into the Past* (eds. C. Hoorn & F.P. Wesselingh), pp. 38-60. Wiley-Blackwell,
621 Chichester, UK.

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57
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59
60
- 622 Mullen, S.P., Savage, W.K., Wahlberg, N. & Willmott, K.R. (2011) Rapid diversifica-
623 tion and not clade age explains high diversity in Neotropical *Adelpha* butterflies. *Pro-*
624 *ceedings of the Royal Society B*, **278**, 1777-1785.
- 625 Müller, F. (1879) *Ituna* and *Thyridia*: a remarkable case of mimicry in butterflies.
626 *Transactions of the Entomological Society of London* 1879. xx-xxix.
- 627 Pagel, M., Meade, A. & Barker, D. (2004) Bayesian estimation of ancestral character
628 states on phylogenies. *Systematic Biology*, **53**, 673-684.
- 629 Paradis, E., Claude, J. & Strimmer, K. (2004) APE: Analysis of phylogenetics and
630 evolution in R language. *Bioinformatics*, **20(2)**, 289-290.
- 631 Pennell, M.W., Sarver, B.A.J. & Harmon, L.J. (2012) Trees of unusual size: biased
632 inference of early bursts from large molecular phylogenies. *PLoS Biology*, **6**, 483-489.
- 633 Perret, M., Chautems, A., Araujo, A.O. & Salamin, N. (2013) Temporal and spatial
634 origin of Gesneriaceae in the New World inferred from plastid DNA sequences. *Botan-*
635 *ical Journal of the Linnean Society*, **171**, 61-79.
- 636 Pybus, O.G. & Harvey, P.H. (2000) Testing macro-evolutionary models using
637 incomplete molecular phylogenies. *Proceedings of the Royal Society B: Biological*
638 *Sciences*, **267**, 2267-2272.
- 639 R Core Development Team. (2010) R (A Language and Environment for Statistical
640 Computing).
- 641 Rabosky, D.L. (2006) Laser: a maximum likelihood toolkit for detecting temporal
642 shifts in diversification rates from molecular phylogenies. *Evolutionary Bioinformatics*,
643 **2**, 247-250.

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60
- 644 Rabosky, D.L. & Lovette, I.J. (2008) Density-dependent diversification in North
645 American wood warblers. *Proceedings of the Royal Society B: Biological Sciences*,
646 **275**, 2363-2371.
- 647 Ree, R.H. & Smith, S.A. (2008) Maximum likelihood inference of geographic range
648 evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, **57**, 4-14.
- 649 Rosser, N., Phillimore, A.B., Huertas, B., Willmott, K.R. & Mallet, J. (2012) Testing
650 historical explanations for gradients in species richness in heliconian butterflies of
651 tropical America. *Biological Journal of the Linnean Society*, **105**, 479-497.
- 652 Rull, V. (2013) Palaeoclimates and Amazon biodiversity. *Journal of Biogeography*, **40**,
653 1413-1414.
- 654 Santos, J.C., Coloma, L.A., Summers, K., Caldwell, J.P., Ree, R. & Cannatella, D.C.
655 (2009) Amazonian amphibian diversity is primarily derived from Late Miocene
656 Andean lineages. *PLoS Biology*, **7**, 448-461.
- 657 Sébrier, M., Mercier, J.L., Macharé, J., Bonnot, D., Cabrera, J. & Blanc, J.L. (1988)
658 The state of stress in an overriding plate situated above a flat slab: the Andes of Central
659 Peru. *Tectonics*. **7**, 895-928.
- 660 Schuller, D. (2000) *The Ecology of Adaptive Radiation*. Oxford University Press,
661 Oxford.
- 662 Tuomisto, H., Ruokolainen, K., Kalliola, K., Linna, R., Danjoy, W. & Rodriguez, Z.
663 (1995) Dissecting Amazonian biodiversity. *Science*, **269**, 63-66.

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60
- 664 Turchetto-Zolet, A.C., Pinheiro, F., Salbueiro, F. & Palma-Silva, C. (2013)
665 Phylogeographical patterns shed light on evolutionary process in South America.
666 *Molecular Ecology*, **22**, 1193-1213.
- 667 Wahlberg, N. & Freitas, A.V.L. (2007) Colonization of and radiation in South America
668 by butterflies in the subtribe Phyciodina (Lepidoptera : Nymphalidae). *Molecular*
669 *Phylogenetics and Evolution*, **44**, 1257-1272.
- 670 Webb, S.D. (2006) The Great American Biota Interchange: patterns and processes.
671 *Annals of the Missouri Botanical Garden*. **93**, 245-257
- 672 Wesselingh, F.P., Räsänen, M.E., Irion, G.E., Vonhof, H.B., Kaandorp, R., Renema,
673 W., Romero Pittman, L. & Gingras, M. (2002) Lake Pebas: a palaeoecological
674 reconstruction of a Miocene, long-lived lake complex in western Amazonia. *Cainozoic*
675 *Research*, **1**, 35-81.
- 676 Whipple, K.X. & Gasparini, N.M. (2014) Tectonic control of topography, rainfall
677 patterns, and erosion during rapid post-12 Ma uplift of the Bolivian Andes.
678 *Lithosphere*. **6**, 251-268.
- 679 Willmott, K.R. & Mallet, J. (2004) Correlations between adult mimicry and larval
680 hostplants in ithomiine butterflies. *Proceedings of the Royal Society London B (Biology*
681 *Letters) Supplement*. **271**, S266-S269.
- 682 Willmott, K.R. & Freitas, A.V.L. (2006) Higher-level phylogeny of the Ithomiinae
683 (Lepidoptera: Nymphalidae): classification, patterns of larval hostplant colonization
684 and diversification. *Cladistics*, **22**, 297-368.

1 685 Willmott, K.R., Hall, J.P.W. & Lamas, G. (2001) Systematics of Hypanartia
2
3
4 686 (Lepidoptera : Nymphalidae : Nymphalinae), with a test for geographical speciation
5
6 687 mechanisms in the Andes. *Systematic Entomology*, **26**, 369-399.
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11 689 SUPPORTING INFORMATION

13 690

16 691 Additional Supporting Information may be found in the online version of this article:

18 692

20 693 **Appendix S1 a.** List of specimen used, GenBank accession numbers and elevation
21
22 694 ranges for each species. **b.** Museum collections from which information was obtained
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24 695 about elevation range and distribution. **c.** Phylogenetic analysis of the Oleriina and
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26 696 timing of diversification – Materials & Methods, Results, References. **d.** PartitionFind-
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28 697 er best substitution models
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31 698 **Appendix S2.** Distribution maps of the Oleriina species.
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37 700 BIOSKETCHES

40 701 **Donna Lisa de-Silva** is interested in understanding the patterns and processes involved
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42 702 in Neotropical diversification. Her work currently focuses on the ithomiine butterflies.
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45 703 The research group of **Julia Day** focuses on the patterns and processes leading to insu-
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47 704 lar and continental radiations. **James Mallet** and his research group study evolution,
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49 705 hybridization, and speciation - mainly in Neotropical butterflies. **Marianne Elias** and
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51 706 her research group study diversification patterns and community ecology of various
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53 707 organisms, with a special emphasis on ithomiine butterflies. **Keith Willmott** has a
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1 708 longstanding research program on the systematics and biogeography of Neotropical
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3 709 butterflies.

