ORIGINAL ARTICLE

Diversification of clearwing butterflies with the rise of the Andes

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ABSTRACT

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

Location Neotropics.

Methods Ancestral elevation and biogeographical ranges were reconstructed using data generated from detailed range maps and applying the dispersal-extinction-cladogenesis model using stratified palaeogeographical time slice matrices. The pattern of diversification through time was examined by comparing constant and variable rate models. We also tested the hypothesis that a change in elevation is associated with speciation.

Results The Oleriina likely originated in the Andes in the Early to Middle Miocene and rapidly diversified to include four genera all of which also originated in the Andes. These clades, together with four species groups, experienced varying spatial and temporal patterns of diversification. An overall early burst and decreasing diversification rate is identified, and this pattern is reflected for most subclades.

Main conclusions Changes in the palaeogeological 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, *Hyposcada*, Ithomiini butterflies, *Megoleria*, Neotropics, *Oleria*, *Ollantaya*

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INTRODUCTION

Like all other species-rich 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 palaeoclimatic 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 palaeogeographical 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 (15 to 3 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 (*c.* 24 to 11.3 Ma) (Wesselingh *et al.*, 2002); the formation of the fluvial 'Acre' System (*c.* 11.3 to 7 Ma), which later became the eastward flowing palaeo-Amazon (*c.* 8 to 5 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 Andean uplift was also detected (Elias *et al.*, 2009). The diversification of *Taygetis* (Nymphalidae: Satyrinae) in the Late Miocene to Pliocene was coincident with the central Andean uplift and the disappearance of geographical barriers such as Lake Pebas (Matos-Maraví *et al.*, 2013). The Andes also played an important role in the radiation of heliconiine butterflies (Nymphalidae: Heliconiinae) and the diversification of the most species-rich genera is coincident with uplift of the Andes (Kozak *et al.*, 2015). Nevertheless, the highest community species richness in most groups is found in the Amazon Basin, where, for example, a large proportion of heliconiine subspecies diversity occurs (Rosser *et al.*, 2012).

To provide further insights into how geological events have shaped Neotropical butterfly diversification processes, we studied the evolutionary history of the diverse butterfly subtribe Oleriina (Nymphalidae: Ithomiini). The Ithomiini represent an ideal group for this purpose because they are widely distributed throughout the Neotropics and are found at all elevations within the Andean mountain range up to around 3000 m. The overall diversity and distribution of the tribe is reflected in the subtribe Oleriina, containing the most species-rich ithomiine genus, *Oleria* (48 species), as well as three genera, *Hyposcada*, *Megoleria* and *Ollantaya*, that are relatively species-poor in comparison. The subtribe therefore offers a valuable system to investigate diversification processes in ithomiine butterflies and may aid our understanding of the diversification of Neotropical butterflies as a whole.

Using a densely sampled (86%), calibrated species-level phylogeny combined with detailed biogeographical and elevation range data, we specifically address the following questions: (1) When and where did the Oleriina originate? (2) What was the biogeographical pattern of colonization of the Neotropics? (3) Did geological events, particularly the uplift of the Andes, influence the timing and pattern of diversification of the focal group?

MATERIALS AND METHODS

Phylogenetic analysis of the Oleriina and timing of diversification

We generated a calibrated species-level phylogeny using an uncorrelated lognormal relaxed clock implemented in BEAST 1.7.2 (Drummond *et al.*, 2012) and implementing secondary calibrations based on Wahlberg *et al.* (2009) (see Appendix S1 in Supporting Information).

Rates of diversification

To visualize the tempo of diversification, lineage-through-time (LTT) plots for 1000 sampled trees from the posterior distribution were generated in APE 3.0-9 (Paradis *et al.*, 2004) in R (R Core Team, 2015). To test whether diversification rates have changed over time the gamma (γ) statistic was calculated (Pybus & Harvey, 2000) for different taxonomic groups using APE 3.0-9. Positive and negative values of γ indicate an increasing and decreasing diversification rate towards the present respectively. The Monte Carlo constant rates test (Pybus & Harvey, 2000) was used to determine if the decreasing diversification rate indicated by the gamma parameter is significant given the number of missing taxa in our dataset. LASER 2.3 (Rabosky, 2006) was used to test specific models of diversification through time (see Table 1). Fit of constant and variable rate models were compared using the Akaike information criterion (AIC; see Table 1).

Ancestral elevation range

To test the hypothesis that a change in elevation is associated with speciation, we used BAYESTRAITS 1.0 (Pagel *et al.*, 2004). BayesMultiState, which reconstructs the evolution of a

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

Clade	Model	R^1	R^2	a	k/x	st	log-lkh	AIC	ΔAIC
Oleriina	Pure-birth	0.174					17.42	−32.84	11.71
	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
Hyposcada	**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
onega 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

finite number of discrete states, was implemented to compare a scenario of gradual evolution [where the branch scaling parameter kappa (κ) is equal to one], with a scenario of punctuational evolution (κ is equal to 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 ML and maximum parsimony (MP) using BayesTraits 1.0 (Pagel *et al.*, 2004) and Mesquite 2.75 (Maddison & Maddison, 2011) respectively. Each species was categorized according to its known elevation range as either low (0–1000 m), mid (750–1700 m), high (>1400 m) or a combination of these ranges (see Appendix S1). 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. A random-walk model of evolution was implemented 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 phylogeny and trait. A λ value of one is consistent with the Brownian motion or constant-variance model of evolution, whereas a value of zero indicates that species are evolving independently. The log-likelihood was calculated in each case and the associated AIC determined.

