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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**

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.

Keywords

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

INTRODUCTION

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).

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) (Sébrier *et al.*, 1988; Ehlers & Poulsen,

2009), although increasing evidence suggests more rapid growth from the Late Miocene (12 Ma) (Kennan *et al.*, 1997; Garzione *et al.*, 2008; 2014; Whipple & Gasparini, 2014); the orogenesis of the Northern Colombian Andes began with the Cordillera Occidental and culminated with the emergence of the Cordillera Oriental (3–15 Ma) (Mora *et al.*, 2008); the formation of the “Pebas System”, a vast network of shallow lakes and wetlands, from the Late Oligocene to the Early Miocene (11.3 to ~24 Ma) (Wesselingh *et al.*, 2002); the formation of the fluvial “Acre” System (7 to ~11.3 Ma), which later became the eastward flowing paleo-Amazon (5 to ~8 Ma), after intense Andean uplift created a continuous barrier and transformed Amazonian drainage patterns (Mora *et al.*, 2010).

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

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

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

130

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.

136

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).

150

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

one), with a scenario of punctuational evolution (κ is represented by zero), and a scenario where κ was estimated by maximum likelihood (ML). Under a model of gradual evolution the probability of a change in elevation is in direct proportion to the branch length whereas under punctuational evolution a change in elevation is associated with speciation.

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

Using BayesTraits 1.0 (Pagel *et al.*, 2004) we first tested ancestral elevation as a discrete trait using BayesMultiState. Ancestral states were reconstructed by fixing the root of each clade at low, mid and high elevation and calculating the AIC in each case to determine if one of the alternative states was significantly more likely. The results obtained for κ were used to reconstruct the ancestral elevation range. Second, BayesContinuous was used to test ancestral elevation as a continuous trait by examining the minimum and maximum elevation range for each species. Random-walk versus directional change models of evolution were compared and the branch scaling parameters κ , delta (δ) and lambda (λ) were estimated. The δ parameter determines if the rate of trait evolution has accelerated or slowed over time. A δ value of less than one is a signature of rapid early diversification followed by slower rates of change and suggests adaptive radiation, whereas a δ value of greater than one indicates a signature of accelerating evolution with time. The parameter λ reveals the phylogenetic signal for a given

182 en phylogeny and trait. A lambda value of one is consistent with the Brownian motion
183 or constant-variance model of evolution whereas a value of zero indicates that species
184 are evolving independently. The log-likelihood was calculated in each case and the
185 associated AIC determined.

186

187 **Ancestral geographical distribution**

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

207

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-

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

Ancestral geographical range

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

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

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

DISCUSSION

Pattern and tempo of diversification

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

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

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

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

In contrast to other Oleriina clades, lineage accumulation in the *amalda* species group and *Hyposcada* is suggested to have proceeded at a near constant rate, although both clades contain a small number of species, potentially limiting the power to investigate diversification. The case of *Hyposcada* is particularly intriguing, because it is an old clade that underwent a change in dietary repertoire with a switch to a new plant family, Gesneriaceae (Willmott & Freitas, 2006). Older clade age and increased ecological opportunities should both favour diversification, through time-for-speciation (Hutter *et al.*, 2013) and adaptive radiation (Schulter, 2000; Kozak *et al.*, 2015), yet this clade is particularly depauperate. Although no significant extinction was recovered at the subtribe level (again, perhaps because of a lack of power in small clades), the long branches leading to *H. illinissa* and *H. taliata*, and to the clade containing the remaining *Hyposcada*, may suggest past extinction in this genus.

Rise of the Andes and biogeographic history of the Oleriina

Our analyses suggest that the ancestral Oleriina diverged from the rest of the Ithomiini during the Early to Middle Miocene between low and high elevations in the Central or Northern Occidental Andes. The subtribe separated into four lineages, which, with the exception of *Megoleria*, all diverged during the Middle to Late Miocene with further diversification during the Pliocene. Diversification within the subtribe is largely consistent with key geological changes in the Neotropical landscape (Garzione *et al.*, 2008) particularly from the Late Oligocene to Pliocene (~3-26 Ma) (Hoorn & Wesseling, 2010).

Hyposcada diversified between low and high elevations on the slopes of the Central or Northern Occidental Andes. The most basal members of this clade, *H. illinissa*

and *H. taliata*, have much older histories than the rest of the clade, having diverged well within the Miocene. However, these species have contrasting histories, with *H. illinissa* thriving at low and mid altitudes, colonizing cis- and trans-Andean habitats and western and eastern Amazonia, while *H. taliata* colonized higher elevation cis-Andean habitats along the eastern slopes of central Peru and Ecuador. A further divergence led to the relatively rapid radiation and formation of two subclades at low altitudes during the Late Pliocene ~3.5 Ma, in which constituent species have a broad biogeographic distribution. The first clade contains the cis-Andean species, *H. kena*, which is commonly found in the east Andean foothills. A further divergence at ~2.5 Ma led to the widely distributed trans-Andean, low-mid elevation, *H. virginiana* and rarer, low elevation, *H. schausi*, which indicates that their ancestor may have crossed the Andes at the 'Western Andean Portal' (WAP). This lowland corridor separated the Northern and Central Andes in northern Peru and southern Ecuador until the Middle Miocene (11-13 Ma) forming a biogeographic barrier to the dispersal of many montane species (Antonelli *et al.*, 2009). The WAP may not have attained altitudes of 1500-2000m before 2-5 Ma (Blandin & Purser, 2013) allowing the dispersal of some low altitude species. Furthermore, evolution of the host plant family Gesneriaceae, in particular, the genera, *Drymonia* and *Columnea*, which are known host plants for *H. virginiana* and other *Hyposcada* species, coincided with intense Northern Andean uplift in the last 10 Ma (Perret *et al.*, 2013). These plants diversified extensively, particularly at mid-elevation in the Northern Andes and Central America. A second clade contains two geographically allopatric species, *H. anchiala* and *H. zarepha*, with the former found in the Andes and western Amazonia and the latter in the Guianas and eastern Amazonia. Their distribution is in accordance with that of Gesneriaceae, which are poorly represented in the Amazon Basin as a whole (Perret *et al.*, 2013).

