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

NICOLAS CHAZOT,*† KEITH R. WILLMOTT,‡ FABIEN L. CONDAMINE,§¶
DONNA LISA DE-SILVA,* ANDRÉ V. L. FREITAS,** GERARDO LAMAS,†† HÉLÈNE MORLON,‡‡
CARLOS E. GIRALDO,§§ CHRIS D. JIGGINS,¶¶ MATHIEU JORON,*** JAMES MALLET,†††
SANDRA URIBE‡‡‡ and MARIANNE ELIAS*
*Institut de Systématique, Évolution, Biodiversité, ISYEB – UMR 7205 – CNRS MNHN UPMC EPHE, Muséum national d'Histoire naturelle, Sorbonne Universités, 57 rue Cuvier CP50, F-75005 Paris, France, †Department of Biology, University of Lund, 223 62 Lund, Sweden, ‡McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA, §CNRS, UMR 5554 Institut des Sciences de l'Evolution (Université de Montpellier), Place Eugène Bataillon, 34095 Montpellier, France, ¶Department of Biological Sciences, University of Alberta, T6G 2E9 Edmonton, AB, Canada, **Departamento de Zoologia and Museu de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil, ††Museo de Historia Natural, Universidad Nacional de San Marcos, Lima, Peru, ‡‡IBENS, Ecole Normale Supérieure, UMR 8197 CNRS, Paris, France, §§Grupo de Investigación de Sanidad Vegetal, Universidad Católica de Oriente, Rionegro, Antioquia, Colombia, ¶¶Department of Zoology, University of Cambridge, Cambridge, UK, ***Centre d'Ecologie Fonctionnelle et Evolutive, CEFE, UMR 5175 CNRS – EPHE – Université de Montpellier – Université Paul Valéry Montpellier, 34293 Montpellier 5, France, †††Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA, ‡‡‡Universidad Nacional de Colombia, sede Medellín, Medellín, Colombia

Abstract

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

Correspondence: Nicolas Chazot, Fax: +33 1 40 79 56 79;
E-mail: chazotn@gmail.com

Introduction

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

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

Valentine (1967) coined the term 'species-pump', referring to the hypothesis that during warm periods mollusc species ranges increased (northward) while during colder periods, species went either to extinction or contracted into small, isolated populations in the remaining optimal areas ('pumps'). These populations were free to evolve independently, before expanding again during the following warm period and becoming sympatric 'species'. Later, Stebbins (1974) expanded this hypothesis to rainforest plants and Fjeldså (1994) applied the 'species-pump' concept to distributional patterns of tropical birds, proposing that climatically buffered Andean regions acted as a 'species-pump' that would 'pump' species generated in the Andes out to the Amazonian region. Fjeldså's (1994) 'species-pump' scenario therefore involves a complex combination of extinction, range contraction, speciation and colonization processes, which makes formal tests difficult to carry out. Importantly, this scenario was originally proposed to explain the species diversity of the Amazonian basin. These terms have later been used by other authors, but often with a different meaning that corresponds to only one or a few aspects of Fjeldså's (1994) scenario. For example, Sedano & Burns (2010) interpreted a high rate of dispersal from the Andes towards adjacent areas as a support for the 'species-pump' hypothesis (see also e.g. Antonelli & Sanmartin 2011). By contrast, Hutter *et al.* (2013) interpreted this hypothesis as a higher net diversification rate in a study designed to investigate Andean diversity. Hutter *et al.* (2013) therefore ignore the 'pumping out' mechanism originally proposed (see also e.g. Smith *et al.* 2007). In fact, the hypothesis of higher speciation rate is also referred to as the 'cradle' hypothesis, often used to explain large patterns of latitudinal gradient of diversity (e.g. Arita & Vázquez-Domínguez 2008; Rolland *et al.* 2014).

A similar confusion occurs with the so-called time-for-speciation and museum hypotheses. Stebbins (1974) proposed that the angiosperm 'centres of diversity' are the result of low disturbance and therefore low extinction rates that lead to museum-like areas with high species diversity and 'primitive' lineages. Stephens & Wiens (2003) used the term 'time-for-speciation' when referring to a process where a specific region was colonized earlier than other ones by a clade, therefore giving more time for diversification. Confusion arose when some authors used the term 'museum' to describe areas that were colonized early and had more time to accumulate species (e.g. Hutter *et al.* 2013; Smith *et al.* 2007), whereas other authors, such as Arita & Vázquez-Domínguez (2008), considered the tropics as a museum if 'origination rate is constant and extinction rate is lower in the tropics' (see also e.g. Chown & Gaston 2000; Condamine *et al.* 2012).

In this study, we propose a framework of four biogeographic scenarios, which are clarified in terms of mechanisms and expectations. The four scenarios rest on the four main evolutionary processes proposed to

explain spatial patterns of biodiversity: speciation, extinction, age of colonization and migration. These four mechanisms are not mutually exclusive but each of them relies on the variation of only one of the following parameters: speciation rate, extinction rate, age of first colonization and colonization rate (Fig. 1). Here, we apply this framework to investigate variation in diversity between Andean and non-Andean regions, but this framework may be used to investigate patterns of diversity among any set of regions. Our hypotheses are as follows:

1 *Cradle*. Andean lineages speciate faster than non-Andean lineages, leading to a rapid accumulation of species over time (Fig. 1a). Indeed, the Andes offer conditions potentially favourable to speciation. The uplift of the different cordilleras generated major barriers to dispersal for many organisms, favouring allopatric divergence. In addition, the slopes of the Andes also display a strong topological heterogeneity, with deep valleys creating further opportunities for geographic divergence (Graham *et al.* 2004; Hughes & Eastwood 2006). Ecological divergence is also

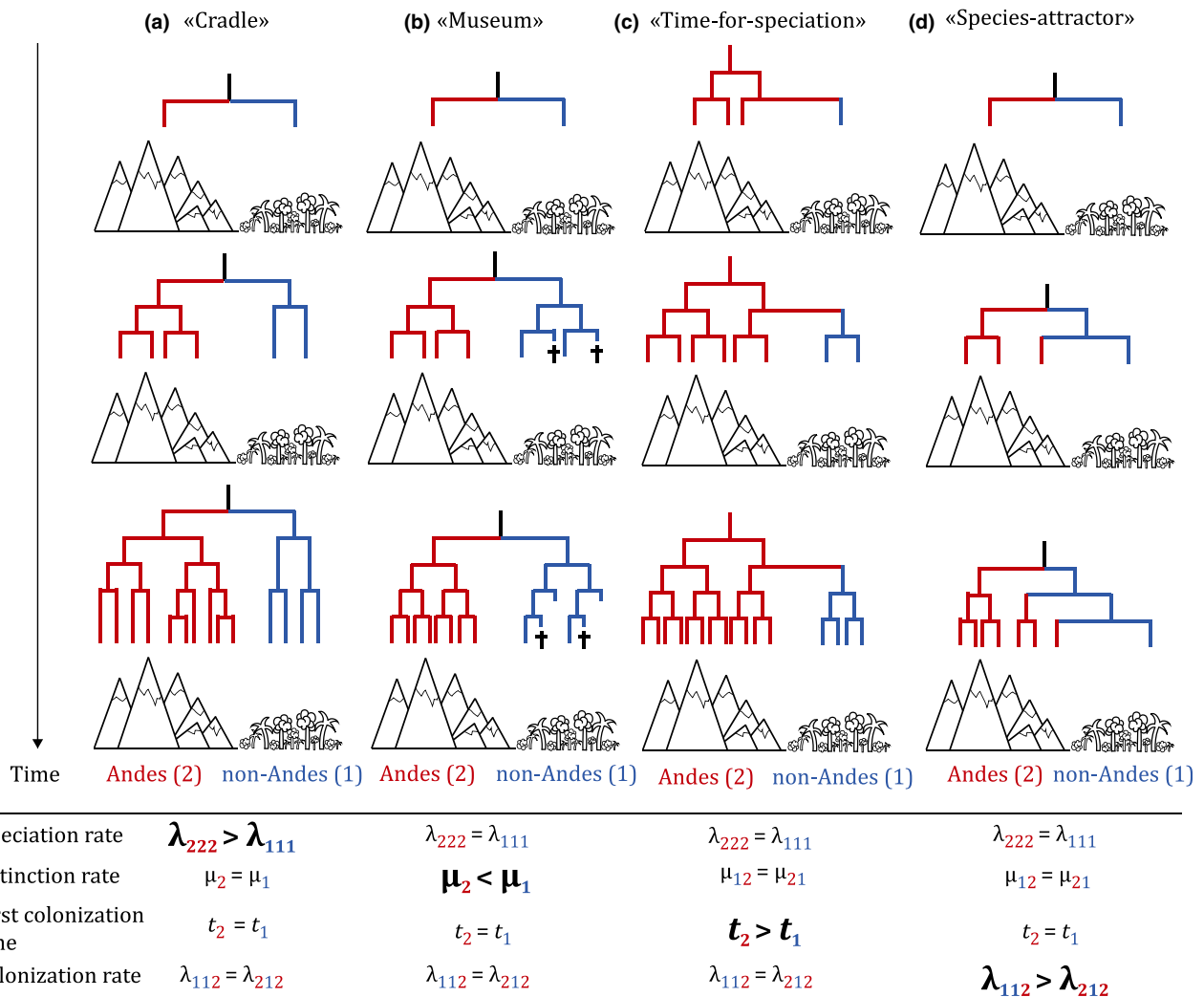|	(a) «Cradle»	(b) «Museum»	(c) «Time-for-speciation»	(d) «Species-attractor»
	Andes (2) non-Andes (1)	Andes (2) non-Andes (1)	Andes (2) non-Andes (1)	Andes (2) non-Andes (1)
Speciation rate	$\lambda_{222} > \lambda_{111}$	$\lambda_{222} = \lambda_{111}$	$\lambda_{222} = \lambda_{111}$	$\lambda_{222} = \lambda_{111}$
Extinction rate	$\mu_2 = \mu_1$	$\mu_2 < \mu_1$	$\mu_{12} = \mu_{21}$	$\mu_{12} = \mu_{21}$
First colonization time	$t_2 = t_1$	$t_2 = t_1$	$t_2 > t_1$	$t_2 = t_1$
Colonization rate	$\lambda_{112} = \lambda_{212}$	$\lambda_{112} = \lambda_{212}$	$\lambda_{112} = \lambda_{212}$	$\lambda_{112} > \lambda_{212}$