Ancestral geographical distribution

The distribution of the Oleriina (see Appendix S2) was delimited on the basis of geological history, range data and previous studies (Santos *et al.*, 2009; Blandin & Purser, 2013) into ten areas (see Figs 1 & 2). The geographical range evolution of the Oleriina was reconstructed using the ML dispersal-extinction-cladogenesis (DEC) model in Lagrange (Ree & Smith, 2008). We used the dated phylogeny generated in beast and extant species distributional data to infer ancestral locations. The maximum number of ancestral areas was set to six, reflecting the maximum number of areas occupied by extant species. Each species was coded as present or absent for each geographical region. Our analyses considered the main palaeogeographical events that have occurred during the past 25 Myr (Fig. 2). This time span, covering the evolution of the Oleriina, was stratified into four time slices each reflecting temporal palaeogeographical constraints. We followed Ree & Smith (2008) and for each time slice a matrix was constructed to scale the probability of dispersal between 0 and 1 according to geographical area connectivity

through time (Fig. 2). Dispersals that involved a change in elevation were therefore multiplied by 0.01 to reflect the low probability of movement (Matos-Maraví *et al.*, 2013). Additional analyses tested the root area of the subtribe by constraining the root to be single areas and combinations of multiple areas. Likelihoods of models under different constraints were compared. A log-likelihood difference of two units was considered significant.

RESULTS

Oleriina phylogeny and timing of diversification

Our analyses indicate that the Oleriina originated *c.* 15.2 Ma [95% highest posterior density (HPD): 25.6–13.2 Ma] and that the diversification of all extant genera followed in the Middle to Late Miocene. The *Oleria* species groups, *onega* and *makrena*, diversified mainly during the Late Miocene and Pliocene (95% HPD: 8.0–3.0 Ma), with the *makrena* group diversifying further and more rapidly during the Pleistocene (95% HPD: 3.0–0.5 Ma). The Pleistocene was also important in the diversification of the *Oleria amalda* species group (Figs 1 & 3).

Diversification through time

Lineage-through-time plots (Fig. 4) and the gamma statistic indicate an overall decreasing diversification rate for the Oleriina ($\gamma = -3.38$, $P = 0.001$ assuming nine missing species). These results are reflected by the gamma statistic for *Oleria* ($\gamma = -4.22$, $P = 0.001$, six missing species) as well as internal clades: *makrena* species group ($\gamma = -3.57$, $P = 0.001$, three missing species); *onega* species group ($\gamma = -2.31$, $P = 0.01$, three species missing). In turn, a constant diversification rate could not be rejected for the *amalda* species group ($\gamma = -0.19$, $P = 0.42$) or for *Hyposcada* ($\gamma = -0.27$, $P = 0.28$, two species missing). Gamma statistic results are in general supported by diversification models, in which rate-variable models (density-dependent logistic and/or Yule-2-rate) were preferred over rate-constant models for Oleriina, *Oleria*, *makrena* and *onega* groups. Conversely, for *Hyposcada* and the *amalda* species group, a rate-constant pure-birth model was better supported although density-dependent models also had high support. (Table 1).

Evolution of elevation range

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

Reconstruction of ancestral elevation was largely congruent between ML and MP analyses, except for basal nodes connecting the different genera, and some internal nodes in the makrena clade (Fig. 3). The Oleriina originated at mid or high elevations (Fig. 3, Table 2). This was followed by two radiations, one into mid/high elevations resulted in the genus Hyposcada. The second radiation led to the origin and diversification of Megoleria, Ollantaya and Oleria. A high elevation origin was well supported for Megoleria (Table 2). A second clade likely evolved at high elevation forming Ollantaya and Oleria. A high elevation origin was strongly supported for Ollantaya, whereas for Oleria, a mid- or high-elevation origin was equally likely (Table 2). Within Oleria, two clades (the amalda group and the onega + aegle groups) colonized and mostly remained at low elevation with a few instances of movement to include mid elevation and one to high elevation. The fourth species group, makrena, originated at mid-high elevations and diversified rapidly in montane areas.

When elevation is scored as a continuous trait, for minimum elevation range and the κ and λ scaling parameters, the best model of evolution is a model without branch length transformation, meaning that evolution of elevation range is gradual and Brownian-motion-like (Table 3). For the δ scaling parameter, models $\delta = 1$ and $\delta = 0.68$ cannot be distinguished. Therefore, minimum elevation 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) and the area spanning the Ecuadorian Andean ranges and Colombian central and western cordilleras (hereafter, Ecuador-Colombia, Area F) (log L – 238.6) or both areas (log L – 237.2) as the most likely ancestral areas of the Oleriina (Fig. 1). 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. 1).