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-

cies (Blandin & Purser, 2013). It is plausible that the demise of the Acre System from 5-7 Ma (Mora *et al.*, 2010), the filling of the deltaic proto-Orinoco Basin (Hoorn *et al.*, 1995) and the establishment of rainforests linking western Amazonia and the Guiana Shield facilitated this eastward dispersal (Gomez *et al.*, 2005). The Vaupés Arch, a paleoarch formed by uplift of the Eastern Cordillera of the Northern Andes, may also have promoted dispersal between these regions (Hoorn *et al.*, 1995).

Relationships within the second *makrena* clade were generally poorly resolved, possibly due to rapid diversification (De-Silva *et al.*, 2010), but the Northern Occidental Andes was likely to have been important in their diversification and several distinct distribution patterns emerge. There are several examples of geographically allopatric sister species, for example, *O. vicina* and *O. quadrata* diverged ~5.4 Ma (95% HPD: 3.7-8.0) with the former restricted to Central America while the latter is found within the Northern Andes and along its western slopes. Although the importance of the supposed recent closure of the Panamanian Isthmus ~3Ma (Coates *et al.*, 2003) in the diversification of some groups (Webb, 2006) is controversial (Baker *et al.*, 2014), the landmasses were in close proximity from the Miocene and dispersal may have occurred via the Atrato Seaway (Kirby *et al.*, 2008; Mullen *et al.*, 2011). *O. santineza* and *O. fumata* separated ~1.8 Ma (95% HPD: 0.9-2.8) and are confined to the east and west slopes of the Northern Oriental/Occidental Andes respectively. Their divergence is coincident with the final uplift of the Cordillera Oriental ~2-5 Ma, which was previously isolated from the proto-Northern Andes by the Magdalena Valley (Mora *et al.*, 2010). *Oleria padilla* is restricted to the eastern slopes of the Central Andes and crosses onto the western slopes of the Northern Andes in the vicinity of the WAP, while *O. makrena* dispersed along the eastern slopes of the Northern Andes.

Ecological adaptation, such as diversification on new host plants, may have been key to the diversification of some sympatric sister species, including

414 *O.athalina/O.fasciata* and *O.attalia/O.cyrene*. *Oleria victorine* has a disjunct distribu-
415 tion and, unlike other *Oleria*, has colonized large swathes of the Neotropics from the
416 Venezuelan Cordilleras to the Atlantic Forest. Causes for this unusually wide distribu-
417 tion are unknown, but expansion in larval diet breadth could have provided opportuni-
418 ties for colonization of new habitats.

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

429 The *onega* group diversified in lowland forest habitats of western Amazonia main-
430 ly during the Late Miocene and Pliocene. Their diversification coincides with the dis-
431 appearance of Lake Pebas and contraction of the Acre System, which are likely to have
432 acted as dispersal barriers between the Andes and Amazonia (Wahlberg & Freitas,
433 2007; Antonelli *et al.*, 2009; Hoorn & Wesseling, 2010). The eastward development of
434 terra firme rainforests prompted dispersal of a relatively high number of species into
435 eastern Amazonia, the Guiana Shield and Atlantic region (see Appendix S2). However,
436 low diversity of the host plant, Solanaceae, within these regions (Knapp, 2002) may
437 have precluded further diversification driven by adaptation to alternative host plants.
438 Indeed, forest productivity is higher on nutrient-rich western Amazonian soils, in con-
439 trast to the nutrient poor soils of the eastern Amazon (Hoorn *et al.*, 2010). Further di-

440 versification within the monotypic *O. aegle* group in eastern Amazonia and the Guian-
441 as may also have been limited by the availability of larval host plants as has been noted
442 with other ithomiine genera in this region (Elias *et al.*, 2009). Several instances of
443 sympatric *onega* group sister species within western Amazonia suggests that fine-scale
444 ecological adaptation, such as specialization on different but related host plant species
445 (Willmott & Mallet, 2004), might have been important in the diversification of this
446 clade.

447 For the Oleriina, in general, distinct Northern Andean distribution patterns have
448 emerged from our analyses. A remarkable number of species exist within the Cordille-
449 ra Occidental, at all elevations, whereas only a few species have colonized the Cordil-
450 lera Oriental, of which only one, *Megoleria susiana*, is a strictly high elevation species;
451 although there are a few instances of mid/high altitude species that have diversified
452 within the last 2 Ma. Other species remain within the eastern Ecuadorian Andes or
453 where the Cordillera Oriental joins the western Colombian Cordilleras. This pattern is
454 consistent with the geologically recent emergence of the east Colombian Cordillera and
455 the appearance of cloud forests between 3-5 Ma (Kattan *et al.*, 2004). There are only
456 three instances of dispersal as far as the Venezuelan Cordilleras, consistent with their
457 emergence as recently as 3.5 Ma (Albert *et al.*, 2006). *Oleria phenomoe* is found only
458 in this region, suggesting the extinction of it or its sister species in Northern Andean
459 ancestral areas. Dispersal into the Atlantic region has occurred rarely, but may have
460 been via the Mato Grosso Arch, which linked the Central Andes to the Brazilian Shield
461 perhaps from the Late Eocene (Hoorn & Wesselingh, 2010), or via continuous forest
462 cover which previously connected eastern Amazonia and the Atlantic Forest (Costa,
463 2003, and references therein). These regions are now linked by interconnecting forest
464 patches through an otherwise open landscape, which may explain the presence of *O.*

465 *aquata* within the northeastern Caatinga and central Cerrado regions of the Brazilian
466 Shield.

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

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

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SUPPORTING INFORMATION

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

Appendix S1 a. List of specimen used, GenBank accession numbers and elevation
ranges for each species. **b.** Museum collections from which information was obtained
about elevation range and distribution. **c.** Phylogenetic analysis of the Oleriina and
timing of diversification – Materials & Methods, Results, References. **d.** PartitionFind-
er best substitution models

Appendix S2. Distribution maps of the Oleriina species.

BIOSKETCHES

Donna Lisa de-Silva is interested in understanding the patterns and processes involved
in Neotropical diversification. Her work currently focuses on the ithomiine butterflies.
The research group of **Julia Day** focuses on the patterns and processes leading to insu-
lar and continental radiations. **James Mallet** and his research group study evolution,
hybridization, and speciation - mainly in Neotropical butterflies. **Marianne Elias** and
her research group study diversification patterns and community ecology of various
organisms, with a special emphasis on ithomiine butterflies. **Keith Willmott** has a

708 longstanding research program on the systematics and biogeography of Neotropical
709 butterflies.