Fig. 1 Schematic representation of the four-hypothesis framework used to investigate the role of the Andes in diversification, and the parameters expected to vary in each hypothesis. Here, we present simple cases were only one parameter varies at a time, but all combinations of varying parameters can also be tested. (a) The 'cradle' hypothesis posits that speciation rate of Andean lineages exceeds that of non-Andean lineages ($\lambda_{222} > \lambda_{111}$). (b) The 'museum' hypothesis posits that extinction rates of the Andean lineages are lower than the non-Andean lineages ($\mu_2 < \mu_1$). (c) The 'time-for-speciation' hypothesis states that the Andes were colonized earlier than non-Andean regions ($t_2 > t_1$), resulting in a longer time for diversification. (d) The 'species-attractor' hypothesis states that the rate of colonization from non-Andean regions to the Andean regions is higher than *vice versa* ($\lambda_{112} > \lambda_{212}$). [Colour figure can be viewed at wileyonlinelibrary.com].

favoured because high turnover of bioclimatic conditions coupled with stratified vegetation types over small distances creates strong ecological gradients.

2 *Museum*. Andean lineages have undergone lower extinction rates than non-Andean lineages (Fig. 1b). Here, we follow Stebbins' original definition of the 'museum' hypothesis (Stebbins 1974).

3 *Time-for-speciation*. The timing of colonization events of the Andes might be older than the colonization of other areas and Andean lineages have thus had more time to accumulate species (Fig. 1c). This is the 'time-for-speciation' hypothesis *sensu* Stephens & Wiens (2003).

4 *Species-attractor*. The last hypothesis posits a higher dispersal and colonization rate into the Andes (Fig. 1d). This scenario has received less attention compared to the other hypotheses (but see Beckman & Witt 2015), but with the formation of the tropical Andes, the availability of newly formed ecosystems may have been accompanied by many independent colonization events. Indeed, vacant ecological niches, such as host plants in the case of oligophagous herbivores, could become occupied by multiple independent lineages. Under identical rates of diversification and time for speciation in Andean and non-Andean regions, multiple colonizations of the Andes could increase species richness in this region (Fig. 1d). Under this hypothesis, the Andes play the role of an 'attractor' for species and colonization rates towards the Andes from adjacent areas are predicted to be higher than the other way around.

Vertebrates, especially birds, prevail in most recent studies of patterns of Neotropical diversification (Weir 2006; Brumfield & Edwards 2007; McGuire *et al.* 2007, 2014; Sedano & Burns 2010; Chaves *et al.* 2011; Hutter *et al.* 2013; Castroviejo-Fisher *et al.* 2014; Fouquet *et al.* 2014; Beckman & Witt 2015; Lynch Alfaro *et al.* 2015; Parada *et al.* 2015; Dantas *et al.* 2016; Rojas *et al.* 2016). Despite their megadiversity and abundance, insects are poorly known in the Neotropics compared to vertebrates. Studies of diversification are often restricted to small groups or suffer from low sampling, taxonomic uncertainty or scarce distribution data. Therefore, attempts to generalize the processes explaining high Andean species richness described in the literature remain rare. Yet, insect clades offer the opportunity to add insights into our understanding of the macroevolutionary processes that shaped Andean biodiversity over time.

One of the best-known and most diverse groups of Neotropical insects is the butterfly tribe Ithomiini (Nymphalidae: Danainae). With *ca.* 47 genera and over 390 species (Lamas 2004) restricted to the Neotropical region, the group has diversified during the last 35 million years (Wahlberg *et al.* 2009). Ithomiini are known for their striking variety of wing patterns, and many groups include species with partially or entirely transparent wings. They are a major component of forest butterfly communities and interact through Müllerian mimicry among themselves and with other Lepidoptera such as *Heliconius* butterflies and arctiid moths (Beccaloni 1997). Three of the most diverse ithomiine genera, *Ithomia*, *Napeogenes* and *Oleria*, exhibit high species richness along the Andean slopes (Jiggins *et al.* 2006; Chazot *et al.* 2015). Of interest to our study, Elias *et al.* (2009) showed that the ithomiine genus *Napeogenes* (25 species), which has a higher diversity in the Andes, probably originated at middle elevations in the Andes and subsequently colonized the lowlands, therefore supporting the 'time-for-speciation' hypothesis. However, there is no indication that this pattern is common to the whole tribe Ithomiini. In this study, we focus on a more speciose Ithomiini clade, the subtribe Godyridina. The Godyridina includes 10 genera and 77 species distributed throughout the Neotropics. They also exhibit particularly high species richness in the Andes (46 species) compared to other Neotropical regions (Fig. 2). Here, we generated and compiled DNA sequences for 206 individuals to infer a time-calibrated molecular phylogeny that contained over 87% of species (67 of 77 species after making taxonomic changes where necessary). Combining historical biogeography, time- and trait-dependent diversification analyses, we applied the above framework to test the four non-mutually exclusive hypotheses proposed to explain Andean species richness: the 'cradle' hypothesis (higher speciation rate in the Andes), the 'museum' hypothesis (lower extinction rate in the Andes), the 'time-for-speciation' hypothesis (older colonization time in the Andes) and the 'species-attractor' hypothesis (higher rates of colonization towards the Andes from adjacent areas) (Fig. 1).

Materials and methods

Individual-level phylogenetic tree and redefinition of species boundaries

Defining species boundaries can be challenging, particularly in the case of mimetic butterflies (Elias *et al.* 2007), so we included as many species and subspecies as possible to represent taxonomic and geographic diversity (Appendix S1, Supporting information). We used material from our own collections (Florida Museum of Natural History, Museo de Historia Natural of Lima, Museu de Zoologia da Universidade de São Paulo, University College London, Muséum National d'Histoire Naturel of Paris) and material kindly provided by colleagues.
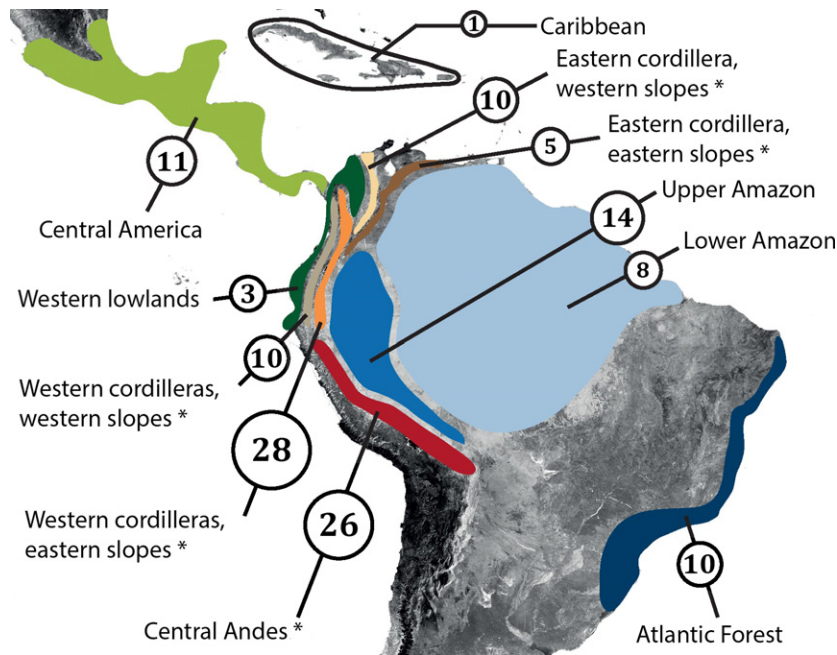
Fig. 2 Map showing the delimitation of biogeographic areas used in the DEC model for ancestral reconstruction and the number of species recorded in each biogeographic region. Stars (*) indicate the Andean areas. The western and eastern cordilleras (eastern and western slopes) constitute the Northern Andes. [Colour figure can be viewed at wileyonlinelibrary.com].