Our results indicate that the Oleriina most likely diverged in situ forming all four genera (Figs 1 & 2). Hyposcada dispersed widely with the exception of the Venezuelan Highlands and Atlantic region. The high elevation genera Megoleria and Ollantaya both remained in Ecuador-Colombia (Area F) but only Megoleria reached the north-east Colombian 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 Andes or Ecuador-Colombia (Area F). Within the amalda group there are two allopatric sub-clades,

the first is restricted to the eastern slopes of the Central Andes, north-east Colombian Andes, Ecuador-Colombia (Area F) and western Amazonia while the second is found on the western coast and slopes of the 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. 1, see Appendix S1). In general, high numbers of sister species pairs are found in the same biogeographical 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 and mimetic pattern has been shown to contribute to reproductive isolation (e.g. Merrill et al., 2012). 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 (Elias et al., 2008; 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 riodinid butterfly genus Ithomiola (Hall, 2005). However, in the case of Oleriina, although shifts in altitudinal ranges are associated with speciation (Table 1), they tend to be rare (Fig. 3). Moreover, 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
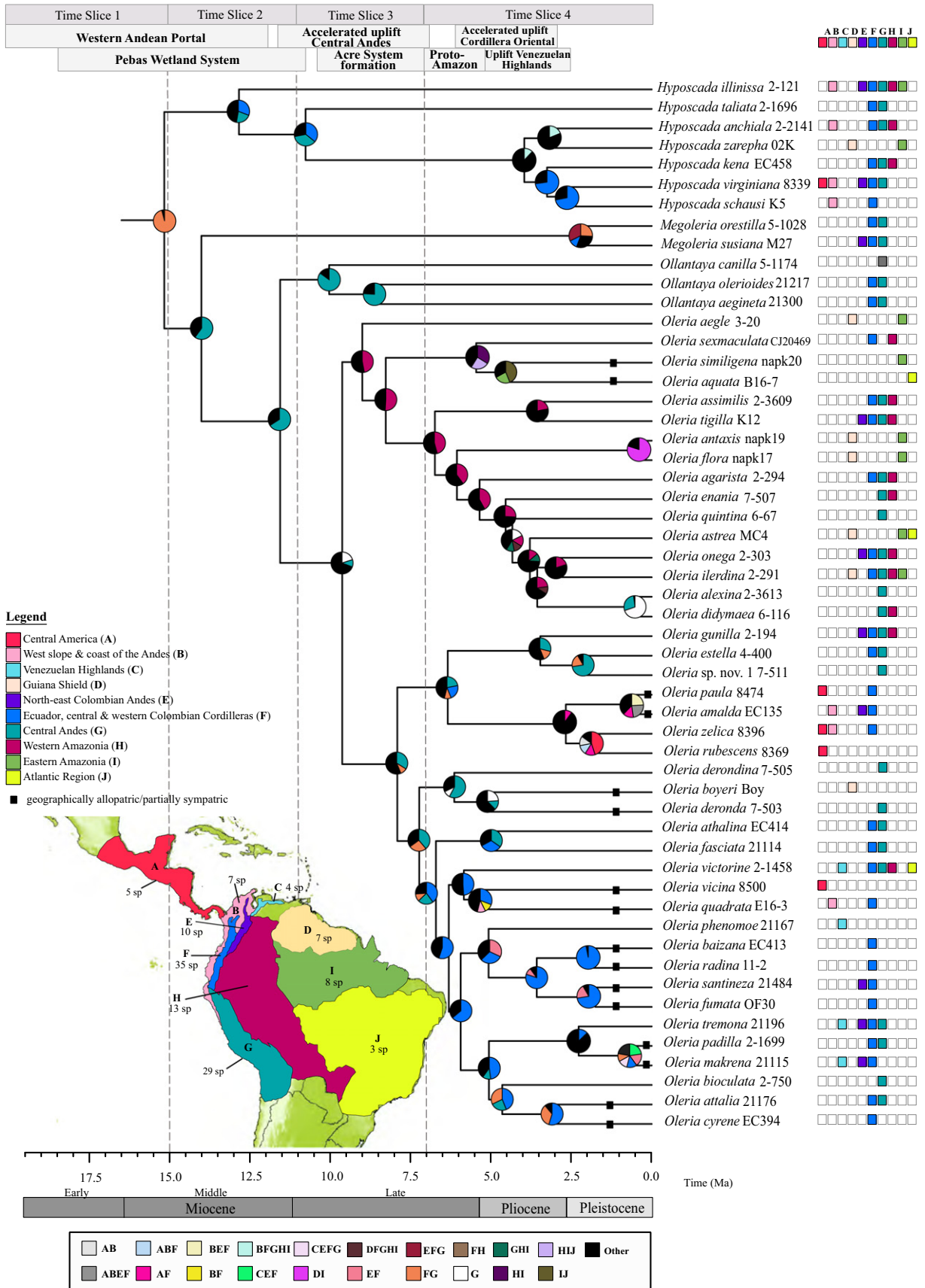
Figure 1 Bayesian dated maximum clade credibility tree for the Oleriina based on an uncorrelated lognormal relaxed clock detailing biogeographical reconstructions of ancestral geographical ranges inferred from dispersal-extinction-cladogenesis implemented in LAGRANGE. The evolution of the Oleriina was divided into four time slices corresponding to notable palaeogeographical events. Coloured squares to the left of the map correspond to the geographical areas indicated. Coloured squares to the right of the tree indicate the geographical range of each extant species and those at the bottom of the tree indicate combined ranges. 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 is indicated in the map.