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7 710 Author contributions: D.L.de-S., M.E. and J.J.D. conceived the ideas; K.W. provided
8
9 711 elevation and distribution data, D.L.de-S. compiled and analysed the data and wrote the
10
11 712 first draft. All co-authors helped revise and approved the manuscript.
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15 713

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18 714 Table 1. Rates of diversification test results using rate-constant (pure-birth, birth-death)
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20 715 and rate-variable (density dependent logistic - DDL and density dependent exponential
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22 716 - DDX, indicative of adaptive radiation; Yule two-rate models; time-varying speciation
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24 717 and constant extinction - SPVAR, time-varying extinction and constant speciation -
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26 718 EXVAR, varying speciation and extinction through time - BOTHVAR (Rabosky &
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28 719 Lovette, 2008)) diversification models. In each case, the best model/s is/are indicated
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30 720 in **bold**. Log-likelihood, AIC and the difference in AIC with the best model (Δ AIC) are
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32 721 shown for each clade examined. R^1 and R^2 indicate initial and, when applicable, final
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34 722 net diversification rates, respectively; st = the time of rate shift in the Yule-2-rate mod-
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36 723 el; a = extinction fraction E/S , k = the k -parameter from the DDL model, and x = the x -
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38 724 parameter from the DDX model.
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Clade	Model	R ¹	R ²	a	k/x	st	log-lkh	AIC	ΔAIC	ΔAIC_2
Oleriina										
	Pure Birth	0.174					17.42	-32.84	11.71	727
	Birth Death	0.174		0			17.42	-30.84	13.71	
	DDL	0.390			63.35		24.16	-44.32	0.23	
	DDX	0.662			0.41		20.67	-37.33	7.21	
	Yule 2-rate	0.230	0.045			1.75	25.27	-44.54	0	
	SPVAR						20.75	-35.51	9.04	
	EXVAR						17.38	-28.77	15.77	
	BOTHVAR						20.77	-33.53	11.01	
Hyoscada										
	Pure Birth	0.101					-9.88	21.75	0	
	Birth Death	0.101		0			-9.88	23.75	2	
	DDL	0.273			7.42		-9.29	22.58	0.82	
	DDX	0.253			0.66		-9.66	23.33	1.57	
	Yule 2-rate	0.081	0.121			3.96	-9.78	25.56	3.81	
	SPVAR						-9.88	25.75	4	
	EXVAR						-9.88	25.75	4	
	BOTHVAR						-9.88	27.75	6	
Oleria										
	Pure Birth	0.205					10.66	-19.33	19.34	
	Birth Death	0.205		0			10.66	-17.33	21.34	
	DDL	0.626			44.18		21.33	-38.66	0	
	DDX	2.136			0.76		18.01	-32.02	6.64	
	Yule 2-rate	0.513	0.118			4.54	20.93	-35.85	2.81	
	SPVAR						19.09	-32.17	6.49	
	EXVAR						10.64	-15.27	23.39	
	BOTHVAR						19.09	-30.17	8.49	
makrena species group										
	Pure Birth	0.191					-8.76	19.52	16.42	
	Birth Death	0.191		0			-8.76	21.52	18.42	
	DDL	0.926			18.58		0.31	3.38	0.27	
	DDX	5.475			1.38		-1.79	7.58	4.48	
	Yule 2-rate	0.898	0.090			4.99	1.45	3.10	0	
	SPVAR						-1.60	9.21	6.1	
	EXVAR						-8.76	23.52	20.42	
	BOTHVAR						-1.62	11.24	8.14	
omega species group										
	Pure Birth	0.190					-9.38	20.75	7.03	
	Birth Death	0.190		0			-9.38	22.75	9.03	
	DDL	0.696			15.01		-5.16	14.32	0.6	
	DDX	1.291			0.90		-7.08	18.17	4.45	
	Yule 2-rate	0.457	0.065			3.55	-3.86	13.72	0	
	SPVAR						-7.31	20.62	6.9	
	EXVAR						-9.38	24.77	11.05	
	BOTHVAR						-7.31	22.62	8.9	
amalda species group										

Pure Birth	0.214			-6.13	14.25	0	
Birth Death	0.214	0		-6.13	16.25	2	
DDL	0.544		7.62	-5.62	15.25	0.99	
DDX	0.398		0.45	-6.00	16.00	1.75	
Yule 2-rate	0.290	0.154		2.12	-5.88	17.75	3.5
SPVAR					-6.13	18.25	4
EXVAR					-6.13	18.25	4
BOTHVAR					-6.13	20.25	6

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For Peer Review

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730 Table 2. Tests of ancestral states of altitudinal ranges (scored as a discrete trait) in dif-
731 ferent clades. In each case, the best model/s is/are indicated in bold.
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Clade	Model	Log lkd	Parameters	AIC	Δ AIC
Oleriina					
	High	-21.09	4	50.17	0
	Low	-23.19	4	54.38	4.21
	Mid	-21.50	4	51.00	0.83
Hyposcada					
	High	-21.15	4	50.30	0
	Low	-23.19	4	54.38	4.08
	Mid	-21.18	4	50.36	0.06
Ollantaya					
	High	-20.69	4	49.37	0
	Low	-25.67	4	59.33	9.96
	Mid	-22.05	4	52.09	7.24
Oleria					
	High	-20.66	4	49.33	0
	Low	-22.16	4	52.32	2.99
	Mid	-20.99	4	49.98	0.65
Megoleria					
	High	-20.69	4	49.39	0
	Low	-25.74	4	59.47	10.09
	Mid	-22.05	4	52.10	2.71

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734 Table 3. Maximum likelihood estimation of ancestral elevation range as a continuous
 735 trait for minimum and maximum elevation ranges. Random walk versus directional
 736 change models of evolution are compared. kappa (κ) = 0 (punctuational evolution), (κ)
 737 = 1 (gradual evolution); delta (δ) < 1 (early rapid evolution followed by slow down), (δ)
 738 > 1 (accelerating evolution with time); lambda (λ) = 1 (Brownian motion evolution),
 739 (λ) = 0 (Independent evolution). In each case, the best model is indicated in **bold**.
 740

Model	Log lkd	Parameters	AIC	Δ AIC	Scaling parameter
Minimum elevation range					
Random walk					
(κ) = 1	-400.71	2	805.41		1
(κ) = 0	-406.55	2	817.09	-11.68	0
(κ) = estimated	-400.69	3	807.37	-2	0.95
Directional					
(κ) = 1	-401.87	3	809.75		1
(κ) = 0	-406.54	3	819.08	-9.34	0
(κ) = estimated	-400.64	4	809.29	0.46	0.95
Random walk					
(δ) = 1	-400.71	2	805.41		1
(δ) = 0	-451.62	2	907.24	-101.83	0
(δ) = estimated	-400.52	3	807.04	-1.63	0.68
Directional					
(δ) = 1	-401.87	3	809.75		1
(δ) = 0.001 (not defined for 0)	-406.63	3	819.27	-9.52	0.001
(δ) = estimated	-400.54	4	809.08	0.67	0.58
Random walk					
(λ) = 1	-400.71	2	805.41		1
(λ) = 0	-424.35	2	852.70	-47.29	0
(λ) = estimated	-400.71	3	807.41	-2	1
Directional					
(λ) = 1	-401.87	3	809.75		1
(λ) = 0	-424.37	3	854.74	-44.99	0
(λ) = estimated	-409.04	4	826.07	-16.32	0.63

Maximum elevation range

Random walk

(κ) = 1	-407.27	2	818.55		1
(κ) = 0	-410.83	2	825.65	0	0
(κ) = estimated	-407.06	3	820.12	-1.57	0.84

Directional

(κ) = 1	-407.4	3	820.8		1
(κ) = 0	-410.76	3	827.52	0	0
(κ) = estimated	-406.9	4	821.8	-1	0.85

Random walk

(δ) = 1	-407.27	2	818.55		1
(δ) = 0	-440	2	884	-65.45	0
(δ) = estimated	-407.27	3	820.54	-2	1.04

Directional

(δ) = 1	-407.4	3	820.8		1
(δ) = 0.001 (not defined for 0)	-414.42	3	834.84	-14.04	0.001
(δ) = estimated	-400.54	4	822.91	-2.11	0.7

Random walk

(λ) = 1	-407.27	2	818.55		1
(λ) = 0	-427.66	2	859.33	-40.78	0
(λ) = estimated	-406.86	3	819.71	-1.17	0.98

Directional

(λ) = 1	-407.4	3	820.8		1
(λ) = 0	-427.71	3	861.42	-40.62	0
(λ) = estimated	-412.79	4	833.59	-12.79	0.64

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743 Figure 1. Bayesian dated maximum clade credibility tree for the *Oleriina* based on an

744 uncorrelated log normal relaxed clock and detailing current and ancestral elevation

745 ranges. Current elevation ranges are shown at the tips of the trees. ML inferred ances-

746 tral elevation ranges are shown for each node on the branch and MP inferred ancestral

747 elevation ranges are shown below the branch where results differ. Bayesian posterior

748 probabilities lower than 0.90 are indicated. Genera and *Oleria* species groups are

749 shown to the right of the tree.