De novo (75%) and published sequences (25%) for three mitochondrial (cytochrome oxidase I, tRNAL, cytochrome oxidase II, 2356 base pairs (bp)) and two nuclear genes (elongation-factor alpha 1, 1260 bp and tektin, 734 bp) were compiled for 206 specimens (see Appendix S1–S2, Supporting information for PCR conditions and GenBank Accession nos.). We could not obtain sequences for 10 species. We added 44 outgroups representing most genera of the subfamily Danainae (Wahlberg *et al.* 2009) to our focal group sampling, for a total data set of 250 individuals. We concatenated all sequences, resulting in a total length of 4350 bp. The data set was then partitioned by gene and codon positions, and the best models of substitution for optimized sets of nucleotides were selected over all models implemented in MrBayes, using the 'greedy' algorithm and linked rates implemented in PARTITION-FINDER 1.1.1 (Lanfear *et al.* 2012). We performed a Bayesian inference of the phylogeny using MRBAYES 3.2.2 (Ronquist *et al.* 2012), allowing it to run for 10 million generations, with four Markov chain Monte Carlo that sampled every 10 000 generations (resulting in 1000 posterior trees). Although the monophyly of the Ithomiini was well established by previous studies (Freitas & Brown 2004; Brower *et al.* 2006, 2014; Willmott & Freitas 2006), it was not recovered in preliminary runs. We therefore constrained the tribe to be monophyletic in the MrBayes runs. We extracted the maximum clade credibility tree using the median of posterior distribution for node ages using TREEANNOTATOR 1.6.2 (Drummond *et al.* 2012) and applied a 20% burn-in. The resulting tree was used to investigate the established taxonomy in the light of our molecular data and to define species to be included in the species-level phylogeny and in subsequent analyses (Appendix 1, Appendix S1–S3, Supporting information).

Species-level phylogeny

To generate a species-level phylogeny of the Godyridina, we used the consensus of concatenated sequences of all individuals belonging to the same species, after redefining species boundaries where applicable (e.g. Condamine *et al.* 2012; Lewis *et al.* 2015; see Appendix 1). We obtained a data set of 67 species of 77 extant Godyridina species (after our revision of species boundaries), which we combined with the sequences of the 44 outgroups used previously. To select the best partition scheme, we used PARTITIONFINDER (Lanfear *et al.* 2012) as before, but tested only the models implemented in BEAST (Drummond *et al.* 2012). First, we generated a maximum likelihood tree using IQ-TREE 1.3.11 (Nguyen *et al.* 2015). We implemented the best partition scheme previously found and performed 1000 ultra-fast bootstrap iterations to get node support (Minh *et al.* 2013). The ML tree is available in Appendix S4 (Supporting information). Second, a

time-calibrated phylogeny was generated using BEAST 1.6.2 (Drummond *et al.* 2012). Following preliminary runs, we implemented a uniform prior for the substitution model of the mitochondrial third position. We selected nine secondary calibration points based on the shared nodes with the phylogeny of Nymphalidae from Wahlberg *et al.* (2009) (Appendix S5, Supporting information). We used conservative uniform priors for secondary calibrations, with upper and lower bounds corresponding to the 95% credibility intervals inferred in Wahlberg *et al.* (2009). We tested the effect of calibrating or not the root of the tree, and of using both Yule process and birth–death process as the branching process prior. This resulted in four independent runs of BEAST. Each run was performed for 30 million generations, sampled every 30 000 generations, resulting in 1000 trees. For each run, the maximum clade credibility tree using the median of posterior distribution for node ages was extracted using TREEANNOTATOR (Drummond *et al.* 2012), applying a 20% burn-in. As differences in node ages between the four independent runs were below two million years, we only used the root-unconstrained and Yule process as the branching process prior in subsequent analyses (Appendix S6–S7, Supporting information).

Historical biogeography

To infer the ancestral colonization events of the Andes, we performed an ancestral reconstruction of biogeographic regions on the maximum clade credibility tree. We used the Dispersion–Extinction–Cladogenesis (DEC) model (Ree & Smith 2008) implemented in the R package BIOGEOBEARS 0.2.1 (Matzke 2014). We did not test the effect of founder-event speciation because this method applies to island-dwelling clades. We defined ten biogeographic regions (Fig. 2) based on the main geological events that occurred in the Cenozoic (Hoorn *et al.* 2010) and previous publications (Elias *et al.* 2009; Condamine *et al.* 2012; Lewis *et al.* 2015). We first ran a model constraining only the connectivity among adjacent areas (see Appendix S8, Supporting information). Secondly, we specified unequal rates of dispersal between areas and time stratification of dispersal rate in BioGeoBEARS: we defined four time bins (0–5, 5–8, 8–14, 14–20 million years ago) and for each of them we specified dispersal multipliers. The time bins and dispersal multipliers were designed to account for the arguably major geological events such as the closure of the Panama Isthmus, the south-to-north uplift of the Andes, the closure of the Western Andean Portal, the retreat of the Pebas System and the creation of *terra firme* forest in the upper Amazon (Appendix S8, Supporting information). Distributional data for Godyridina species were obtained from fieldwork, literature and museum collections. Each species was assigned to biogeographic areas based on their current known distribution combined with data on their altitudinal distribution. We allowed for up to 6 areas to form an ancestral geographic range.

Trait-dependent diversification

Using trait-dependent models of diversification, we tested whether (i) increased speciation rates in the Andes ('cradle'), (ii) lower extinction rate in the Andes ('museum'), (iii) longer colonization rate ('time-for-speciation') or (iv) higher rates of colonization of the Andes ('species-attractor') explain the pattern of higher species richness in the Andes (Fig. 1). We classified species into either Andean or non-Andean regions, based on their current known distributions. We fitted Cladogenetic State-dependent Speciation and Extinction models (ClaSSE, Goldberg & Igic 2012) implemented in the DIVERSITREE 0.9-7 R package (FitzJohn 2012), which estimates speciation rates, extinction rates and transition rates of multiple states of a trait (here, the Andean or non-Andean distribution). Specifically, this model allows both cladogenetic (at nodes) and anagenetic (along branches) character changes. For a two-state character, the model accounts for up to six speciation rates, two extinction rates (μ_2, μ_1) and two anagenetic transition rates (q_{12}, q_{21}). Two speciation rates account for speciation events without character state change (λ_{222}, λ_{111}). Two other rates account for speciation accompanied by character state change of one of two descendant species (λ_{112}, λ_{212}) and the last two speciation rates account for cases where speciation involved character state change of the two descendant species (λ_{122}, λ_{211}) (cladogenetic character changes in the two latter cases (Goldberg & Igic 2012; Rolland *et al.* 2014). We used the ClaSSE rather than the Geographic State change Speciation and Extinction model (GeoSSE, Goldberg *et al.* 2011) because Andean species are typically not present outside of the Andes (and reciprocally). To avoid overparametrization of the models, we imposed several constraints on the models by excluding parameters that are not meaningful in terms of biogeographic events. Similarly to Rolland *et al.* (2014), we constrained to zero speciation rates involving simultaneous character state change in the two descendant species. We also constrained to zero the anagenetic transition rates because we considered that transition from one region to another was accompanied by a speciation event. Transitions between regions were therefore modelled by the parameters λ_{112} and λ_{212}. We tested for all possible combinations of models, constraining or not speciation, extinction and transition rates to be equal among states. Therefore, we ended up with 10 models, which

were fitted on 300 trees randomly sampled from the posterior distribution, accounting for incomplete sampling in each region (Andean: 88%, non-Andean: 90%). Models were compared using corrected Akaike information criterion scores (AICc). The strength of the ClaSSE model is that it allows simultaneously testing of the nonmutually exclusive 'cradle', 'museum' and 'species-attractor' hypotheses.