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 biogeographical 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 mid and high elevations in the Central Andes or Ecuador-Colombia (Area F). 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 (~26–3 Ma) (Hoorn & Wesseling, 2010; Figs 1 & 2).

Hyposcada diversified between mid and high elevations on the slopes of the Central Andes or Ecuador-Colombia (Area F). 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 *c.* 3.5 Ma, in which constituent species have a broad biogeographical distribution. The first clade contains the cis-Andean species, *H. kena*, which is commonly found in the east Andean foothills. A further divergence at *c.* 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 corridor, which was perhaps covered by water, separated the Northern (Areas

E and F) and Central Andes in northern Peru and southern Ecuador until the Middle Miocene (13–11 Ma) forming a biogeographical barrier to the dispersal of many montane species (Antonelli *et al.*, 2009; Blandin & Purser, 2013). More recently, this region, which remained at a lower altitude than the neighbouring Andes, may have allowed 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).

In contrast to *Hyposcada*, *Megoleria* originated and remained at high elevation within the Central Andes. *Megoleria* diverged from *Oleria* + *Ollantaya* at around 14.0 Ma (95% HPD: 18.7–9.4), but split into only two partially sympatric species relatively recently at 2.2 Ma (95% HPD: 4.9–0.5). *Megoleria*, similar to *Hyposcada*, feeds on the plant family Gesneriaceae (Willmott & Freitas, 2006), whose high species richness in the mountain forests of the Northern Andes should provide ample opportunity for ecological speciation driven by adaptation to alternative host plants. Yet, similar to *Hyposcada*, *Megoleria* does not seem to have taken advantage of the switch.

Ollantaya diversified at high elevation in the Central Andes forming *O. canilla,* and *O. olerioides* and *O. aegineta*, which separated *c.* 8.7 Ma (95% HPD: 12.2–5.7). The Central Andean endemic *O. canilla* may have been unable to cross the WAP because of the low elevation of this area at that time. The subsequent diversification of the genus following the closure of the WAP corridor led to the dispersal of *O. olerioides* and *O. aegineta* throughout the high elevation Andes possibly due to the availability of potential host plants.

Oleria likely originated at mid or high elevation and our findings show that four distinct clades diverged almost simultaneously within a preferred altitudinal range (De-Silva *et al.*, 2010). The most species-rich clade, *makrena*, diverged from its sister clade, the *amalda* group at *c.* 7.9 Ma (95% HPD: 10.8–5.2) within the Central Andes. The *makrena*

Time slice 1: 25 - 15 Ma
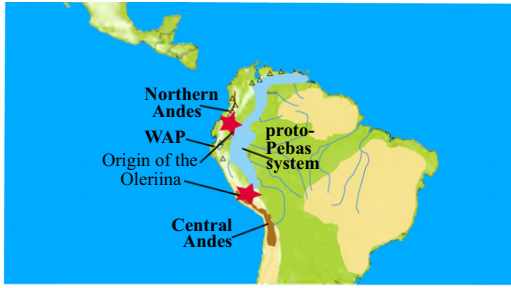
	A	B	C	D	E	F	G	H	I	J
A	-									
B	0.1	-								
C	0.01	0.25	-							
D	0	0.1	0.1	-						
E	0.01	0.5	0.25	0.1	-					
F	0.01	0.05	0.025	0.025	0.025	-				
G	0	0.025	0	0.01	0.01	0.25	-			
H	0	0.025	0.025	0.25	0.25	0.025	0.025	-		
I	0	0.01	0.1	0.5	0.1	0.01	0.01	0.5	-	
J	0	0	0	0.25	0	0	0.025	0.25	0.5	-

Time slice 2: 15 - 11 Ma

	A	B	C	D	E	F	G	H	I	J
A	-									
B	0.1	-								
C	0.01	0.25	-							
D	0	0.01	0.1	-						
E	0.01	0.05	0.025	0.1	-					
F	0.01	0.05	0.01	0.01	0.25	-				
G	0	0.025	0	0	0.01	0.1	-			
H	0	0.025	0.25	0.25	0.025	0.01	0.025	-		
I	0	0.01	0.1	0.5	0.01	0	0.01	0.5	-	
J	0	0	0	0.25	0	0	0.025	0.25	0.5	-