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1 751 Figure 2. Bayesian dated maximum clade credibility tree for the Oleriina based on an
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3 752 uncorrelated log normal relaxed clock detailing biogeographical reconstructions of
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5 753 ancestral geographical ranges inferred from dispersal-extinction-cladogenesis imple-
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7 754 mented in Lagrange. The evolution of the Oleriina was divided into four time slices
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9 755 corresponding to notable paleogeographic events. Coloured squares to the left of the
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11 756 map correspond to the geographical areas indicated and those below the map to multi-
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13 757 ple areas. Coloured squares to the right of the tree indicate the geographical range of
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15 758 each extant species. Pie charts represent the relative probabilities of ancestral ranges.
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17 759 Ancestral area probabilities < 0.1 were combined (black sections of the pie charts). The
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19 760 number of extant species for each geographical region are indicated.
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26 762 Figure 3. Lineage-through-time (LTT) plots based on 1000 sampled Bayesian trees for
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28 763 a. Oleriina, b. *Hyposcada*, c. *Oleria*, d. 'makrena' species group, e. 'amalda' species
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30 764 group, f. 'onega' species group.
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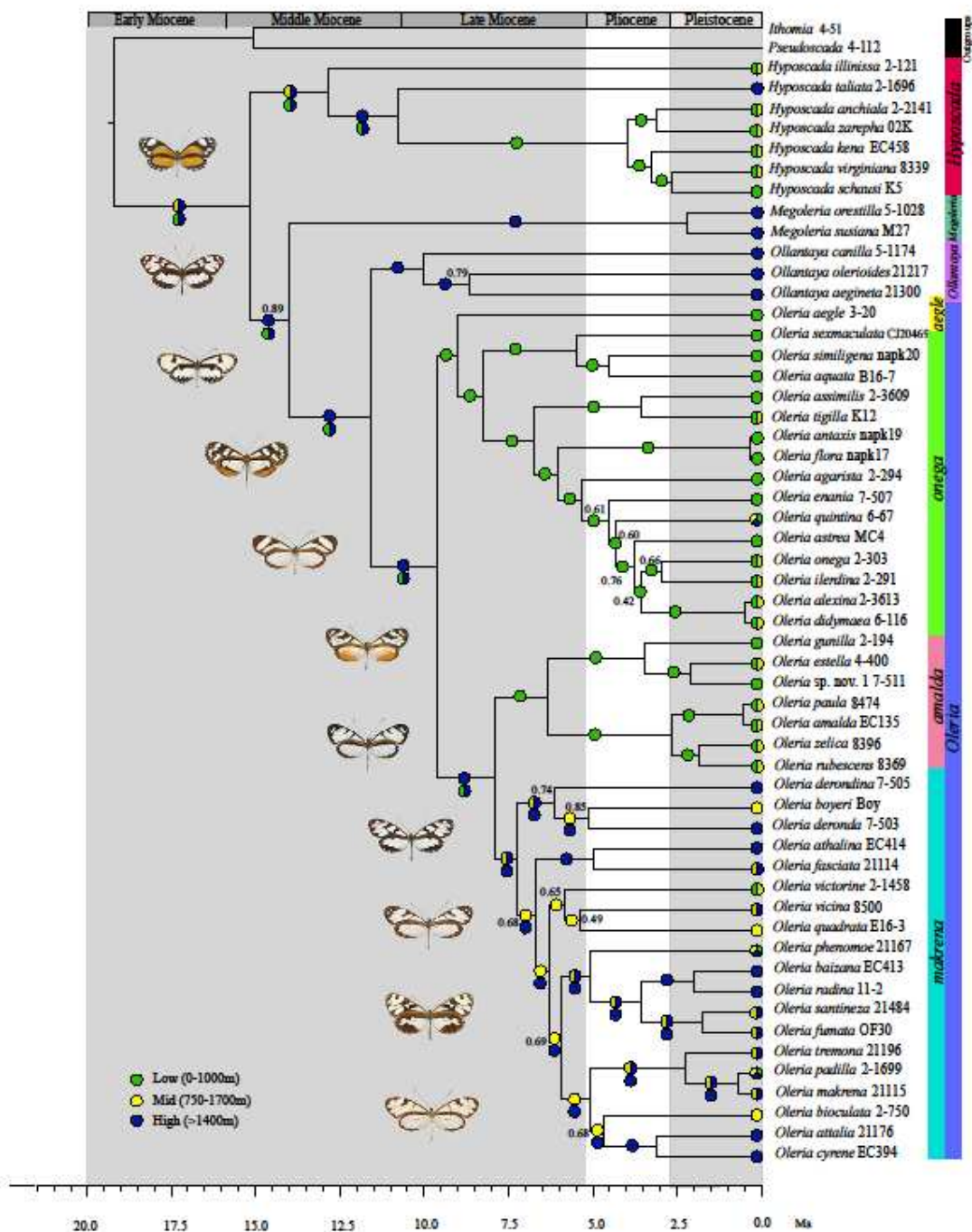
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34 766 Figure 4. Paleogeographical model used in the dispersal-extinction-cladogenesis anal-
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36 767 yses of biogeographical events. The four time slices used in the analyses and dispersal
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38 768 rates for each biogeographic area are shown. Maps are modified from Hoorn & Wes-
39
40 769 seling, (2010); Condamine *et al.*, (2013); Matos-Maraví *et al.*, (2013). Maps show dis-
41
42 770 persal and diversification of each Oleriina genus. Dispersal rates highlighted indicate a
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44 771 constraint on dispersal. A. Central America; B. western slopes and lowlands of the
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46 772 Northern Andes including Colombia, Ecuador and northwest Peru; C. Venezuelan
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48 773 Highlands including the Cordillera de Mérida and Cordillera de la Costa; D. Guiana
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50 774 Shield; E. Northern Oriental Andes; F. Northern Occidental Andes including the Co-
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52 775 lombian Cordillera Occidental, Cordillera Central and Ecuador; G. Central Andes; H.
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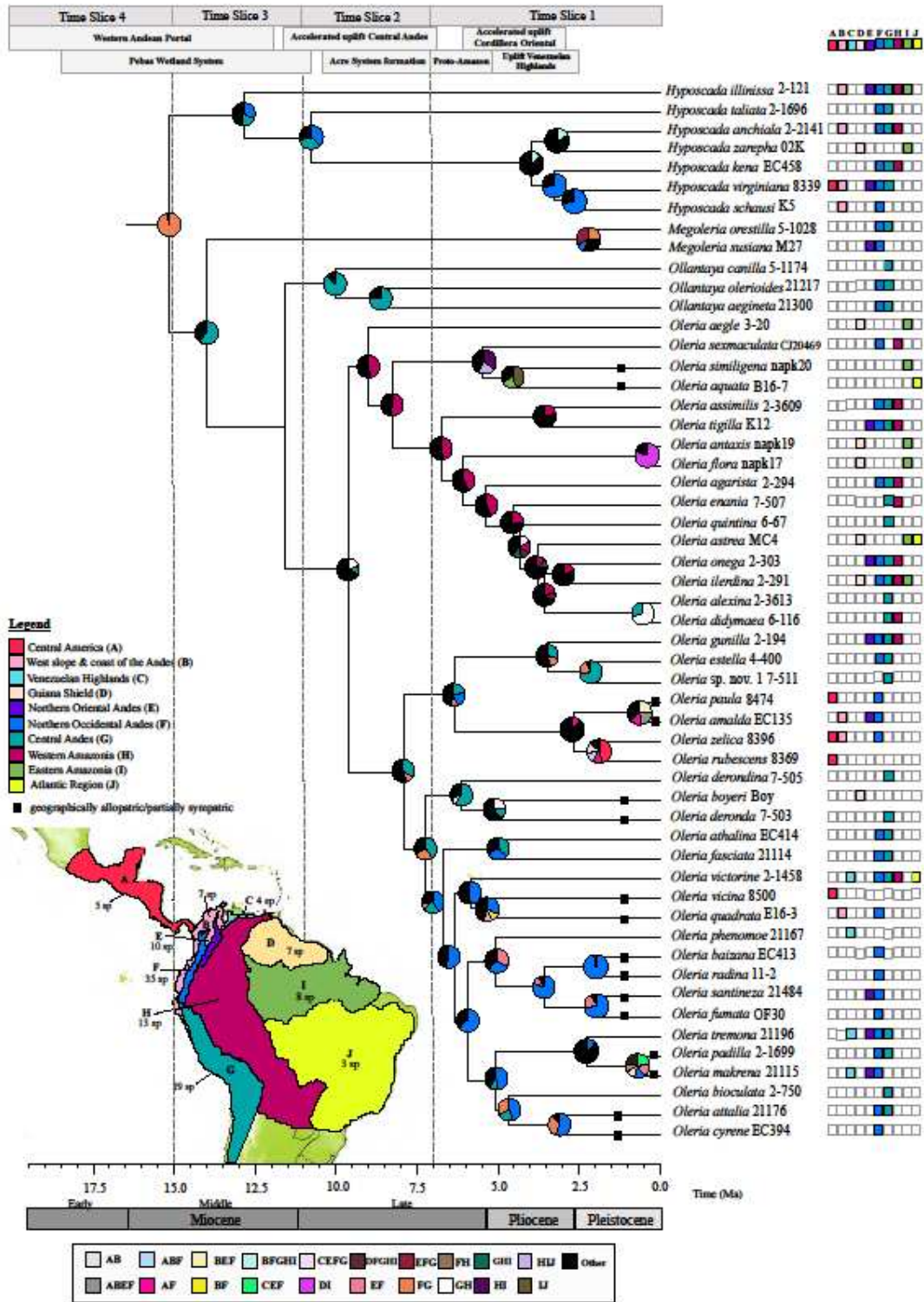
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776 western Amazonia; I. central and eastern Amazonia; J. Atlantic region including the
777 Atlantic Forest and Cerrado.