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

713

714 Table 1. Rates of diversification test results using rate-constant (pure-birth, birth-death)
715 and rate-variable (density dependent logistic - DDL and density dependent exponential
716 - DDX, indicative of adaptive radiation; Yule two-rate models; time-varying speciation
717 and constant extinction - SPVAR, time-varying extinction and constant speciation -
718 EXVAR, varying speciation and extinction through time - BOTHVAR (Rabosky &
719 Lovette, 2008)) diversification models. In each case, the best model/s is/are indicated
720 in **bold**. Log-likelihood, AIC and the difference in AIC with the best model (Δ AIC) are
721 shown for each clade examined. R^1 and R^2 indicate initial and, when applicable, final
722 net diversification rates, respectively; st = the time of rate shift in the Yule-2-rate mod-
723 el; a = extinction fraction E/S , k = the k -parameter from the DDL model, and x = the x -
724 parameter from the DDX model.

A726

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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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.
732

| Clade | Model | Log lkd | Parameters | AIC | ΔAIC |
|------------------|-------------|---------------|------------|--------------|-------------|
| <i>Oleriina</i> | | | | | |
| | High | -21.09 | 4 | 50.17 | 0 |
| | Low | -23.19 | 4 | 54.38 | 4.21 |
| | Mid | -21.50 | 4 | 51.00 | 0.83 |
| <i>Hyposcada</i> | | | | | |
| | High | -21.15 | 4 | 50.30 | 0 |
| | Low | -23.19 | 4 | 54.38 | 4.08 |
| | Mid | -21.18 | 4 | 50.36 | 0.06 |
| <i>Ollantaya</i> | | | | | |
| | High | -20.69 | 4 | 49.37 | 0 |
| | Low | -25.67 | 4 | 59.33 | 9.96 |
| | Mid | -22.05 | 4 | 52.09 | 7.24 |
| <i>Oleria</i> | | | | | |
| | High | -20.66 | 4 | 49.33 | 0 |
| | Low | -22.16 | 4 | 52.32 | 2.99 |
| | Mid | -20.99 | 4 | 49.98 | 0.65 |
| <i>Megoleria</i> | | | | | |
| | 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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Table 3. Maximum likelihood estimation of ancestral elevation range as a continuous trait for minimum and maximum elevation ranges. Random walk versus directional change models of evolution are compared. kappa (κ) = 0 (punctuational evolution), (κ) = 1 (gradual evolution); delta (δ) < 1 (early rapid evolution followed by slow down), (δ) > 1 (accelerating evolution with time); lambda (λ) = 1 (Brownian motion evolution), (λ) = 0 (Independent evolution). In each case, the best model is indicated in **bold**.

| Model | Log lkd | Parameters | AIC | Δ AIC | Scaling parameter |
|--|----------------|------------|---------------|--------------|-------------------|
| Minimum elevation range | | | | | |
| <u>Random walk</u> | | | | | |
| (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 |
| <u>Directional</u> | | | | | |
| (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 |
| <u>Random walk</u> | | | | | |
| (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 |
| <u>Directional</u> | | | | | |
| (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 |
| <u>Random walk</u> | | | | | |
| (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 |
| <u>Directional</u> | | | | | |
| (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

| | | | | | |
|---------------------------------|---------|---|--------|--------|-------|
| <u>Random walk</u> | | | | | |
| (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 |
| <u>Directional</u> | | | | | |
| (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 |
| <u>Random walk</u> | | | | | |
| (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 |
| <u>Directional</u> | | | | | |
| (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 |
| <u>Random walk</u> | | | | | |
| (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 |
| <u>Directional</u> | | | | | |
| (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 |

Figure 1. Bayesian dated maximum clade credibility tree for the Oleriina based on an uncorrelated log normal relaxed clock and detailing current and ancestral elevation ranges. Current elevation ranges are shown at the tips of the trees. ML inferred ancestral elevation ranges are shown for each node on the branch and MP inferred ancestral elevation ranges are shown below the branch where results differ. Bayesian posterior probabilities lower than 0.90 are indicated. Genera and *Oleria* species groups are shown to the right of the tree.

Figure 2. Bayesian dated maximum clade credibility tree for the Oleriina based on an uncorrelated log normal relaxed clock detailing biogeographical reconstructions of ancestral geographical ranges inferred from dispersal-extinction-cladogenesis implemented in Lagrange. The evolution of the Oleriina was divided into four time slices corresponding to notable paleogeographic events. Coloured squares to the left of the map correspond to the geographical areas indicated and those below the map to multiple areas. Coloured squares to the right of the tree indicate the geographical range of each extant species. Pie charts represent the relative probabilities of ancestral ranges. Ancestral area probabilities < 0.1 were combined (black sections of the pie charts). The number of extant species for each geographical region are indicated.