Time slice 3: 11 - 7 Ma

	A	B	C	D	E	F	G	H	I	J
A	-									
B	0.25	-								
C	0.01	0.05	-							
D	0	0.025	0.25	-						
E	0.01	0.05	0.5	0.25	-					
F	0.01	0.05	0.01	0.1	0.5	-				
G	0	0.05	0.01	0	0.05	0.5	-			
H	0	0.025	0.05	0.5	0.05	0.05	0.025	-		
I	0	0.01	0.025	0.5	0.025	0.025	0.01	0.5	-	
J	0	0	0	0.25	0	0	0.025	0.25	0.25	-

Time slice 4: 7 Ma - Present

	A	B	C	D	E	F	G	H	I	J
A	-									
B	0.5	-								
C	0.025	0.01	-							
D	0.01	0.01	0.025	-						
E	0.025	0.05	0.05	0.1	-					
F	0.025	0.05	0.01	0.01	0.5	-				
G	0.025	0.05	0.01	0.01	0.25	0.5	-			
H	0.01	0.025	0.05	0.5	0.05	0.05	0.05	-		
I	0	0.01	0.025	0.5	0.025	0.025	0.025	0.5	-	
J	0	0	0	0.25	0	0	0.05	0.25	0.5	-

Legend

Origin of:
- ★ Oleriina
- ★ *Hyposcada*
- ★ *Megoleria*
- ★ *Ollantaya*
- → Major dispersal
- ★ Diversification event

- ● *makrena*
- ● *onega*
- ● *amalda*
- ● *aegle*
- ∫ River

- ▨ Mountains/hills
- ▨ Upland area
- ▨ Lowland area
- ▨ Lake/wetland
- ▨ Ocean

Western Andean Portal (WAP)   **Vaupes Arch**   **Pebas Wetland System**
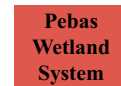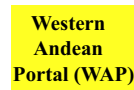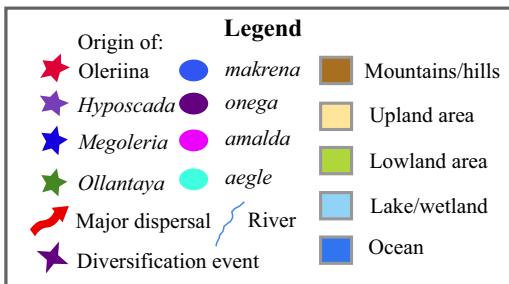
Dispersal rates:

0.5 = areas are contiguous; 0.25 = two areas separated by another; 0.1 = two areas are separated by two additional areas or by one other and a shift in elevation is required; 0.1 = elevation shift required; 0 = dispersal not possible.

Figure 2 Palaeogeographical model used in the dispersal-extinction-cladogenesis analyses of biogeographical events. The four time slices used in the analyses and dispersal rates for each biogeographical 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 north-west Peru; (C) Venezuelan Highlands including the Cordillera de Mérida and Cordillera de la Costa; (D) Guiana Shield; (E) north-east Colombian Andes; (F) Northern Andes including Ecuador and the central & western Colombian Cordilleras; (G) Central Andes; (H) western Amazonia; (I) central and eastern Amazonia; (J) Atlantic region including the Atlantic Forest and Cerrado.

group radiated rapidly at mid to high elevation (> 750 m) during the Late Miocene and Pliocene between 7–3 Ma and separated into two clades. Within the first *makrena* clade, the sister species, *O. boyeri* and *O. deronda* have a disjunct distribution with the former endemic to the Guiana Shield and the latter occurring along the eastern slopes of the Central Andes (see Appendix S2), a pattern also observed in other butterfly species (Blandin & Purser, 2013). It is plausible that the demise of the Acre System from 7 to 5 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 palaeoarch 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 Ecuador-Colombia (Area F) 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 *c.* 5.4 Ma (95% HPD: 8.0–3.7) 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 *c.* 3 Ma (Coates *et al.*, 2003) in the diversification of some groups (Webb, 2006) is controversial (Baker *et al.*, 2014; Montes *et al.*, 2015), 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 *c.* 1.8 Ma (95% HPD: 2.8–0.9) and are confined to the east and west slopes of the north-east Colombian Andes/Ecuador-Colombia (Area F) respectively. Their divergence is coincident with the final uplift of the north-east Colombian Andes *c.* 5–2 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 formation of some sympatric sister species, including *O. athalina*/*O. fasciata* and *O. attalia*/*O. cyrene*. *Oleria victorine* has a disjunct distribution and, unlike other *Oleria*, has colonized large swathes of the Neotropics from the Venezuelan Cordilleras to the Atlantic Forest. Causes for this unusually wide distribution are unknown, but expansion in larval diet breadth could have provided opportunities for colonization of new habitats.

The less diverse *amalda* species group diversified in the Central Andes or Ecuador-Colombia (Area F), but, in contrast to the *makrena* group, this occurred at low elevation. The *amalda* group has two allopatric subclades, an Amazonian clade that colonized the eastern slopes of the Central and Northern Andes and Amazonia, and a trans-Andean clade that diversified along the western slopes of the Andes and Ecuador-Colombia (Area F) before dispersal into Central America. The distribution of these clades suggests that their low altitude common ancestor crossed the Andes in the region of the WAP around 6.4 Ma (95% HPD: 8.9–4.1) before the WAP attained sufficient altitude to prevent further dispersal. This provided an alternative dispersal route and further opportunities for diversification of the group.