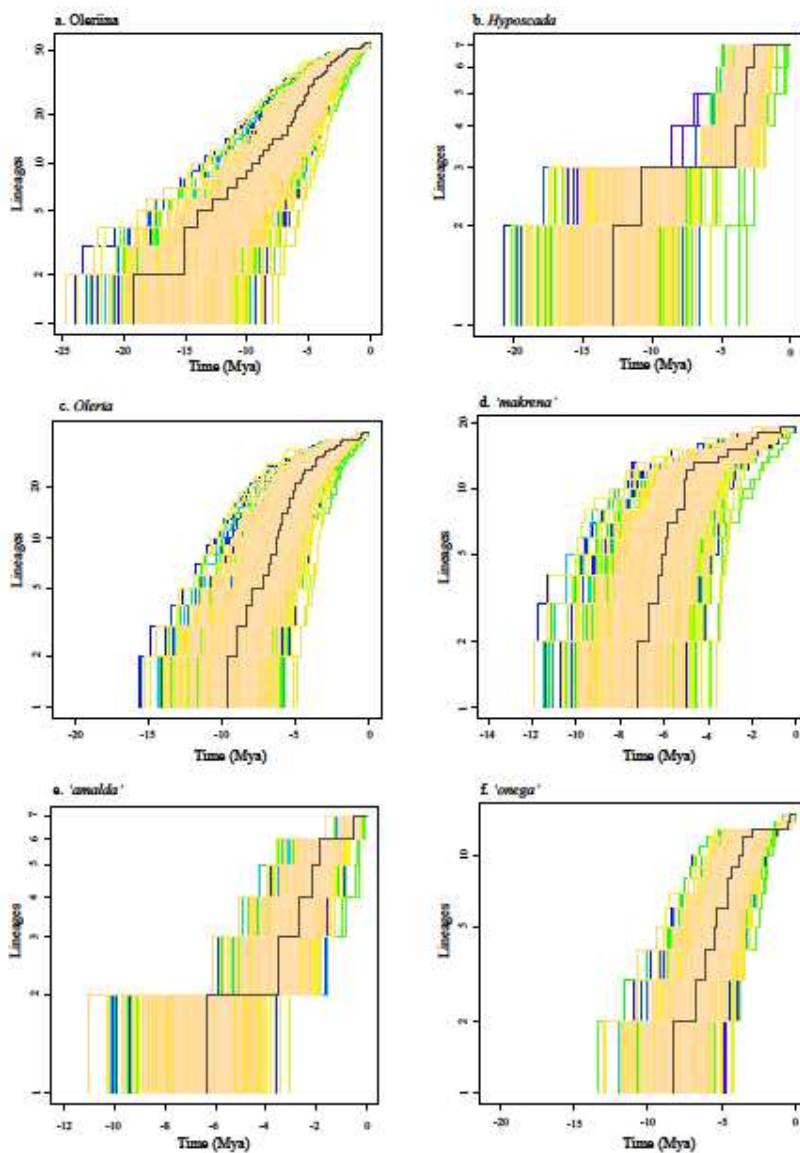
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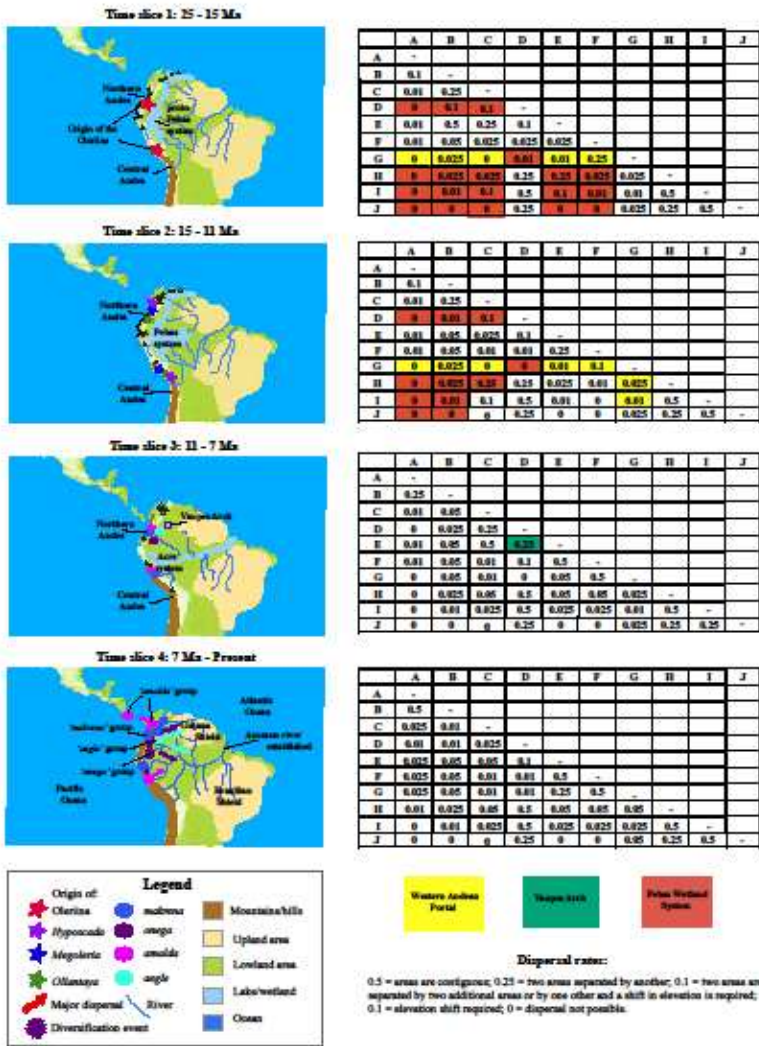