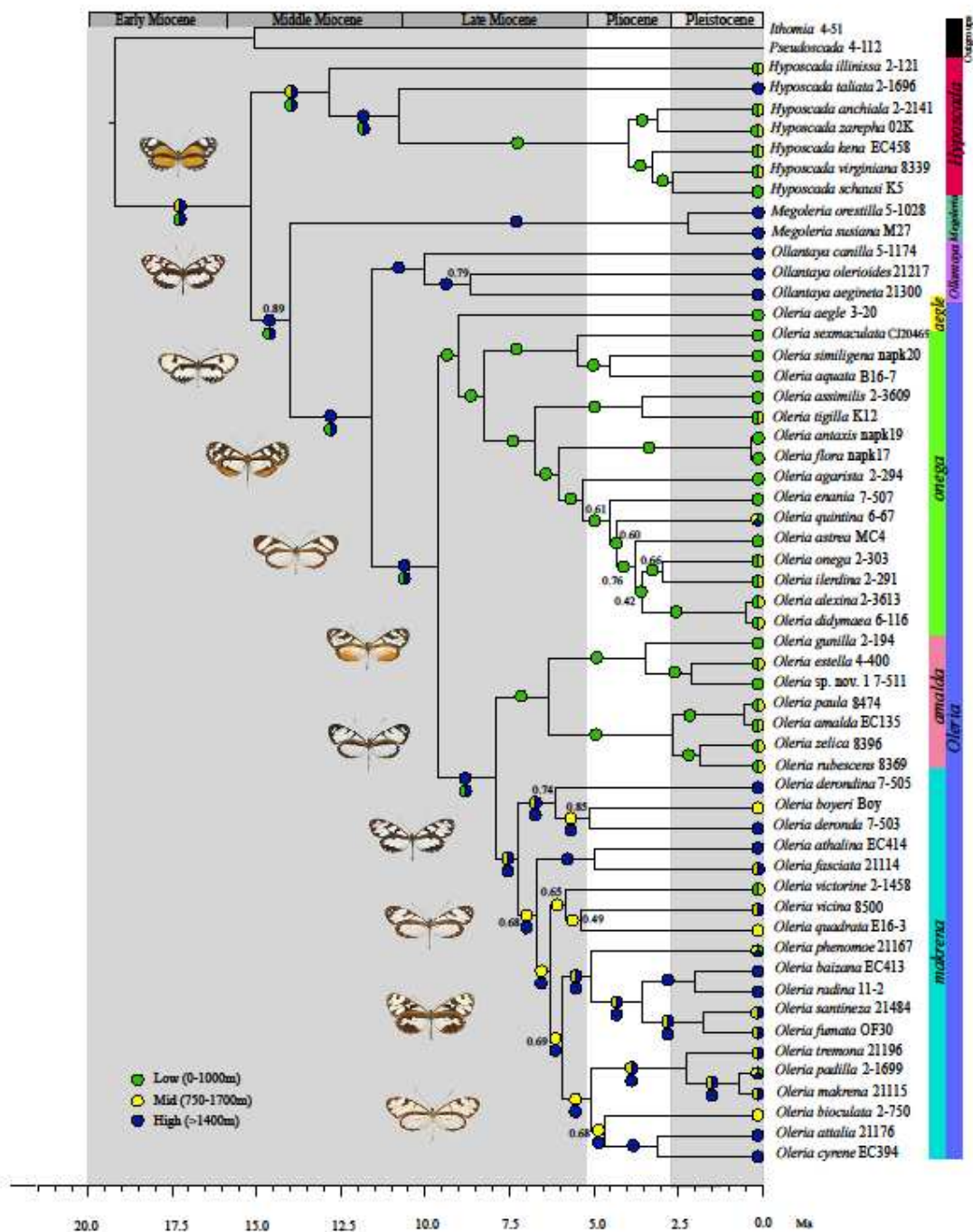
Figure 3. Lineage-through-time (LTT) plots based on 1000 sampled Bayesian trees for a. Oleriina, b. *Hyposcada*, c. *Oleria*, d. 'makrena' species group, e. 'amalda' species group, f. 'onega' species group.

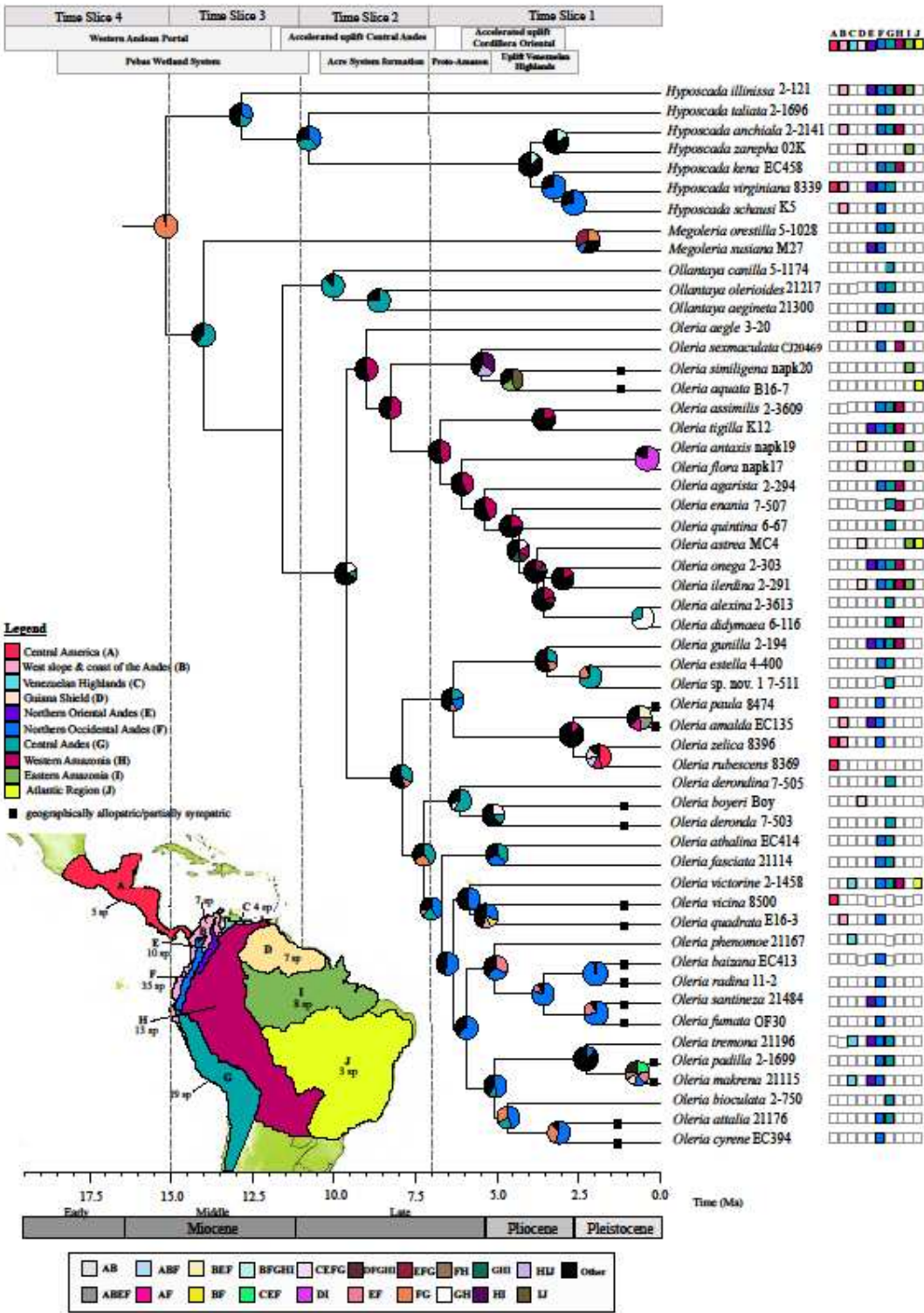
Figure 4. Paleogeographical model used in the dispersal-extinction-cladogenesis analyses of biogeographical events. The four time slices used in the analyses and dispersal rates for each biogeographic area are shown. Maps are modified from Hoorn & Wesseling, (2010); Condamine *et al.*, (2013); Matos-Maraví *et al.*, (2013). Maps show dispersal and diversification of each Oleriina genus. Dispersal rates highlighted indicate a constraint on dispersal. A. Central America; B. western slopes and lowlands of the Northern Andes including Colombia, Ecuador and northwest Peru; C. Venezuelan Highlands including the Cordillera de Mérida and Cordillera de la Costa; D. Guiana Shield; E. Northern Oriental Andes; F. Northern Occidental Andes including the Colombian Cordillera Occidental, Cordillera Central and Ecuador; G. Central Andes; H.