To test the 'time-for-speciation' hypothesis, we needed to infer ancestral state for each node, which is not currently implemented in ClaSSE models. Therefore, we fitted the Binary State Speciation and Extinction model (BiSSE, FitzJohn 2012) equivalent to the best-fitting ClaSSE model on the maximum clade credibility tree, which fits anagenetic instead of cladogenetic changes, and confirmed that parameter values inferred from BiSSE were consistent with those inferred from ClaSSE. This allowed us to estimate the probabilities of ancestral states at each node. Finally, we used this ancestral state reconstruction to represent the accumulation (speciation and colonization events through time) of Andean and non-Andean lineages.

Time-dependent diversification

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

Results

Phylogenetic tree and taxonomical revisions

The individual-level phylogeny of Godyridina was generally well supported, except for the positions of *Greta clavijoi* and for relationships within the clade containing

the genera *Brevioleria, Mcclungia, Pachacutia* and some *Hypoleria* species (Appendix S3, S4, S7, Supporting information). Based on the relationships between individuals in this phylogeny, reassessment of morphological characters in some cases and distributional data, we re-evaluated the current species and genera status and propose a number of formal and informal taxonomic changes (Appendix 1, Appendix S1–S3, Supporting information).

Estimates of divergence times and historical biogeography

Based on the secondary calibrations from Wahlberg *et al.* (2009), the subtribe Godyridina was inferred to be 17.08 million years old (95% highest posterior density: 14.99–19.16 million years) (Appendix S6, Supporting information). Based on our biogeographic reconstructions, the most likely ancestral areas were the Central Andes for the *Velamysta*/*Veladyris* clade and the upper Amazon for the remaining ingroup (Fig. 3). The inference at the root was not well resolved. Then diversification occurred in three main areas: Central Andes where the *Veladyris*, *Velamysta* and *Godyris* diversified, the western cordillera of Northern Andes where the *Hypomenitis* diversified, and the upper Amazon in which the *Brevioleria*, *Hypoleria*, *Mcclungia*, *Pachacutia* and *Heterosais* diversified (Fig. 3). The genera *Velamysta* and *Veladyris* originated in the Central Andes and have slowly accumulated species in this region. From 15 to 10 million years ago, four speciation events occurred in the upper Amazon, a region partly covered during this period by the Pebas System, a complex semi-aquatic ecosystem, which even occasionally transformed into marine environment (Hoorn *et al.* 2010; Wesselingh *et al.* 2010; Blandin & Purser 2013; Boonstra *et al.* 2015). As there were probably emergent lowlands, especially along the eastern side of the Andes, we did not forbid dispersal into this region and instead allowed a low dispersal probability. One of these early lowland lineages started diversifying intensively in the upper Amazon from around 8 million years ago, after the drainage of the Pebas, leading to the clade currently grouping *Hypoleria* and the *Brevioleria* clade. A major colonization event of the Northern Andes occurred around 10 million years ago, subsequently giving birth to the entire *Hypomenitis* clade (largely distributed in the Western cordillera). Around 4–5 million years ago, another colonization of the Andes occurred in the genus *Godyris*, followed by local diversification. We also recovered several independent colonizations of the Andes on terminal or subterminal branches, mainly in the Northern Andes. The clade formed by *Pseudoscada* and Genus2 had a much more complex spatial diversification history.
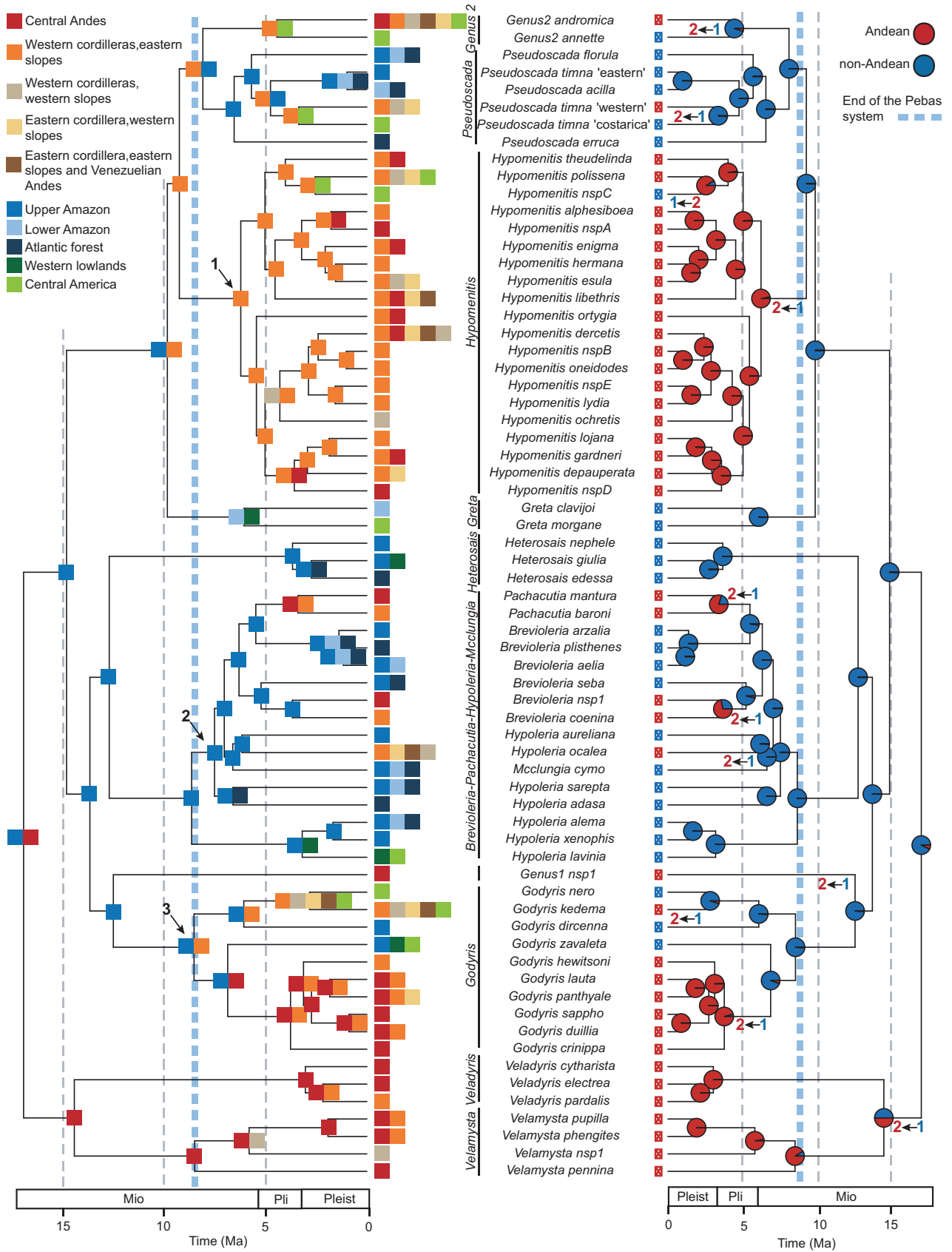
Fig. 3 Time-calibrated tree of the Godyridina. On the left, the most likely ancestral areas inferred using the DEC model implemented in BioGeoBEARS are represented. On the right, the probabilities for each node of being Andean (red) or non-Andean (blue) are represented. This ancestral reconstruction was obtained from the best-fitting model of character state-dependent diversification (ClaSSE analysis, see text). Numbers on the left panel indicate the three subclades for which we tested a shift in diversification rate: 1-*Hypomenitis*, 2-*Brevioleria* clade: *Brevioleria, Hypoleria, Mcclungia, Pachacutia*, 3-*Godyris*. On the right panel, colonization events are represented (2←1: non-Andean towards Andean area, 1←2: Andean towards non-Andean region). *Pleist = Pleistocene, Pli = Pliocene, Mio = Miocene.*

Secondary colonizations of lowlands were inferred in the western part of the Andes for some species and in the eastern part for others. This group now occurs from Central America to the Brazilian Atlantic forest region. Generally, Central America and Brazilian Atlantic forest faunas were the result of several independent colonizations, with very few within-region diversification events.