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Appendix S1a. Specimens used in the phylogeny and associated GenBank accession numbers. Elevation range data was obtained from museum collections (see Appendix S1b.), records of collaborators and the University College London butterfly database.

genus	species group	species	ssp and voucher	elevation range	COI-COII	Wg	EF1a	Tektin	RpL5	Tpi
<i>Hyposcada</i>										
		<i>H. anchiala</i>	<i>mendax</i> ; 2141	100-1200m	DQ078361	FN545690	FN551006	FN568118	FN666690	FN666923
		<i>H. attilodes</i>	-	1200-1600m	-	-	-	-	-	-
		<i>H. dujardini</i>	-	0-1400m	-	-	-	-	-	-
		<i>H. gallardi</i>	-	200-400m	-	-	-	-	-	-
		<i>H. ilinissa</i>	<i>margarita</i> ; 2-121	50-1450m	FN646233	FN545700	FN551020	FN568128	FN666701	-
		<i>H. kena</i>	<i>kena</i> ; EC458	100-1425m	FN646238	DQ143825	FN551039	FN568142	FN666719	FN666936
		<i>H. schausi</i>	<i>lactea</i> ; K5	450-800m	FN646240	FN545705	FN551026	FN568135	FN666709	-
		<i>H. taliata</i>	ssp. nov.; 2-1696	1500-2200m	FN646241	DQ143826	FN551027	-	FN666710	FN666930
		<i>H. virginiana</i>	<i>evanides</i> ; 8339	0-1300m	FN646247	DQ143829	FN551035	FN568138	FN666715	-
		<i>H. zarepha</i>	<i>zarepha</i> ; 02K	0-1400m	-	DQ143830	FN551044	FN568147	FN666723	FN666940
<i>Megoleria</i>										
		<i>M. orestilla</i>	<i>orestilla</i> ; 5-1028	1250-2700m	FN646248	FN545715	FN551047	FN568149	-	-
		<i>M. susiana</i>	<i>susiana</i> ; M27	1200-2500m	-	DQ143833	-	-	-	-
<i>Ollantaya</i>										
		<i>O. aegineta</i>	<i>inelegans</i> ; 21300	1350-2100m	FN646252	FN545717	FN551049	FN568151	FN666727	FN666944
		<i>O. canilla</i>	-; 5-1174	1400-2100m	FN646253	FN545718	FN551050	FN568152	-	-
		<i>O. sp. nov.</i>	-	1800-2500m	-	-	-	-	-	-
		<i>O. olerioides</i>	ssp. nov.; 21217	1400-2200m	FN646255	FN545722	FN551055	FN568155	FN666795	-
<i>Oleria</i>										
	<i>aegle</i>	<i>O. aegle</i>	<i>egra</i> ; 3-20	0-500m	FN646257	FN545724	FN551057	FN568157	FN666728	FN666945
	<i>amalda</i>	<i>O. amalda</i>	<i>modesta</i> ; EC135	0-1500m	FN646263	DQ143838	FN551065	FN568162	FN666738	-
		<i>O. estella</i>	<i>estella</i> ; 4-400	600-1470m	FN646295	FN545755	FN551098	FN568191	FN666768	-
		<i>O. gunilla</i>	<i>serdolis</i> ; 2-194	100-850m	DQ078378	FN545762	FN551112	-	FN666783	FN666960
		<i>O. paula</i>	-; 8474	30-1750m	FN646319	DQ143861	FN551150	-	-	-
		<i>O. rubescens</i>	-; 8369	30-1540m	DQ085460	DQ085443	DQ085455	FN568240	FN666826	FN666987
		<i>O. sp. nov. 1</i>	-; 7-511	500-1000m	FN651633	-	-	-	FN666853	-
		<i>O. zelica</i>	<i>pagasa</i> ; 8396	0-1550m	FN646346	FN545812	FN551178	FN568261	FN666857	-
	<i>makrena</i>	<i>O. athalina</i>	<i>banjana</i> ; EC414	1200-2700m	FN646269	FN545737	FN551074	FN568170	FN666750	-
		<i>O. attalia</i>	<i>tabera</i> ; 21176	1200-2400m	FN646276	FN545742	FN551079	FN568176	FN666752	-
		<i>O. baizana</i>	<i>baizana</i> ; EC413	2000-2450m	FN646281	DQ143842	FN551084	FN568181	-	-
		<i>O. sp. nov. 2</i>	-	1310-2000m	-	-	-	-	-	-
		<i>O. bioculata</i>	<i>tapio</i> ; 2-750	1250-1600m	FN646282	FN545746	FN551086	FN568183	FN666757	-
		<i>O. boyeri</i>	-; Boy	900-1475m	FN646285	-	FN551087	-	-	-
		<i>O. sp. nov. 3</i>	-	1600-2400m	-	-	-	-	-	-
		<i>O. cyrene</i>	<i>solida</i> ; EC394	1600-2600m	FN646287	DQ143844	FN551089	-	FN666767	FN666952
		<i>O. deronda</i>	<i>valida</i> ; 7-503	1400-2200m	FN651636	-	-	-	-	-
		<i>O. derondina</i>	ssp. nov.; 7-505	1800-2850m	FN651637	-	-	-	-	-
		<i>O. fasciata</i>	<i>fasciata</i> ; 21114	1300-2200m	FN646298	FN545757	FN551102	FN568194	FN666772	-
		<i>O. fumata</i>	-; OF30	1000-2500m	FN646300	FN545761	FN551106	FN568198	FN666774	-