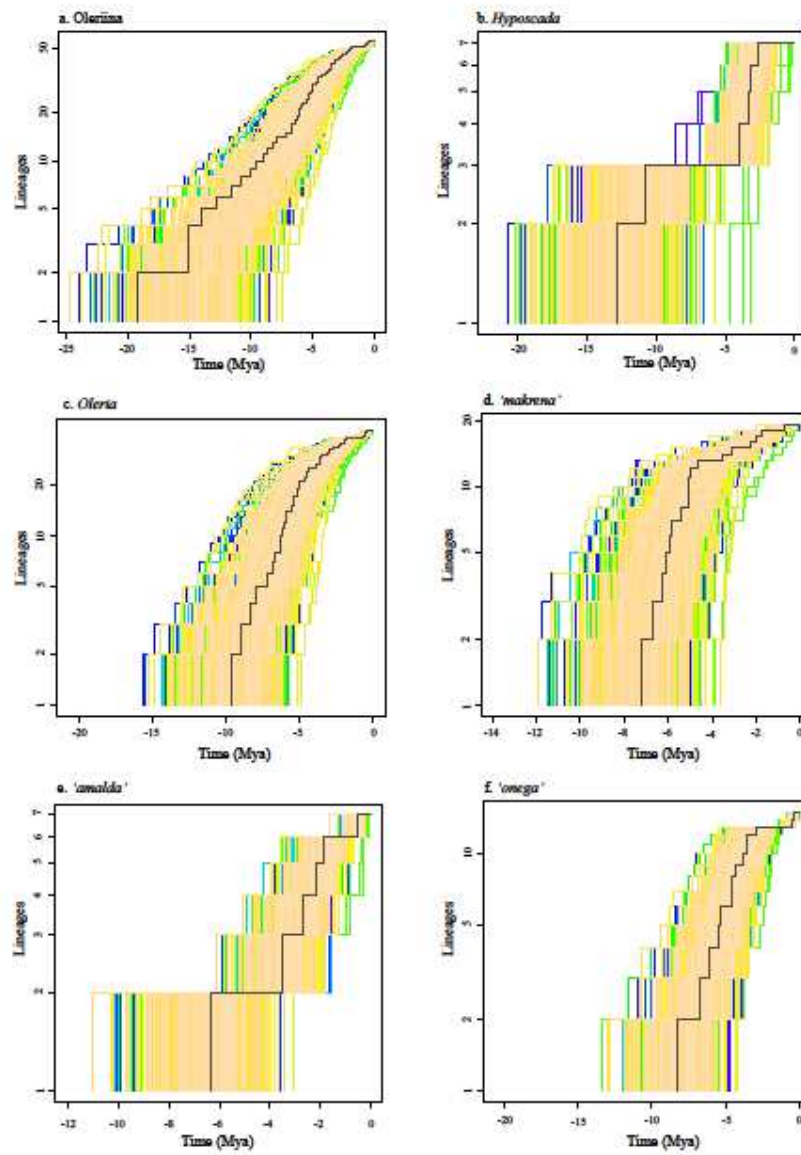
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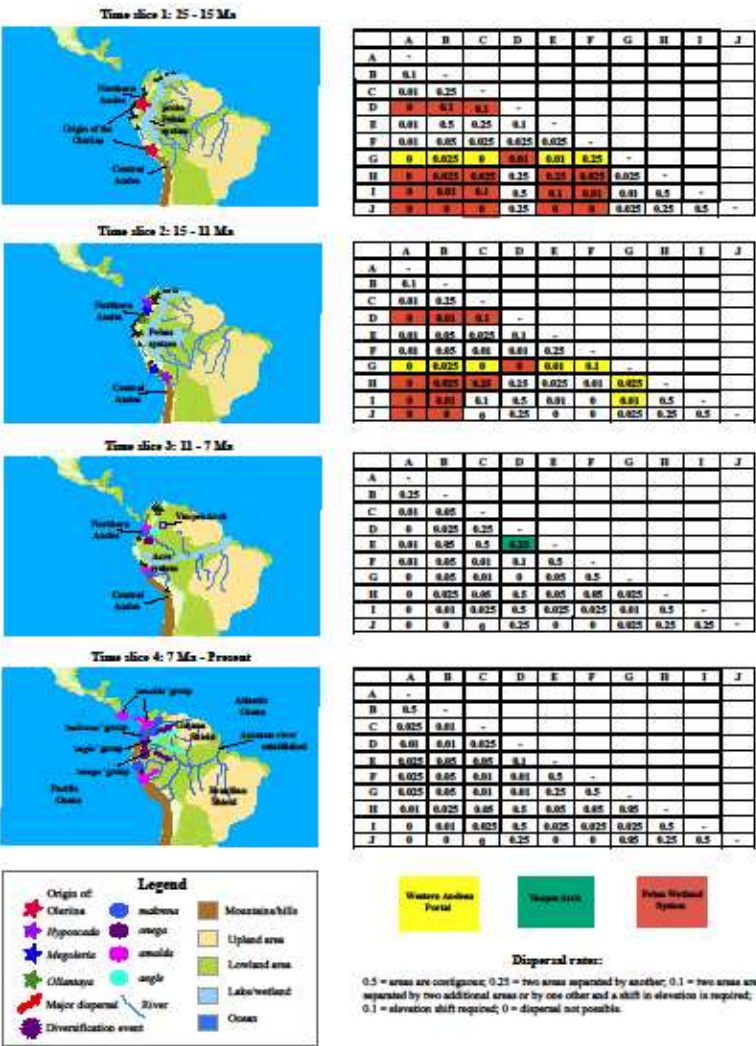
776 western Amazonia; I. central and eastern Amazonia; J. Atlantic region including the
777 Atlantic Forest and Cerrado.