The *onega* group diversified in lowland forest habitats of western Amazonia mainly during the Late Miocene and Pliocene. Their diversification coincides with the disappearance of Lake Pebas and contraction of the Acre System, which are likely to have acted as dispersal barriers between the Andes and Amazonia (Wahlberg & Freitas, 2007; Antonelli *et al.*, 2009; Hoorn & Wesseling, 2010). The eastward development of terra firme rainforests prompted dispersal of a relatively high number of species into eastern Amazonia, the Guiana Shield and Atlantic region (see Appendix S2). However, low diversity of the host plant, Solanaceae, within these regions (Knapp, 2002) may have precluded further diversification driven by adaptation to alternative host plants. Indeed, forest productivity is higher on nutrient-rich western Amazonian soils, in contrast to the nutrient-poor soils of the eastern Amazon (Hoorn *et al.*, 2010). Further diversification within the monotypic *O. aegle* group in eastern Amazonia and the Guianas may also have been limited by the availability of larval host plants as has been noted with other ithomiine genera in this region (Elias *et al.*, 2009). Several instances of sympatric *onega* group sister species within western Amazonia suggests that fine-scale ecological adaptation, such as specialization on different but related host plant species (Willmott & Mallet, 2004), might have been important in the diversification of this clade.
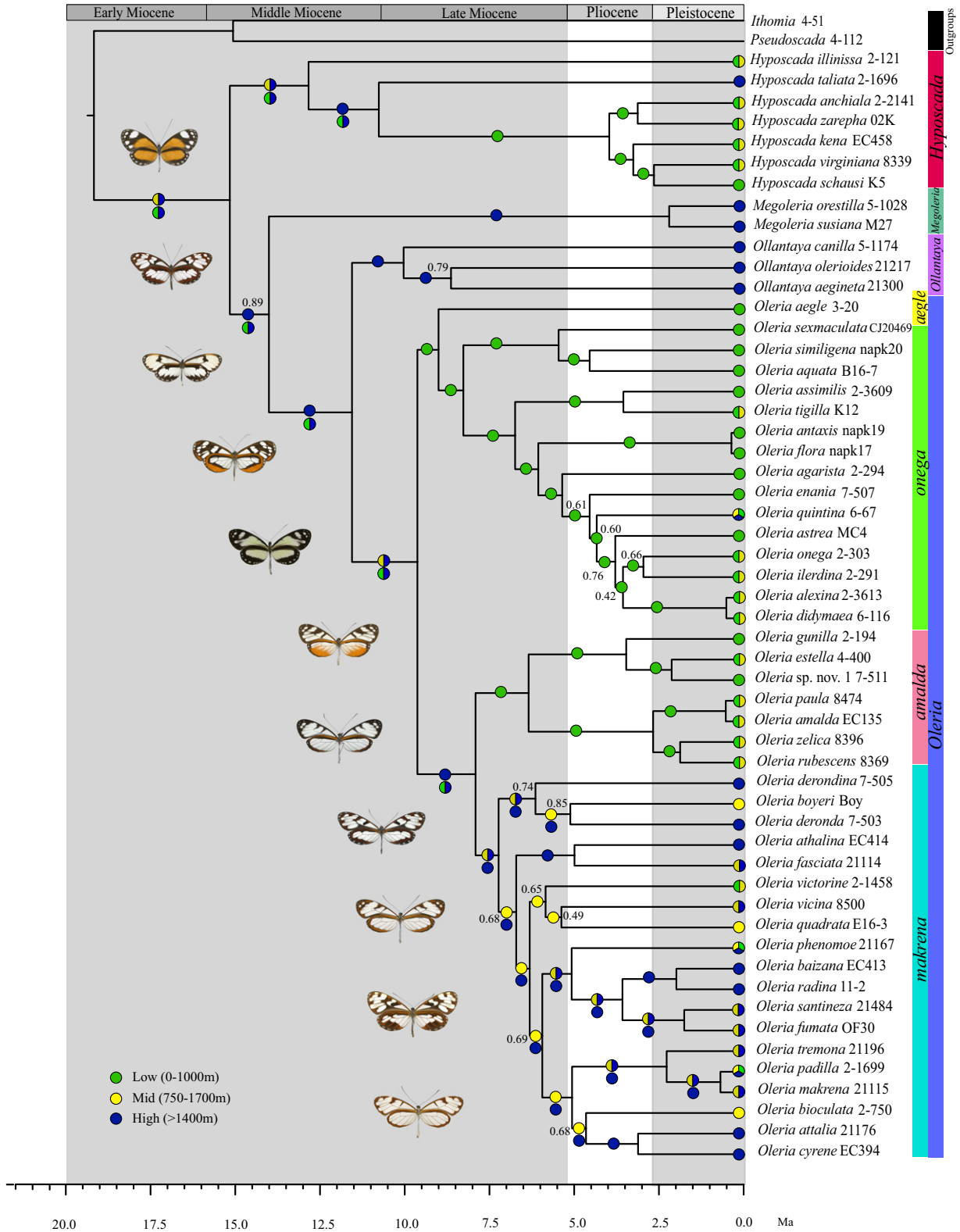
Figure 3 Bayesian dated maximum clade credibility tree for the Oleriina based on an uncorrelated log normal relaxed clock and detailing current and ancestral elevation ranges. Current elevation ranges are shown at the tips of the trees. ML inferred ancestral elevation ranges are shown for each node on 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 and photographs of Oleriina species are to the left. Elevation range categories are indicated in the legend.
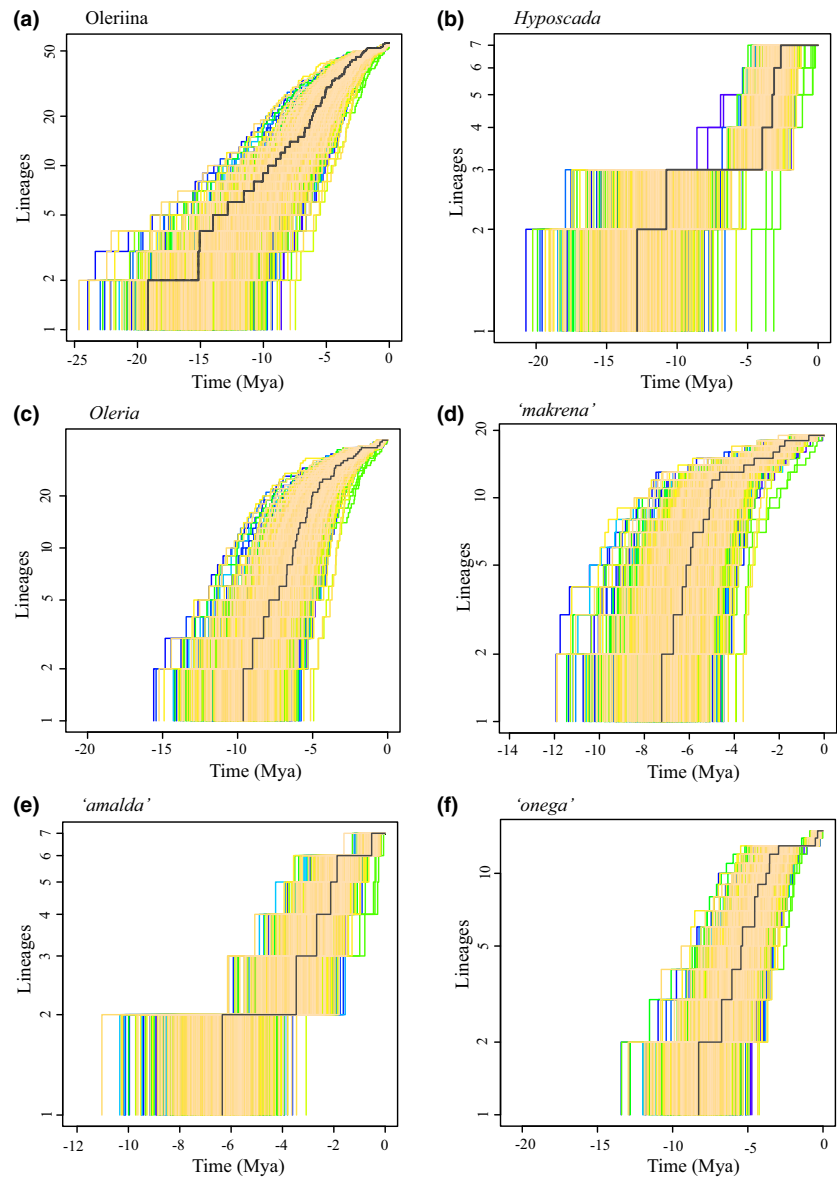
Figure 4 Lineage-through-time (LTT) plots based on 1000 sampled Bayesian trees for (a) Oleriina, (b) *Hyposcada*, (c) *Oleria*, (d) *makrena* species group, (e) *amalda* species group, (f) *onega* species group.