1		<i>O. makrena</i>	<i>makrenita</i> ; 21115	950-2500m	FN651624	FN545771	FN551126	FN568216	FN666792	-
2		<i>O. padilla</i>	<i>pseudamakrena</i> ; 2-1699	500-2500m	FN646313	DQ143860	FN551142	-	FN666813	-
3		<i>O. phenomoe</i>	<i>phenomoe</i> ; 21167	480-1835m	FN651627	FN545789	-	FN568235	FN666821	-
4		<i>O. quadrata</i>	<i>quadrata</i> ; E16-3	900-1550m	DQ168619	DQ168621	DQ168617	-	FN666822	-
5		<i>O. radina</i>	ssp. nov.; 11-2	1700-2400m	FN646326	DQ143862	FN551154	FN568239	FN666825	FN666986
6		<i>O. santineza</i>	<i>santineza</i> ; 21484	1200-2400m	FN651629	FN545797	FN551158	FN568244	FN666829	-
7		<i>O. tremona</i>	ssp. nov.; 21196	1300-2400m	FN651631	FN545806	FN551166	FN568248	FN666843	-
8		<i>O. vicina</i>	-; 8500	1200-2000m	FN646335	DQ143864	FN551168	FN568250	FN666847	FN666991
9		<i>O. victorine</i>	<i>sarilis</i> ; 2-1458	25-1650m	FN646338	DQ143866	FN551171	FN568253	FN666851	-
10		<i>O. zea</i>	-	1200-2000m	-	-	-	-	-	-
11	<i>onega</i>	<i>O. sp. nov. 4</i>	-	0-500m	-	-	-	-	-	-
12		<i>O. agarista</i>	<i>agarista</i> ; 2-294	120-600m	DQ078368	FN545725	FN551059	FN568159	FN666730	-
13		<i>O. alexina</i>	-; 2-3613	120-1300m	FN646260	-	FN551061	-	-	-
14		<i>O. antaxis</i>	<i>antaxis</i> ; napk19	100-450m	TBA	TBA	TBA	-	-	-
15		<i>O. aquata</i>	-; B16-7	0-1100m	DQ168618	DQ168620	DQ168616	FN568165	FN666741	-
16		<i>O. assimilis</i>	ssp. nov.; 2-3609	120-900m	DQ085456	DQ085438	DQ085450	FN568167	FN666743	-
17		<i>O. astrea</i>	<i>burchelli</i> ; MC4	25-1000m	FN651635	FN545733	-	-	FN666745	-
18		<i>O. didymaea</i>	ssp. nov.; 6-116	100-1200m	FN646293	FN545751	FN551092	FN568186	FN666778	-
19		<i>O. enania</i>	<i>enania</i> ; 7-507	130-650m	FN651638	-	-	-	-	-
20		<i>O. flora</i>	ssp. nov.; napk17	100-820m	KJ566622	KJ545893	KJ496140	-	-	-
21		<i>O. ileridina</i>	<i>lerida</i> ; 2-291	10-1400m	DQ078373	FN545765	FN551116	FN568208	-	FN666964
22		<i>O. onega</i>	<i>janarilla</i> ; 2-303	100-1550m	DQ078389	DQ143853	FN551133	FN568223	-	FN666973
23		<i>O. quintina</i>	-; 6-67	500-2100m	FN646323	FN545790	-	FN568236	FN666823	-
24		<i>O. sexmaculata</i>	<i>sexmaculata</i> ; CJ20469	120-600m	FN646332	FN545801	FN551162	FN568247	FN666836	-
25		<i>O. similigena</i>	ssp. nov.; napk20	400-820m	TBA	TBA	TBA	-	-	-
26		<i>O. synnova</i>	-	50-120m	-	-	-	-	-	-
27		<i>O. thiemei</i>	-	400-500m	-	-	-	-	-	-
28		<i>O. tigilla</i>	<i>tigilla</i> ; K12	12-1200m	FN662763	FN545804	-	-	FN666840	-

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2 Appendix S1b. Museum collections from which information was obtained about elevation range and distribution of the *Oleriina* species.

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4 AMNH - American Museum of Natural History, New York, USA

5 BMB - Booth Museum of Natural History, Brighton, UK

6 BMNH - British Museum (Natural History), London, UK

7 CMNH - Carnegie Museum of Natural History, Pittsburgh, USA

8 FLMNH - Florida Museum of Natural History, Gainesville, USA

9 IAVH - Instituto de Investigación de los Recursos Biológicos Alexander von Humboldt, Villa de Leiva, Boyacá, Colombia

10 IOC - Instituto Oswaldo Cruz, C.P. 926, Avenida Brasil, Manguinhos, Rio de Janeiro, Brazil

11 MECM - Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador

12 MEFLG - Museo Entomológico Francisco Luís Gallego, Universidad Nacional de Colombia, Medellín, Colombia

13 MHNUC - Museo de Historia Natural, Universidad de Cauca, Popayán, Colombia

14 MNHN - Muséum National d'Histoire Naturelle, Paris, France

15 MNRJ - Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil

16 MUSM - Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Avenida Arenas 11434, Lima, Peru

17 MZSP - Museo de Zoologia da Universidade de São Paulo, Brasil

18 OUM - Oxford University Museum, Parks Road, Oxford, UK

19 RMS - Royal Museum of Scotland, Edinburgh, UK

20 SMF - Forschungsinstitut und Natur-Museum Senckenberg, Senckenberg-Anlage 25, 6000 Frankfurt-am-Main 1, Germany

21 SMNS - Staatliches Museum für Naturkunde, Stuttgart, Germany

22 SMTD - Staatliches Museum für Tierkunde, Dresden, Germany

23 USNM - National Museum of Natural History, Washington, D.C. 20560, USA

24 ZMHU - Zoologisches Museum, Humboldt Universität, Berlin, Germany

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31 Appendix S1c. MATERIAL & METHODS. Phylogenetic analysis of the *Oleriina* and timing of diversification

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34 We used published sequences of 53 of 63 known species from the subtribe *Oleriina* (De-Silva *et al.*, 2010; Brower *et al.*, 2014) for the mitochondrial gene region spanning COI-COII
35 and for nuclear genes *Wg*, *EF1a*, *Tektin*, *RpL5* and *Tpi* (4407 bp in total). We also obtained from colleagues unpublished sequences for *Oleria similigena*, as well as additional
36 genes for *O. antaxis*, *Ithomia* and *Pseudoscada* were used as outgroups.

37
38 A species-level phylogeny was generated for the *Oleriina*, selecting a single representative taxa per species (De-Silva *et al.*, 2010). The program Partition Finder
39 (Lanfear *et al.*, 2012) was selected to statistically find the best-fit partitioning scheme and best-fit substitution model for each subset, using the Bayesian Information Criterion
40 (BIC), unlinked branch lengths and greedy search algorithm. Using BEAST version 1.7.2 (Drummond *et al.*, 2012), a Bayesian uncorrelated lognormal relaxed clock model was
41 implemented and the dataset was partitioned and models of sequence evolution selected according to the results obtained from PartitionFinder. Two independent Markov chain
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2 Monte Carlo analyses were run using a random starting tree for 100,000,000 generations using a constant rate Yule speciation prior and sampling every 10,000 generations
3 (10 % burn-in). All other priors were left to the default settings. Tracer version 1.5 (Rambaut & Drummond, 2009) was used to ensure each MCMC run had converged on a
4 stationary distribution by confirming the Effective Sample Size (ESS) values were greater than 200. Trees were combined using LogCombiner version 1.7.2 (Drummond *et al.*, 2012)
5 and the posterior distribution of trees was summarized to obtain the maximum clade credibility tree with average branch lengths using TreeAnnotator version 1.7.2
6 (Drummond *et al.*, 2012).
7

8 A recent calibration for the entire Nymphalidae butterfly family was implemented where minimum age constraints were based on seven fossils dating from the Eocene, Oligocene
9 and Miocene and maximum times of divergence were constrained by the ages of plant families for six butterfly clades (Wahlberg *et al.*, 2009). Based on node ages estimated from
10 that study, two secondary calibration points were used, one on the node incorporating the Oleriina and its sister lineage, *Ithomia*, 20.1 Ma (14.27, 27.07) and the other on the node
11 containing the genera, *Oleria* and *Ollantaya* 15.64 Ma (9.51, 22.48). A normal prior was imposed on both nodes.
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14 RESULTS. Phylogenetic analysis of the Oleriina and timing of diversification

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16 PartitionFinder recovered a total of 9 partitions for the concatenated dataset (see Appendix S1c). Selection of an alternative partitioning scheme had little effect on the phylogeny
17 compared to previous findings (De-Silva *et al.*, 2010) with the exception of relationships between *Oleria agarista*, *O. enania*, *O. quintina* and *O. astrea*, which are largely
18 unresolved. The addition of two further species of *Oleria* to the phylogeny also had little effect on the overall topology (De-Silva *et al.*, 2010). *O. similigena* is recovered with
19 high-support within the *O. onega* species group and as sister to *O. aquata* (Fig. 1). The addition of a sample of *O. antaxis* with additional gene regions confirmed the placement
20 of this species within the *O. onega* species group but as sister to *O. flora* (BPP 100) rather than *O. assimilis* as suggested by previous phylogenetic hypotheses
21
22 (De-Silva *et al.*, 2010). The dated phylogeny obtained from BEAST suggests that the Oleriina diverged from other Ithomiini during the Late Oligocene / Early Miocene at around
23 19.2 Ma (12.6-30.0) (Fig.1). The subtribe is suggested to have diverged during the Early-Middle Miocene 15.2 Ma (10.3-20.3) into two clades comprising *Hyposcada* and a
24 clade containing the rest of the Oleriina. While the species *H. illinissa* and *H. taliata* are suggested to have persisted since the Middle Miocene, the rest of *Hyposcada*
25 diversified more recently in the Plio-Pleistocene. The species-poor genus *Megoleria* also diverged during the Middle Miocene (from the clade comprising *Oleria* and *Ollantaya*),
26 while its constituent species diversified during the Plio-Pleistocene. *Oleria* and *Ollantaya* diverged during the Middle Miocene with both clades diversifying soon afterwards
27 (7.7-15.6 Ma); however, in contrast to *Hyposcada* and *Megoleria*, *Ollantaya* appears to have diversified early in its history during the Middle Miocene.
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31 REFERENCES