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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>Hypocada</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. illinissa</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 | - |

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| 1 | | | | | | | | | |
| 2 | | <i>O. makrena</i> | <i>makrenita</i> ; 21115 | 950-2500m | FN651624 | FN545771 | FN551126 | FN568216 | FN666792 |
| 3 | | <i>O. padilla</i> | <i>pseudmakrena</i> ; 2-1699 | 500-2500m | FN646313 | DQ143860 | FN551142 | - | FN666813 |
| 4 | | <i>O. phenomoe</i> | <i>phenomoe</i> ; 21167 | 480-1835m | FN651627 | FN545789 | - | FN568235 | FN666821 |
| 5 | | <i>O. quadrata</i> | <i>quadrata</i> ; E16-3 | 900-1550m | DQ168619 | DQ168621 | DQ168617 | - | FN666822 |
| 6 | | <i>O. radina</i> | <i>ssp. nov.</i> ; 11-2 | 1700-2400m | FN646326 | DQ143862 | FN551154 | FN568239 | FN666825 |
| 7 | | <i>O. santineza</i> | <i>santineza</i> ; 21484 | 1200-2400m | FN651629 | FN545797 | FN551158 | FN568244 | FN666829 |
| 8 | | <i>O. tremona</i> | <i>ssp. nov.</i> ; 21196 | 1300-2400m | FN651631 | FN545806 | FN551166 | FN568248 | FN666843 |
| 9 | | <i>O. vicina</i> | -; 8500 | 1200-2000m | FN646335 | DQ143864 | FN551168 | FN568250 | FN666847 |
| 10 | | <i>O. victorine</i> | <i>sarilis</i> ; 2-1458 | 25-1650m | FN646338 | DQ143866 | FN551171 | FN568253 | FN666851 |
| 11 | | <i>O. zea</i> | - | 1200-2000m | - | - | - | - | - |
| 12 | <i>onega</i> | <i>O. sp. nov. 4</i> | - | 0-500m | - | - | - | - | - |
| 13 | | <i>O. agarista</i> | <i>agarista</i> ; 2-294 | 120-600m | DQ078368 | FN545725 | FN551059 | FN568159 | FN666730 |
| 14 | | <i>O. alexina</i> | -; 2-3613 | 120-1300m | FN646260 | - | FN551061 | - | - |
| 15 | | <i>O. antaxis</i> | <i>antaxis</i> ; napk19 | 100-450m | TBA | TBA | TBA | - | - |
| 16 | | <i>O. aquata</i> | -; B16-7 | 0-1100m | DQ168618 | DQ168620 | DQ168616 | FN568165 | FN666741 |
| 17 | | <i>O. assimilis</i> | <i>ssp. nov.</i> ; 2-3609 | 120-900m | DQ085456 | DQ085438 | DQ085450 | FN568167 | FN666743 |
| 18 | | <i>O. astrea</i> | <i>burchelli</i> ; MC4 | 25-1000m | FN651635 | FN545733 | - | - | FN666745 |
| 19 | | <i>O. didymaea</i> | <i>ssp. nov.</i> ; 6-116 | 100-1200m | FN646293 | FN545751 | FN551092 | FN568186 | FN666778 |
| 20 | | <i>O. enania</i> | <i>enania</i> ; 7-507 | 130-650m | FN651638 | - | - | - | - |
| 21 | | <i>O. flora</i> | <i>ssp. nov.</i> ; napk17 | 100-820m | KJ566622 | KJ545893 | KJ496140 | - | - |
| 22 | | <i>O. ilerdina</i> | <i>lerida</i> ; 2-291 | 10-1400m | DQ078373 | FN545765 | FN551116 | FN568208 | - |
| 23 | | <i>O. onega</i> | <i>janarilla</i> ; 2-303 | 100-1550m | DQ078389 | DQ143853 | FN551133 | FN568223 | - |
| 24 | | <i>O. quintina</i> | -; 6-67 | 500-2100m | FN646323 | FN545790 | - | FN568236 | FN666823 |
| 25 | | <i>O. sexmaculata</i> | <i>sexmaculata</i> ; CJ20469 | 120-600m | FN646332 | FN545801 | FN551162 | FN568247 | FN666836 |
| 26 | | <i>O. similigena</i> | <i>ssp. nov.</i> ; napk20 | 400-820m | TBA | TBA | TBA | - | - |
| 27 | | <i>O. synnova</i> | - | 50-120m | - | - | - | - | - |
| 28 | | <i>O. thiemei</i> | - | 400-500m | - | - | - | - | - |
| 29 | | <i>O. tigilla</i> | <i>tigilla</i> ; K12 | 12-1200m | FN662763 | FN545804 | - | - | FN666840 |

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

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

BMB - Booth Museum of Natural History, Brighton, UK

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

CMNH - Carnegie Museum of Natural History, Pittsburgh, USA

FLMNH - Florida Museum of Natural History, Gainesville, USA

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

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

MECM - Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador

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

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

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

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

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

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

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

RMS - Royal Museum of Scotland, Edinburgh, UK

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

SMNS - Staatliches Museum für Naturkunde, Stuttgart, Germany

SMTD - Staatliches Museum für Tierkunde, Dresden, Germany

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

ZMHU - Zoologisches Museum, Humboldt Universität, Berlin, Germany

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

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 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 genes for *O. antaxis*, *Ithomia* and *Pseudoscada* were used as outgroups.

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 (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 (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 implemented and the dataset was partitioned and models of sequence evolution selected according to the results obtained from PartitionFinder. Two independent Markov chain

1 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
2 (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
3 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)
4 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
5 (Drummond *et al.*, 2012).
6

7 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
8 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
9 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
10 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
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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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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.)