For the Oleriina, in general, distinct Northern Andean distribution patterns have emerged from our analyses. A remarkable number of species exist within Ecuador-Colombia (Area F), at all elevations, whereas only a few species have colonized the northeast Colombian Andes, of which only one, *Megoleria susiana,* is a strictly high elevation species; although there are a few instances of mid/high altitude species that have diversified within the last 2 Myr. Other species remain within the eastern Ecuadorian Andes or where the north-east Colombian Andes joins the western and central Colombian Cordilleras. This pattern is consistent with the geologically recent emergence of the north-east Colombian Cordillera and the appearance of cloud forests between 5 and 3 Ma (Kattan *et al.*, 2004). There are only three instances of dispersal as far as the Venezuelan Cordilleras, consistent with their emergence as recently as 3.5 Ma (Albert *et al.*, 2006). *Oleria phenomoe* is found only in this region,

suggesting the extinction of it or its sister species in Northern Andean ancestral areas. Dispersal into the Atlantic region has occurred rarely, but may have been via the Mato Grosso Arch, which linked the Central Andes to the Brazilian Shield perhaps from the Late Eocene (Hoorn & Wesseling, 2010), or via continuous forest cover which previously connected eastern Amazonia and the Atlantic Forest (Costa, 2003 and references therein). These regions are now linked by interconnecting forest patches through an otherwise open landscape, which may explain the presence of *O. aquata* within the north-eastern Caatinga and central Cerrado regions of the Brazilian Shield.