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- 33
34 Brower, A.V.Z., Willmott, K.R., Silva-Brandão, K.L., Garzón-Orduña, I.J. & Freitas, A.V.L. (2014) Phylogenetic relationships of ithomiine butterflies (Lepidoptera: Nymphalidae:
35 Danainae) as implied by combined morphological and molecular data. *Systematic Biology*, **12**, 133-147.
36
37 De-Silva, D.L., Day, J.J., Elias, M., Willmott, K., Whinnett, A. & Mallet, J. (2010) Molecular phylogenetics of the neotropical butterfly subtribe Oleriina (Nymphalidae: Danainae:
38 Ithomiini). *Molecular Phylogenetics and Evolution*, **55**, 1032-1041.
39
40 Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology & Evolution*, **29**, 1969-1973.
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3 Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular*
4 *Biology & Evolution*, 29, 1695-1701.

5
6
7 Rambaut, A. & Drummond, A.J. (2009) Tracer v1.5, Available from <http://beast.bio.ed.ac.uk/Tracer>.

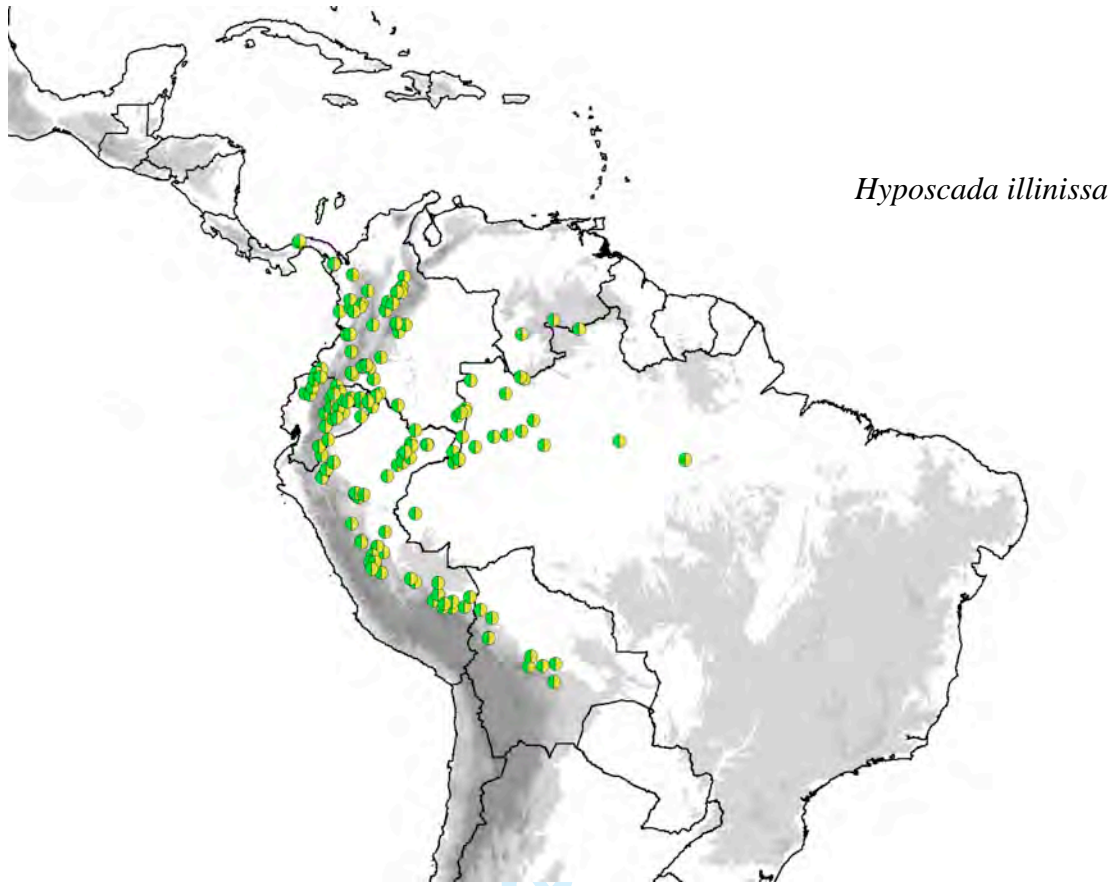
8
9 Wahlberg, N., Leneuve, J., Kodandaramaiah, U., Peña, C., Nylin, S., Freitas, A.V.L. & Brower, A.V.Z. (2009) Nymphalid butterflies diversify following near demise at the Cretaceous/
10 Tertiary boundary. *Proceedings of the Royal Society B: Biological Sciences*, 276, 4295-4302.

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14 Appendix S1d. PartitionFinder best substitution models for the program BEAST v1.7 selected using BIC and partitioned by gene region and codon position.

Gene region/Codon position	Model
COI-COII/Codon1	GTR+I+G
COI-COII/Codon2	GTR+I+G
COI-COII/Codon3	HKY+I+G
Wg/Codon1, Wg/Codon2, Ef-1a/Codon2	HKY+I
Wg/Codon3, Ef-1a/Codon1, Tektin/Codon2	HKY+G
Ef-1a/Codon3	HKY
Tektin/Codon1, Tektin/Codon3	HKY+G
RpL5/Codon1, RpL5/Codon2, RpL5/Codon3, Tpi/Codon1, Tp	GTR+G
Tpi/Codon3	HKY+G

Appendix S2. Distribution maps of the Oleriina species. Localities were recorded from extensive examination of museum collections and records of collaborators. The distribution of the Oleriina is well known in all biogeographic areas with the exception of central Amazonia, which forms part of western and eastern Amazonia (Areas H and I, see Fig.2.)