Trait-dependent diversification

Two models of trait-dependent diversification were found within an interval of 2 AICc scores. The model with the lowest AICc score had three parameters: a unique speciation rate for Andean and non-Andean lineages ($\lambda = 0.158$), and two significantly different cladogenetic transition rates (Table 1). Transitions from non-Andean to Andean areas ($\lambda_{112} = 0.060$) were 10-fold more frequent than from the Andes to non-Andean areas ($\lambda_{212} = 0.005$), as expected under the 'species-attractor' hypothesis (Table 1). The second best-fitting model involved two different transition rates (values similar to those of the best model, Table 1) and also two different speciation rates among the two regions. Speciation rate in the Andes ($\lambda_{222} = 0.176$) was slightly higher than in non-Andean regions ($\lambda_{111} = 0.140$). The latter result is expected under the 'cradle' hypothesis. For these two best models, we fitted the equivalent BiSSE model on the MCC tree and estimated the probabilities of character states at each node. Both reconstructions gave identical results and we only represent the reconstruction based on the best model (Fig. 3). The root was inferred to be non-Andean (Fig. 3), rejecting the 'time-for-speciation' hypothesis. Major colonizations of the Andes followed by diversification occurred three times, leading to the *Veladyris/Velamysta* clade, part of the genus *Godyris*, and the genus *Hypomenitis*. In addition, six colonization events on terminal branches were recovered, totalling nine independent colonizations of the Andes. Conversely, we only found one colonization event from the Andes towards a non-Andean region (*Hypomenitis* nspC in Central America, Fig. 3). The ancestral state reconstruction based on a trait-dependent model of diversification was very congruent with the reconstruction based on the biogeographic model. Finally, lineage accumulation through time showed that speciation of non-Andean lineages slowed down around 6 million years ago (Fig. 4). Almost half of non-Andean speciation events (12 of 27) occurred in a time frame of 3 million years (between 9 and 6 million years ago). By contrast, Andean lineages intensively accumulated in the last 7 million years (Fig. 4) through either speciation or colonization.

Time-dependent diversification

The model with four distinct diversification dynamics (*Brevioleria* clade, *Hypomenitis*, *Godyris* and the remaining backbone) was significantly better supported than the others (Table 2). The mainly non-Andean *Brevioleria* clade followed a model of decreasing speciation rate through time with an initial rate of speciation higher than that of the backbone at the same period followed by an inflexion starting about 6 million years ago (Fig. 4a). The mainly Andean *Godyris* and *Hypomenitis* genera followed a constant speciation rate model, with a speciation rate higher than that of the backbone (*Godyris*: 0.190, *Hypomenitis*: 0.226, backbone: 0.128). Models with extinction had a significantly worse fit than models without extinction (Table 2).

Discussion

In this study, we propose a revision of the systematics of the ithomiine subtribe Godyridina, using a comprehensive sampling of individuals that includes new undescribed species. Based on this revision, we infer the first time-calibrated species-level phylogeny of this subtribe. Our time calibrations are secondary calibrations based on the time-calibrated tree of Nymphalid genera (Wahlberg *et al.* 2009). Apart from *Veladyris* and *Velamysta*, which feed on *Solanum* (Greeney *et al.* 2009) and *Cuatresia* (Willmott, unpublished data), respectively, all Godyridina species feed almost exclusively on *Cestrum* species (Solanaceae) (Willmott & Freitas 2006), which they do not share with any other ithomiine groups. In a recent phylogenetic study of the entire family Solanaceae, *Cestrum* is inferred to have diversified in the last 7 million years (Särkinen *et al.* 2013), which is younger than our estimates for Godyridina diversification (14.9 ± 2 million years ago excluding *Veladyris* and *Velamysta*). Thus, we cannot exclude the

Table 1 Models and results of the ClaSSE analysis run over 300 trees randomly sampled from the posterior distribution (mean values are given), ordered by increasing AICc. Constraints of each model are indicated in the four-first columns. 1 = non-Andean, 2 = Andean, $\lambda_{111}/\lambda_{111}$ = within-region speciation rates, $\lambda_{112}/\lambda_{212}$ = cladogenetic transition rates, μ = extinction rates, d.f. = degree of freedom (number of parameters), logL = log-likelihood, AICc = Akaike information criterion score corrected for sample size, ΔAICc = difference between the model and the best-fitting model. Anagenetic transition rates and cladogenetic transition rates involving a character state change in both descendent lineages were constrained to 0 and are therefore not included in the table. The two first models are retained (models with ΔAICc < 2)

| $\lambda_{111}/\lambda_{222}$		$\lambda_{112}/\lambda_{212}$	μ	d.f.	logL	AICc	ΔAIC	λ_{111}	Λ_{222}	Λ_{112}	λ_{212}	μ_1	μ_2
$\lambda_{111} = \lambda_{222}$	$\neq$	$\lambda_{112} \neq \lambda_{212}$	$\mu_1 = \mu_2$	4	−209.175	426.996	0	0.158	0.158	0.061	0.005	2.7E-06	2.7E-06
$\lambda_{111} \neq \lambda_{222}$	$\neq$	$\lambda_{112} \neq \lambda_{212}$	$\mu_1 = \mu_2$	5	−208.813	428.610	1.614	0.141	0.176	0.060	0.005	6.8E-07	6.8E-07
$\lambda_{111} = \lambda_{222}$	$\neq$	$\lambda_{112} \neq \lambda_{212}$	$\mu_1 \neq \mu_2$	5	−209.142	429.268	2.272	0.162	0.162	0.058	0.005	0.013	4.6E-07
$\lambda_{111} = \lambda_{222}$	$\neq$	$\lambda_{112} = \lambda_{212}$	$\mu_1 = \mu_2$	3	−212.167	430.715	3.720	0.155	0.155	0.035	0.035	5.3E-07	5.3E-07
$\lambda_{111} \neq \lambda_{222}$	$\neq$	$\lambda_{112} \neq \lambda_{212}$	$\mu_1 \neq \mu_2$	6	−208.813	431.026	4.030	0.141	0.176	0.060	0.005	1.6E-05	2.6E-06
$\lambda_{111} \neq \lambda_{222}$	$\neq$	$\lambda_{112} = \lambda_{212}$	$\mu_1 = \mu_2$	4	−211.647	431.939	4.944	0.132	0.175	0.036	0.036	7.5E-07	7.5E-07
$\lambda_{111} = \lambda_{222}$	$\neq$	$\lambda_{112} = \lambda_{212}$	$\mu_1 \neq \mu_2$	4	−212.039	432.723	5.727	0.165	0.035	0.165	0.035	0.032	6.7E-07
$\lambda_{111} \neq \lambda_{222}$	$\neq$	$\lambda_{112} = \lambda_{212}$	$\mu_1 \neq \mu_2$	5	−211.647	434.279	7.283	0.132	0.175	0.036	0.036	6.4E-06	4.1E-06
$\lambda_{111} = \lambda_{222}$	$=$	$\lambda_{112} = \lambda_{212}$	$\mu_1 = \mu_2$	2	−223.265	450.717	23.721	0.095	0.095	0.095	0.095	1.0E-06	1.0E-06
$\lambda_{111} = \lambda_{222}$	$=$	$\lambda_{112} = \lambda_{212}$	$\mu_1 \neq \mu_2$	3	−223.255	452.892	25.896	0.141	0.141	0.141	0.141	1.6E-05	2.6E-06
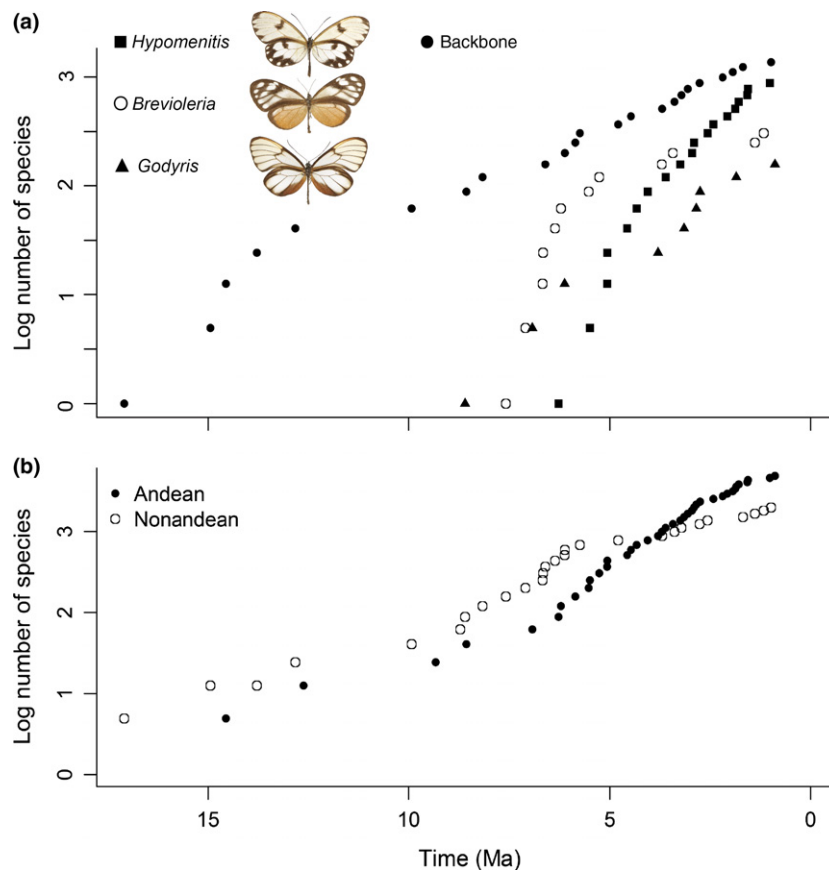
Fig. 4 (a) Lineage-through-time plots of the three subclades with diversification rate shifts (*Hypomenitis*, *Godyris* and *Brevioleria* clade) and for the remaining backbone. (b) Lineage-through-time plots of non-Andean and Andean lineages based on the ancestral reconstruction of trait-dependent diversification model. [Colour figure can be viewed at wileyonlinelibrary.com].