In general, changes in elevation occurred rarely in the Oleriina, as in other butterflies (Willmott *et al.*, 2001; Elias *et al.*, 2009; Chazot *et al.*, 2014). Butterflies are likely to be limited by physiological and ecological constraints, particularly among ithomiines where mimetic species often share

the same altitudinal niche (Chazot *et al.*, 2014). However, exceptions are found in some groups such as the riodinid butterfly genus *Ithomiola* that radiated across an elevational gradient in the Andes (Hall, 2005).

In summary, our results reveal that the Andean orogeny instigated and had a profound influence on the diversification of the Oleriina, in agreement with the ithomiine genera *Napeogenes* and *Ithomia* (Elias *et al.*, 2009), and other butterfly groups such as *Morpho* (Blandin & Purser, 2013), *Taygetis* (Matos-Maraví *et al.*, 2013) and *Lymanopoda* (Casner &

Pyrcz, 2010). The evolution of the Oleriina occurred when the Central Andes had attained at least 1000-1500 m (Garzione *et al.*, 2008). It is therefore unlikely that the uplift of the Andes was a direct driver of altitudinal diversification except perhaps in those species that occur at higher elevations of more than 2000 m that were attained more recently. The Oleriina apparently dispersed throughout the Andes and into newly available cis- and trans-Andean habitats when dispersal barriers such as the Acre System retreated and with the closure of the WAP. Our data support a clear role for the low lying WAP as a dispersal corridor between northern Peru and the eastern and/or western slopes of the Ecuadorian Andes. It also acted as a temporary barrier for higher elevation species. The Colombian Cordilleras Occidental and Central were probably connected to the Ecuadorian Andes a long time before the uplift of the Cordillera Oriental and this may provide an explanation for the continuity of many species ranges from the eastern Ecuadorian slopes to the Occidental and Central Cordilleras. The Andes formed a barrier causing vicariant speciation in some instances and the geologically recent uplift of the Colombian Cordillera Oriental helped to foster the rapid radiation of the *Oleria makrena* species group. Much of the Oleriina diversity remained within the Andes, but our findings suggest the Andes also acted as a source for lowland lineages.

Table 2 Tests of ancestral states of altitudinal ranges (scored as a discrete trait) in different clades. Low (0–1000 m), Mid (750–1700 m), High (> 1400 m). Log-likelihood, AIC and the difference in AIC (ΔAIC) are shown. In each case, the best model/s (ΔAIC) is/are indicated in bold.

Clade	Model	Log lkd	Parameters	AIC	ΔAIC
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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Table 3 Maximum likelihood estimation of ancestral elevation range as a continuous trait for minimum and maximum elevation ranges. 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	ΔAIC	Scaling parameter
Minimum elevation range					
(κ) = 1	**−400.71**	**2**	**805.41**	**0**	**1**
(κ) = 0	−406.55	2	817.09	11.68	0
(κ) = estimated	−400.69	3	807.37	2	0.95
(δ) = 1	**−400.71**	**2**	**805.41**	**0**	**1**
(δ) = 0	−451.62	2	907.24	101.83	0
(δ) = estimated	**−400.52**	**3**	**807.04**	**1.63**	**0.68**
(λ) = 1	**−400.71**	**2**	**805.41**	**0**	**1**
(λ) = 0	−424.35	2	852.70	47.29	0
(λ) = estimated	−400.71	3	807.41	2	1
Maximum elevation range					
(κ) = 1	**−407.27**	**2**	**818.55**	**0**	**1**
(κ) = 0	−410.83	2	825.65	7.10	0
(κ) = estimated	**−407.06**	**3**	**820.12**	**1.57**	**0.84**
(δ) = 1	**−407.27**	**2**	**818.55**	**0**	**1**
(δ) = 0	−440	2	884	65.45	0
(δ) = estimated	−407.27	3	820.54	2	1.04
(λ) = 1	**−407.27**	**2**	**818.55**	**0**	**1**
(λ) = 0	−427.66	2	859.33	40.78	0
(λ) = estimated	**−406.86**	**3**	**819.71**	**1.17**	**0.98**

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SUPPORTING INFORMATION

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

Appendix S1 (a) List of specimens 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 and Methods, Results, References. (d) PARTITIONFINDER best substitution models.
Appendix S2. Distribution maps of the Oleriina species.

BIOSKETCH

Donna Lisa de-Silva is interested in understanding the patterns and processes involved in Neotropical diversification. Her work currently focuses on the ithomiine butterflies.

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

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