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Hyposcada anchiala



Hyposcada zarepha

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Hyposcada kena



Hyposcada virginiana

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Hyposcada schausi



Megoleria orestilla

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Megoleria susiana



Ollantaya canilla

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Oleria aegle



Oleria sexmaculata

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Oleria assimilis



Oleria tigilla

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Oleria sp. nov. 1



Oleria paula

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Oleria boyeri

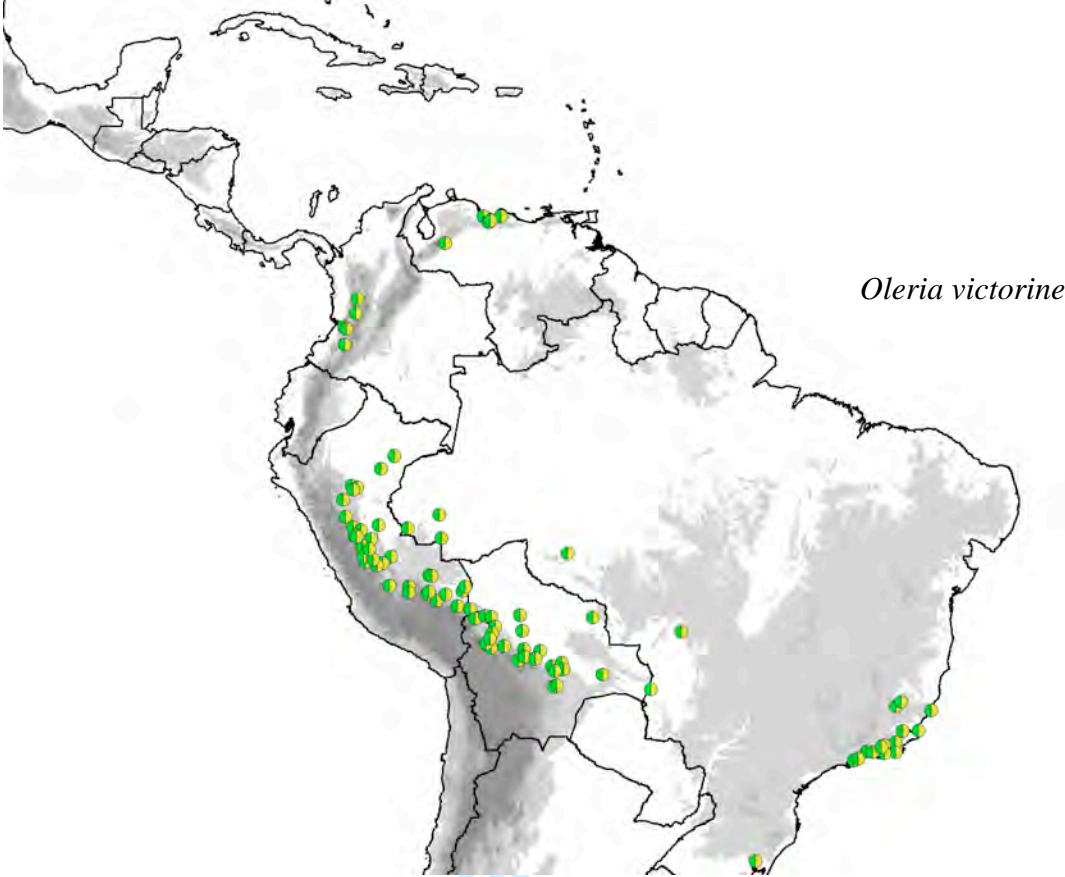


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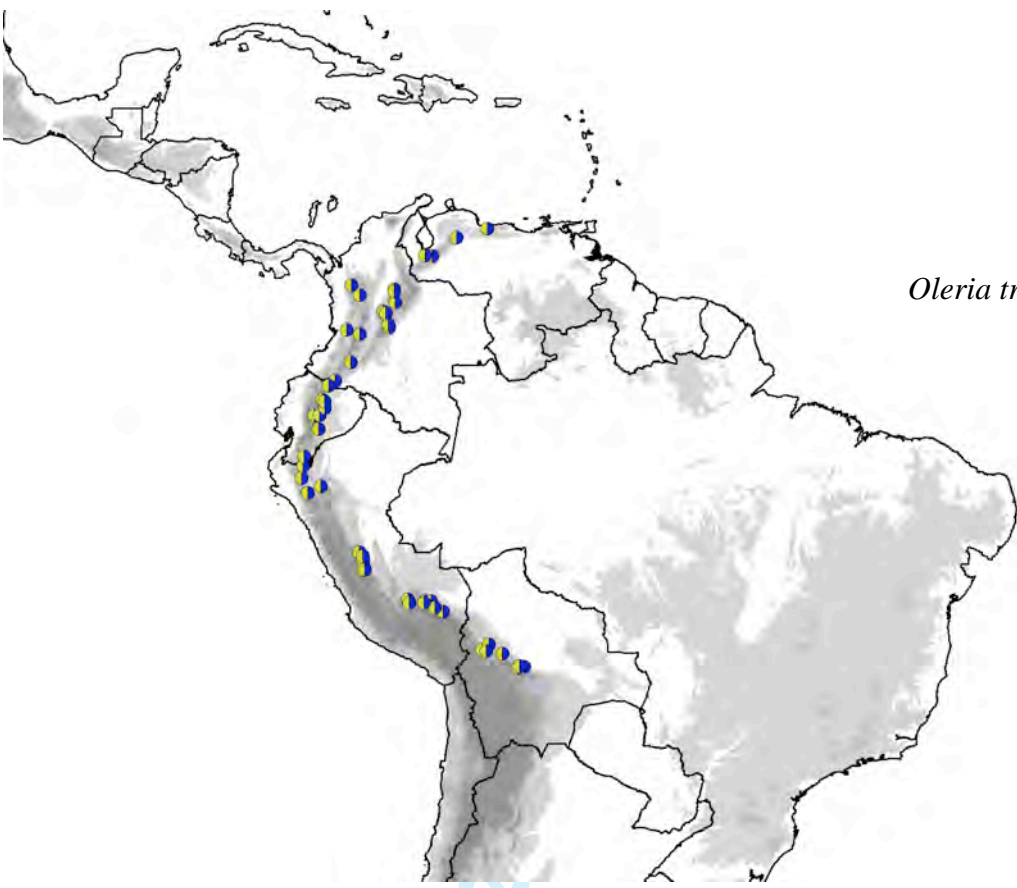
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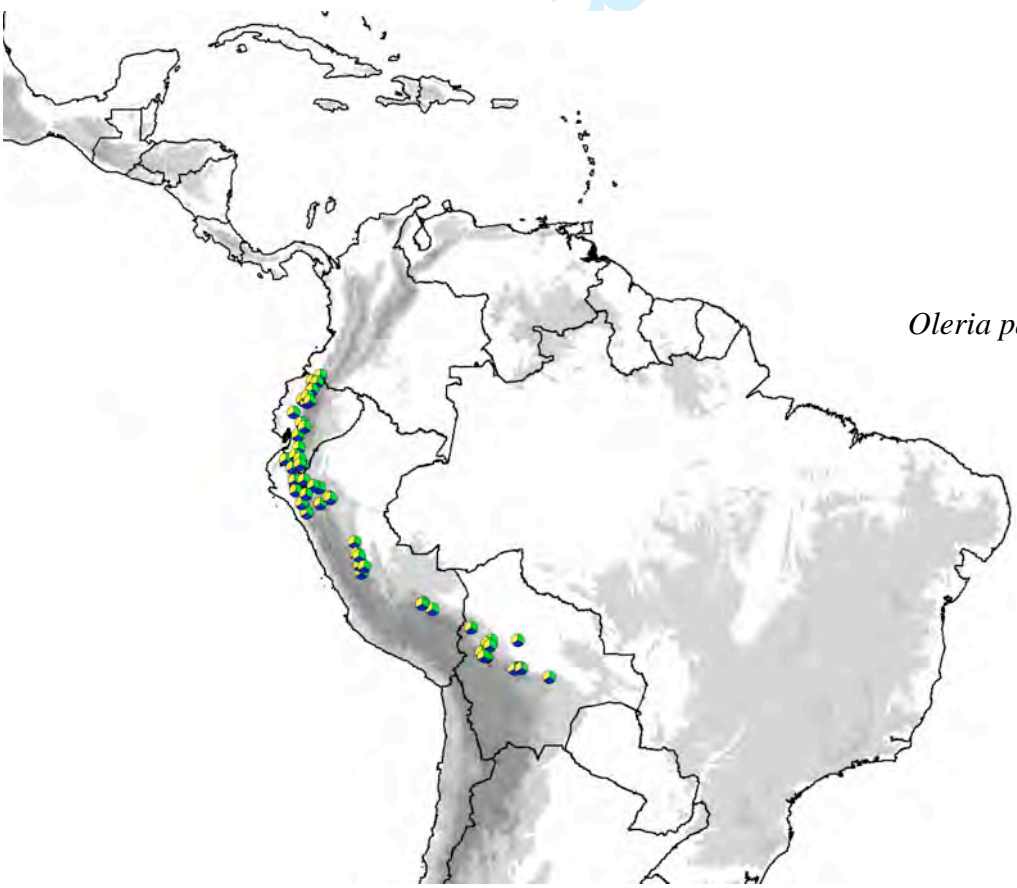
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Oleria tremona



Oleria padilla

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Oleria attalia



Oleria cyrene