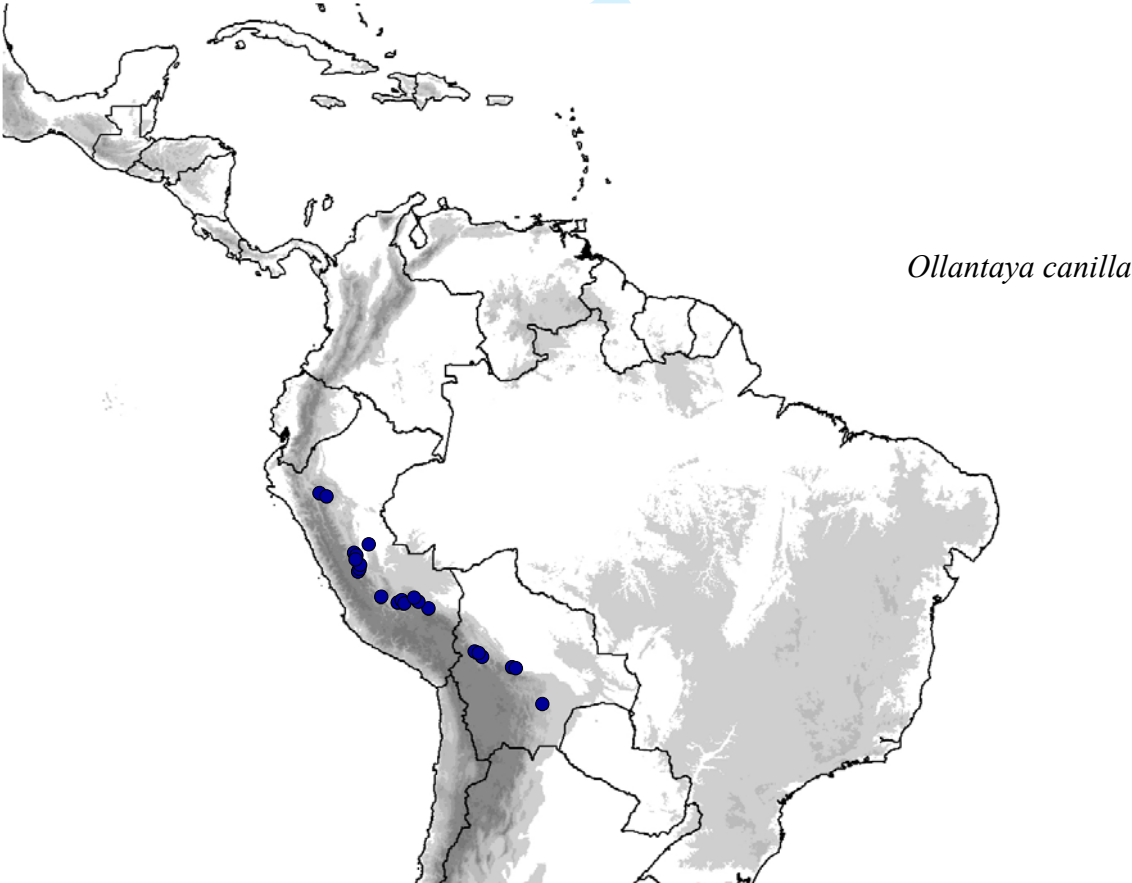


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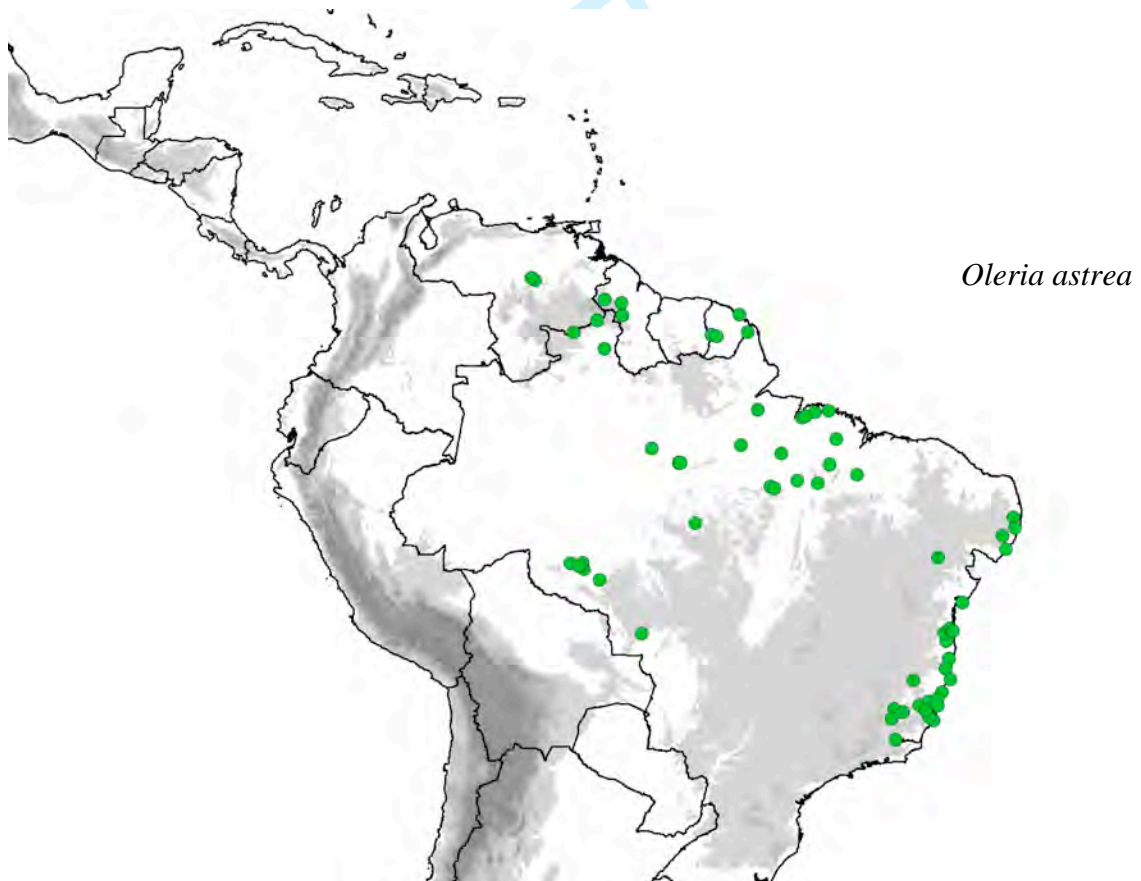
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