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

Shifts	Subtree	Model	Parameter	log L	p(LRT)	λ	α
Best model:	Backbone	BCST	1	−46.307		0.128	
Brevioleria clade + *Hypomenitis* + *Godyris*	*Brevioleria* clade	BVAR	2	−28.135		0.044	0.350
	Hypomenitis	BCST	1	−72.027		0.226	
	Godyris	BCST	1	−21.945		0.190	
	Total		5	−168.415			
Brevioleria clade + *Hypomenitis*	Backbone	BCST	1	−70.484		0.150	
	Brevioleria clade	BVAR	2	−28.135		0.044	0.350
	Hypomenitis	BCST	1	−72.027		0.226	
	Total		4	−170.647	0.0346		
Brevioleria clade + *Godyris*	Backbone	BCST	1	−120.654		0.187	
	Brevioleria clade	BVAR	2	−28.135		0.044	0.350
	Godyris	BCST	1	−21.945		0.190	
	Total		4	−170.734	0.0313		
Brevioleria clade	Backbone	BCST	1	−144.247		0.190	
	Brevioleria clade	BVAR	2	−28.135		0.044	0.350
	Total		3	−172.382	0.0189		
Whole tree		BCST	1	−175.429	0.0072	0.188	
Hypomenitis + *Godyris*	Backbone	BCST	1	−79.473		0.151	
	Hypomenitis	BCST	1	−72.027		0.226	
	Godyris	BCST	1	−21.945		0.190	
	Total		3	−173.445	0.0065		
Hypomenitis	Backbone	BCST	1	−103.383		0.162	
	Hypomenitis	BCST	1	−72.027		0.226	
	Total		2	−175.411	0.0029		
Godyris	Backbone	BCST	1	−153.325		0.188	
	Godyris	BCST	1	−21.945		0.190	
	Total		2	−175.270	0.0033		

hypothesis that Godyridina are younger than inferred here using secondary calibration points (Garzón-Orduña *et al.* 2015). However, the dating of the Solanaceae phylogeny was limited by the quality of available fossils, forcing the authors to downgrade taxonomic assignment of the fossils. This limitation, in combination with a strong prior on fossil ages, incurred a bias towards younger ages, as acknowledged by the authors of the study (Särkinen *et al.* 2013). The actual age of *Cestrum* is therefore likely older than the estimate of Särkinen *et al.* (2013), in better agreement with Wahlberg *et al.* (2009)'s and our ages for the subtribe Godyridina.

The time-calibrated phylogeny was used to infer the geographic and temporal patterns of diversification of the butterfly subtribe Godyridina, which exhibits a higher species diversity in the Andes, a common ecological pattern in the Neotropics (Luebert & Weigend 2014). To evaluate historical explanations for this pattern of diversity, we explicitly tested four nonmutually

exclusive hypotheses: the 'cradle' hypothesis, the 'time-for-speciation' hypothesis, the 'museum' hypothesis and the 'species-attractor' hypothesis (Fig. 1). We found a strong support for the 'species-attractor' hypothesis in the Godyridina, suggesting an important role of multiple colonization events of the Andes. We also found moderate support for a slightly higher speciation rate within the Andes, which is confirmed by the detection of a shift towards higher speciation rates in two Andean genera, in agreement with the 'cradle' hypothesis.

The four hypotheses jointly tested in our study have received mixed support in the literature. Very few studies explicitly tested for higher speciation rate in the Andes (here referred to as the 'cradle' hypothesis). Hutter *et al.* (2013) used trait-dependent diversification models to understand mid-altitude species richness patterns in Andean glassfrogs. Because they divided the Andes into altitudinal bands, interpretations may be

oriented towards altitude-dependent diversification processes instead of Andean vs. non-Andean processes, but they found no support for a higher speciation rate in the Andes. Conversely, Beckman & Witt (2015), who applied an approach similar to ours in a study of New World goldfinches and siskins, found a higher speciation rate in the Andes. Plant groups have shown more evidence of increased rates of speciation associated with the colonization of the Andes, such as, *Lupinus* (Hughes & Eastwood 2006), *Astragalus* (Scherson *et al.* 2008), *Bromeliaceae* (Givnish *et al.* 2014), *Hedyosmum* (Antonelli & Sanmartin 2011). However, the diversification of highland flora may differ from that of the fauna, with, for example, an important role for long-distance dispersal and dispersal of pre-adapted temperate plant lineages from the Nearctic region.

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

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

The 'time-for-speciation' hypothesis, defined as a longer presence in the Andes (Stephens & Wiens 2003), has been supported in several studies (e.g. Santos *et al.* 2009). For instance, Hutter *et al.* (2013) showed that glassfrogs first originated at mid-altitudes and subsequently diversified at both higher and lower altitudes. An Andean origin followed by subsequent colonization of the lowlands was also reported in other Ithomiini lineages, such as the genera *Napeogenes* and *Ithomia* (Elias *et al.* 2009) and the subtribe Oleriina (De-Silva *et al.* 2016). In the Godyridina, the ancestral range inferred using two independent methods does not support an Andean origin. From our results, the subtribe likely originated in a non-Andean region, probably at the lowland interface between the Andes and the future upper Amazon. In addition, the oldest Andean clade, formed by the two sister genera *Veladyris* and *Velamysta*, underwent only moderate diversification (eight species when accounting for a new species of *Veladyris* from Peru not included in the phylogeny) despite the longer time available for speciation.

The 'species-attractor' hypothesis, which posits that the Andes offer opportunities for multiple independent colonization events, has rarely been tested explicitly but has been discussed in the literature. Rates of biotic exchange between regions have been estimated in some studies (e.g. Brumfield & Edwards 2007; Elias *et al.* 2009; Sedano & Burns 2010; Castroviejo-Fisher *et al.* 2014; Beckman & Witt 2015). In Ithomiini, Elias *et al.* (2009) and De-Silva *et al.* (2016) found higher rates of dispersal towards low altitudes, as did Beckman & Witt (2015) for goldfinches and siskins. In contrast, other studies found that dispersal towards the Andes is

generally more frequent, with a limited number of reversals. For instance, in the butterfly genus *Ithomiola* (Riodinidae: Mesosemiini), a small clade of 11 species, Hall (2005) showed that diversification within the group consisted of repeated speciation events across different altitudes, including several colonization events of the Andes from other areas. Hutter *et al.* (2013) also reported that the inferred number of colonization events of each altitudinal band by glassfrogs tends to correlate with species richness. Therefore, higher rates of colonization from lowlands may also have contributed to higher species richness in the Andes, but Hutter *et al.* (2013) did not explicitly test this hypothesis. In plants, Moonlight *et al.* (2015) found that the Andean diversity of *Begonia* arose from multiple dispersal events into the Andes, while Givnish *et al.* (2014) reported an important number of independent colonization events of high elevations areas in Bromeliaceae.

In the Godyridina, the inferred higher colonization rate of the Andes from non-Andean regions (a pattern that we refer to as 'species-attractor') was almost 10-fold higher than in the other direction. We identified up to ten independent events of colonization of the Andes, but only one for non-Andean colonization (Fig. 3). From our ancestral state reconstruction, we found that the accumulation of species in the Andean region accelerated during the very late Miocene, and mostly occurred during Pliocene and early Pleistocene periods through either colonization or speciation events, a time frame that corresponds to the most intense orogeny phase of the Andes (Hoorn *et al.* 2010). By contrast, most of the diversification of non-Andean lineages appears to have occurred by the end of the Miocene. The Andes could drive colonization and speciation in many ways, involving biotic factors, such as the availability of new habitats, new predator communities, host-plant diversity, and abiotic factors such as temperature, precipitation, environment heterogeneity and topography. It is also worth noting that the Andes, extending all along the western side of South America, provide ample opportunity for colonization on both sides of the cordilleras. Besides, from 20 to 10 million years ago, the semi-aquatic Pebas System covered most of the upper Amazon region, with even occasional marine incursions (Hoorn *et al.* 2010; Wesselingh *et al.* 2010; Blandin & Purser 2013). During this period, the Northern and Central Andes started to slowly increase in elevation (Hoorn *et al.* 2010). Sediment deposits from the Andes towards the east accompanied this uplift (Roddaz *et al.* 2010), and around 10 million years ago *terra firme* forest probably started to form. The Acre System and then the Amazon River were formed, and by 8 million years ago, the Amazon region was mostly emerged. This semi-aquatic Pebas system probably prevented

important faunal and floral exchange between the Andes and Amazonia. The retreat of this system may thus have produced a broad connection between these regions, thereby allowing colonizations both into (e.g. the Godyridina, this study) and out of the Andes (e.g. *Napeogenes*, Elias *et al.* 2009).

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

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

Acknowledgements

References

Antonelli A, Sanmartin I (2011) Mass extinction, gradual cooling, or rapid radiation? Reconstructing the spatiotemporal evolution of the ancient angiosperm genus *Hedyosmum* (Chloranthaceae) using empirical and simulated approaches. *Systematic Biology*, **60**, 596–615.

Arita HT, Vázquez-Domínguez E (2008) The tropics: cradle, museum or casino? A dynamic null model for latitudinal gradients of species diversity. *Ecology Letters*, **11**, 653–663.

Beccaloni GW (1997) Ecology, natural history and behaviour of ithomiine butterflies and their mimics in Ecuador (Lepidoptera: Nymphalidae: Ithomiinae). *Tropical Lepidoptera*, **8**, 103–124.

Beckman EJ, Witt CC (2015) Phylogeny and biogeography of the New World siskins and goldfinches: rapid diversification in the Central Andes. *Molecular Phylogenetics and Evolution*, **87**, 28–45.

Bershaw J, Garzione CN, Higgins P, MacFadden BJ, Anaya F, Alvarenga H (2010) Spatial–temporal changes in Andean plateau climate and elevation from stable isotopes of mammal teeth. *Earth and Planetary Science Letters*, **289**, 530–538.

Blandin P, Purser B (2013) Evolution and diversification of neotropical butterflies: insights from the biogeography and phylogeny of the genus *Morpho* Fabricius, 1807 (Nymphildae: Morphinae), with a review of the geodynamics of South America. *Tropical Lepidoptera Research*, **23**, 62–85.

Boonstra M, Ramos MIF, Lammertsma EI, Antoine P-O, Hoorn C (2015) Marine connections of Amazonia: evidence from foraminifera and dinoflagellate cysts (early to middle Miocene, Colombia/Peru). *Palaegeography, Palaeclimatology, Palaeoecology*, **417**, 176–194.

Brower AVZ, Freitas AVL, Lee MM, Silva-Brandão KL, Whinnett A, Willmott KR (2006) Phylogenetic relationships among the Ithomiini (Lepidoptera: Nymphalidae) inferred from one mitochondrial and two nuclear gene regions. *Systematic Entomology*, **31**, 288–301.

Brower AV, Willmott KR, Silva-Brandão KL, Garzón-Orduña IJ, Freitas AV (2014) Phylogenetic relationships of ithomiine butterflies (Lepidoptera: Nymphalidae: Danainae) as implied by combined morphological and molecular data. *Systematics and Biodiversity*, **12**, 133–147.

Brumfield RT, Edwards SV (2007) Evolution into and out of the Andes: a Bayesian analysis of historical diversification in *Thamnophilus* antshrikes. *Evolution*, **61**, 346–367.

Castroviejo-Fisher S, Guayasamin JM, Gonzalez-Voyer A, Vilà C (2014) Neotropical diversification seen through glassfrogs. *Journal of Biogeography*, **41**, 66–80.

Chaves JA, Weir JT, Smith TB (2011) Diversification in *Adelomyia* hummingbirds follows Andean uplift. *Molecular Ecology*, **20**, 4564–4576.

Chazot N, Willmott K, Freitas AVL, de-Silva DL, Pellens R, Elias M (2015) Patterns of species, phylogenetic and mimicry diversity of clearwing butterflies in the Neotropics. In: *Biodiversity Conservation and Phylogenetic Systematics: Species Protection in an Extinction Crisis* (eds Pellens R, Grandcolas P), pp. 333–354. Springer, New York.

Chown SL, Gaston KJ (2000) Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology & Evolution*, **15**, 311–315.

Condamine FL, Silva-Brandão KL, Kergoat GJ, Sperling FA (2012) Biogeographic and diversification patterns of Neotropical Troidini butterflies (Papilionidae) support a museum model of diversity dynamics for Amazonia. *BMC Evolutionary Biology*, **12**, 82.

Dantas SM, Weckstein JD, Bates JM *et al.* (2016) Molecular systematics of the new-word screech-owls (*Megascops*: Aves, Strigidae): biogeographic and taxonomic implications. *Molecular Phylogenetics and Evolution*, **94**, 626–634.

De-Silva DL, Elias M, Willmott K, Mallet J, Day JJ (2016) Diversification of clearwing butterflies with the rise of the Andes. *Journal of Biogeography*, **43**, 44–58.

Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, **29**, 1969–1973.

Duellman WE (1999) *Patterns of Distribution of Amphibians: A Global Perspective*. Johns Hopkins University Press, Baltimore.

Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. *Evolution*, **18**, 586–608.

Elias M, Hill RI, Willmott KR *et al.* (2007) Limited performance of DNA barcoding in a diverse community of tropical butterflies. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2881–2889.

Elias M, Joron M, Willmott K *et al.* (2009) Out of the Andes: patterns of diversification in clearwing butterflies. *Molecular Ecology*, **18**, 1716–1729.

FitzJohn RG (2012) Diversitree: comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution*, **3**, 1084–1092.

Fjeldså J (1994) Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiversity & Conservation*, **3**, 207–226.

Fjeldså J, Bowie RC, Rahbek C (2012) The role of mountain ranges in the diversification of birds. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 249–265.

Fouquet A, Santana CC, Haddad FBC, Pech N, Trefaut RM (2014) Species delimitation, patterns of diversification and historical biogeography of the Neotropical frog genus *Adenomera* (Anura, Leptodactylidae). *Journal of Biogeography*, **41**, 855–870.

Freitas AVL, Brown KS (2004) Phylogeny of the Nymphalidae (Lepidoptera). *Systematic Biology*, **53**, 363–383.

Garzione CN, Hoke GD, Libarkin JC *et al.* (2008) Rise of the Andes. *Science*, **320**, 1304–1307.

Garzón-Orduña IJ, Silva-Brandão KL, Willmott KR, Freitas AV, Brower AV (2015) Incompatible ages for clearwing butterflies based on alternative secondary calibrations. *Systematic Biology*, **64**, 752–767.

Givnish TJ, Barfuss MH, Van Ee B et al. (2014) Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. Molecular Phylogenetics and Evolution, 71, 55–78.

Goldberg EE, Igic B (2012) Tempo and mode in plant breeding system evolution. Evolution, 66, 3701–3709.

Goldberg EE, Lancaster LT, Ree RH (2011) Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. Systematic Biology, 60, 451–465.

Graham CH, Ron SR, Santos JC, Schneider CJ, Moritz C (2004) Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. Evolution, 58, 1781–1793.

Greeney HF, Hill RI, Simbaña WR, Gentry G (2009) The immature stages and natural history of Veladyris pardalis (Salvin, 1869) in eastern Ecuador (Lepidoptera: Nymphalidae: Ithomiinae). Journal of Insect Science, 9, 6.

Hall JP (2005) Montane speciation patterns in Ithomiola butterflies (Lepidoptera: Riodinidae): are they consistently moving up in the world? Proceedings of the Royal Society B: Biological Sciences, 272, 2457–2466.

Hoorn C, Wesselingh F, Ter Steege H et al. (2010) Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science, 330, 927–931.

Hughes C, Eastwood R (2006) Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. Proceedings of the National Academy of Sciences, 103, 10334–10339.

Hutter CR, Guayasamin JM, Wiens JJ (2013) Explaining Andean megadiversity: the evolutionary and ecological causes of glassfrog elevational richness patterns. Ecology Letters, 16, 1135–1144.