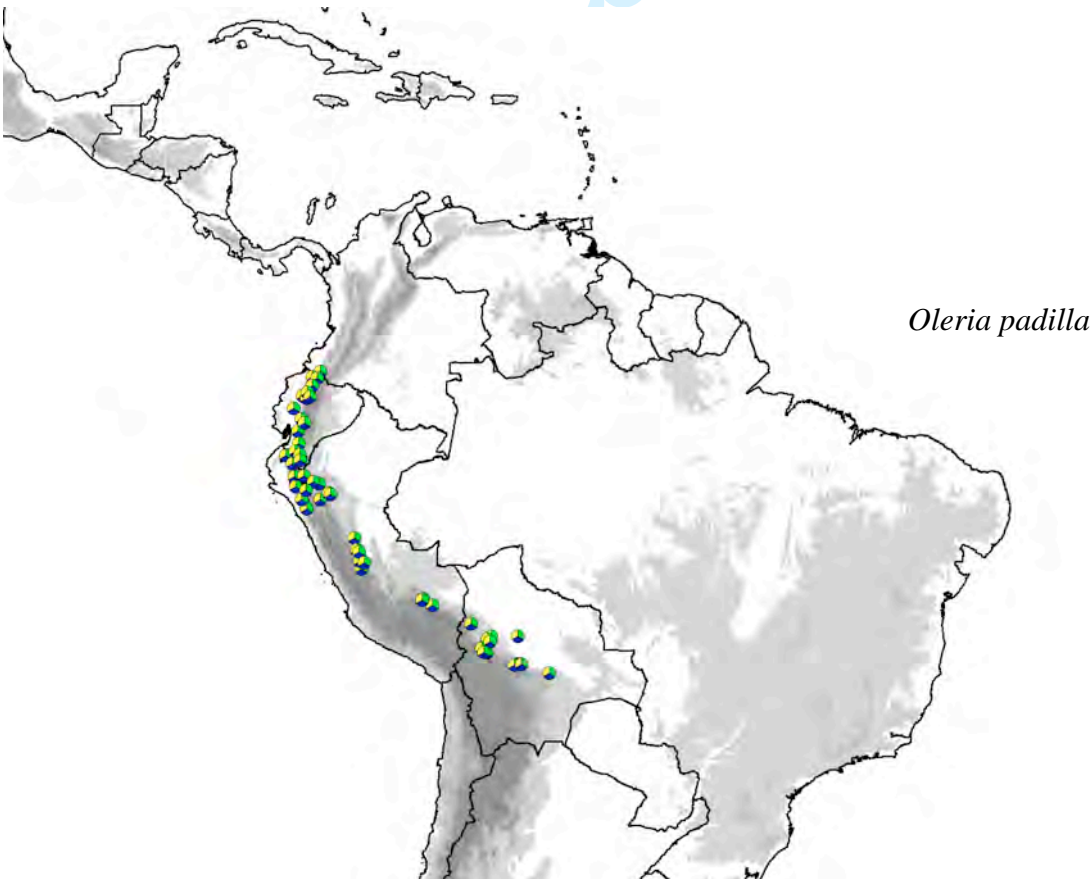
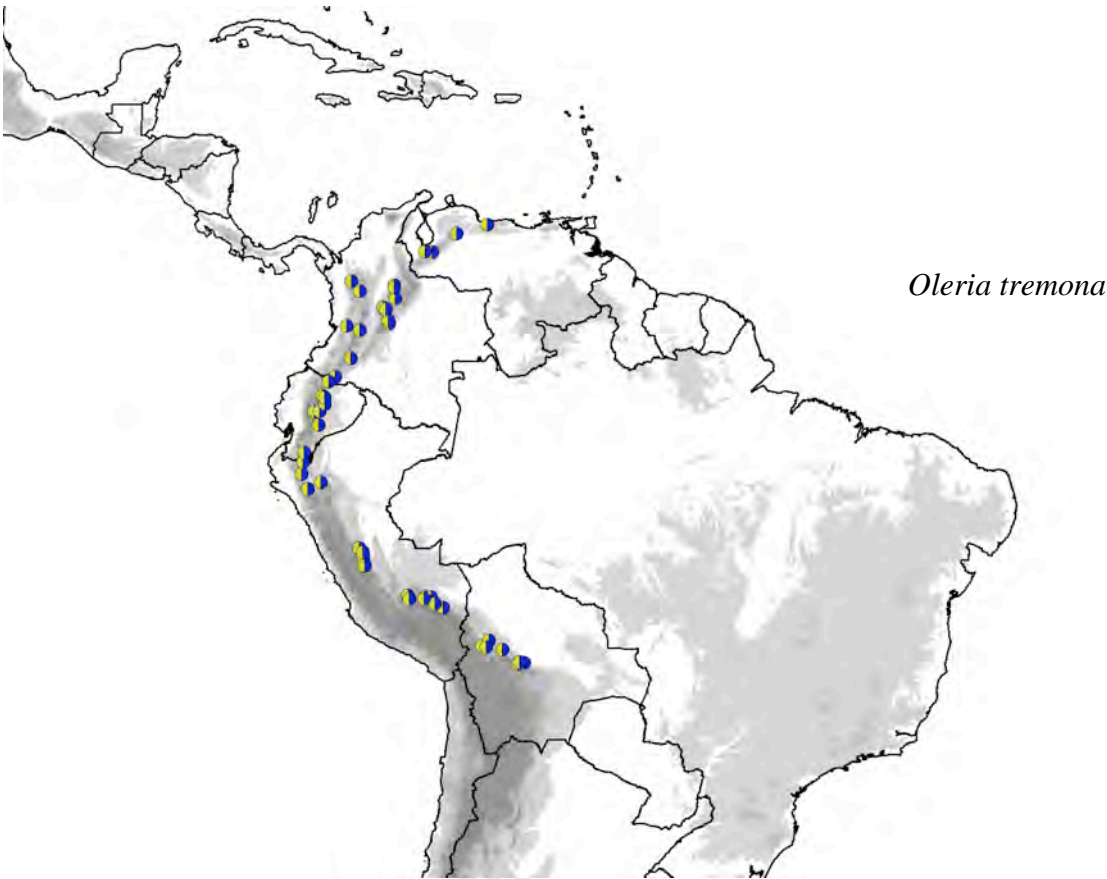


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