Janz N, Nylin S, Wahlberg N (2006) Diversity begets diversity: host expansions and the diversification of plant-feeding insects. BMC Evolutionary Biology, 6, doi: 10.1186/1471-2148-6-4.

Jiggins CD, Mallarino R, Willmott KR, Bermingham E (2006) The phylogenetic pattern of speciation and wing pattern change in neotropical Ithomia butterflies (Lepidoptera: Nymphalidae). Evolution, 60, 1454–1466.

Kozak KH, Wiens JJ (2010) Niche conservatism drives elevational diversity patterns in Appalachian salamanders. The American Naturalist, 176, 40–54.

Lamas G (2004) Ithomiinae. Checklist: Part 4A. Hesperioidea – Papilionoidea. In: Atlas of Neotropical Lepidoptera (ed Heppner JB), pp. 261–274. Association for Tropical Lepidoptera/Scientific Publishers, Gainsville.

Lanfear R, Calcott B, Ho SYW, Guindon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution, 29, 1695–1701.

Lewis DS, Sperling FA, Nakahara S, Cotton AM, Kawahara AY, Condamine FL (2015) Role of Caribbean Islands in the diversification and biogeography of Neotropical Heraclides swallowtails. Cladistics, 31, 1–24.

Luebert F, Weigend M (2014) Phylogenetic insights into Andean plant diversification. Evolutionary and Population Genetics, 2, 27.

Lynch Alfaro JW, Cortès-Ortiz L, Di Fiore A, Boubli JP (2015) Special issue: comparative biogeography of Neotropical primates. Molecular Phylogenetics and Evolution, 82, 518–529.

Matzke NJ (2014) Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. Systematic Biology, 63, 951–970.

McCain CM, Colwell RK (2011) Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. Ecology Letters, 14, 1236–1245.

McGuire JA, Witt CC, Altshuler DL, Remsen J (2007) Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. Systematic Biology, 56, 837–856.

McGuire JA, Witt CC, Remsen J et al. (2014) Molecular phylogenetics and the diversification of hummingbirds. Current Biology, 24, 910–916.

Minh BQ, Nguyen MAT, von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution, 30, 1188–1195.

Moonlight PW, Richardson JE, Tebbitt MC et al. (2015) Continental-scale diversification patterns in a megadiverse genus: the biogeography of Neotropical Begonia. Journal of Biogeography, 42, 1137–1149.

Morlon H, Parsons TL, Plotkin JB (2011) Reconciling molecular phylogenies with the fossil record. Proceedings of the National Academy of Sciences of the United States of America, 108, 16327–16332.

Mullen SP, Savage WK, Wahlberg N, Willmott KR (2011) Rapid diversification and not clade age explains high diversity in neotropical Adelpha butterflies. Proceedings of the Royal Society B: Biological Sciences, 278, 1777–1785.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature, 403, 853–858.

Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Molecular Biology and Evolution, 32, 268–274.

Papageorgis C (1975) Mimicry in neotropical butterflies. American Scientist, 63, 522–532.

Parada A, D'Elía G, Palma RE (2015) The influence of ecological and geographical context in the radiation od Neotropical sigmodontine rodents. BMC Evolutionary Biology, 15, 172.

Ree RH, Smith SA (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Systematic Biology, 57, 4–14.

Roddaz M, Hermoza W, Mora A, et al. (2010) Cenozoic sedimentary evolution of the Amazonian foreland basin system. In: Amazonia, Landscape and Species Evolution (eds Hoorn C., Wesselingh F.), pp. 61–88. Wiley-Blackwell, Chichester, UK.

Rojas D, Warsi OM, Dávalos LM (2016) Bats (Chiroptera: Noctilionoidea) challenge a recent origin of extant neotropical diversity. Systematic Biology, 65, 432–448.

Rolland J, Condamine FL, Jiguet F, Morlon H (2014) Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. Plos Biology, 12, e1001775.

Ronquist F, Teslenko M, van der Mark P et al. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology, 61, 539–542.

Rosser N, Phillimore AB, Huertas B, Willmott KR, Mallet J (2012) Testing historical explanations for gradients in species richness in heliconiine butterflies of tropical America. *Biological Journal of the Linnean Society*, **105**, 479–497.

Santos JC, Coloma LA, Summers K, Caldwell JP, Ree R, Cannatella DC (2009) Amazonian amphibian diversity is primarily derived from late Miocene Andean lineages. *PLoS Biology*, **7**, e1000056.

Särkinen T, Bohs L, Olmstead RG, Knapp S (2013) A phylogenetic framework for evolutionary study of the nightshades (Solanaceae): a dated 1000-tip tree. *BMC Evolutionary Biology*, **13**, 214.

Scherson RA, Vidal R, Sanderson MJ (2008) Phylogeny, biogeography, and rates of diversification of New World Astragalus (Leguminosae) with an emphasis on South American radiations. *American Journal of Botany*, **95**, 1030–1039.

Sedano RE, Burns KJ (2010) Are the Northern Andes a species pump for Neotropical birds? Phylogenetics and biogeography of a clade of Neotropical tanagers (Aves: Thraupini). *Journal of Biogeography*, **37**, 325–343.

Smith SA, De Oca ANM, Reeder TW, Wiens JJ (2007) A phylogenetic perspective on elevational species richness patterns in Middle American treefrogs: why so few species in lowland tropical rainforests? *Evolution*, **61**, 1188–1207.

Stebbins GL (1974) *Flowering Plants: Evolution Above the Species Level*, p. 399. Arnold XVIII, London.

Stephens PR, Wiens JJ (2003) Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *The American Naturalist*, **161**, 112–128.

Valentine JW (1967) The influence of climatic fluctuations on species diversity within the tethyan provincial system. In: *Aspects of Tethyan Biogeography* (eds Adams CG, Ager DV), pp. 153–166. Systematics Ass. Publ. 7.

Wahlberg N, Leneveu J, Kodandaramaiah U *et al.* (2009) Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 4295–4302.

Weir JT (2006) Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution*, **60**, 842–855.

Wesselingh FP, Hoorn C, Kroonenberg SB, *et al.* (2010) On the origin of Amazonian landscapes and biodiversity: a synthesis. In: *Amazonia, Landscape and Species Evolution* (eds Hoorn C., Wesselingh F.), pp. 61–88. Wiley-Blackwell, Chichester, UK.

Willmott KR, Freitas AVL (2006) Higher-level phylogeny of the Ithomiinae (Lepidoptera: Nymphalidae): classification, patterns of larval hostplant colonization and diversification. *Cladistics*, **22**, 297–368.

Data accessibility

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

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

Classification in this study	Lamas (2004) classification	Resulting formal classification	Explanation
Brevioleria plisthenes	*Brevioleria aelia plisthenes*	*Brevioleria aelia plisthenes* (d'Almeida, 1958)	We treat *Brevioleria plisthenes* as a distinct species in this study, based on its quite isolated distribution from other *B. aelia* (Hewitson, 1852) taxa (where it was placed by Lamas 2004) and its stable and distinctive wing pattern. Nevertheless, *Brevioleria* remains taxonomically highly complex and a thorough revision of the genus is required, so we do not make any formal changes here
Godyris hewitsoni	*Godyris nepos hewitsoni*	*Godyris hewitsoni* (Haensch, 1903) rev. stat	We treat *Godyris hewitsoni* as a species distinct from *Godyris nepos* (Weymer, 1875), as it differs in wing venation, having the base of vein M3 nearer the wing base than the

Appendix 1 *Continued*

Classification in this study	Lamas (2004) classification	Resulting formal classification	Explanation
			base of vein M1 on both wings (the opposite is true in *nepos*). As similar differences in venation separate three sympatric *Godyris* species in Ecuador (*G. duillia* (Hewitson, 1854), *G. hewitsoni* and *G. panthyale* (C. & R. Felder, 1862)), we regard such differences as likely to be significant at the species level. In addition, *G. nepos* has a distinctive wing pattern, with reddish HW markings that are more similar to those of *G. duillia* than other *Godyris*. Finally, no slightly intermediate forms or subspecies are known between *G. hewitsoni* and *G. nepos*, and we have not found any characters that suggest that these are sister taxa
Genus1 nsp1	*Greta* n. sp.	*Greta* n. sp.	An undescribed species from Peru included by Lamas (2004) in the genus *Greta*, here is hypothesized to be sister to *Godyris*. Its generic status requires confirmation with detailed morphological study, but there is no reason to suspect that the current DNA-based topology is incorrect
Genus2 *andromica*	*Greta andromica*	*Greta andromica* (Hewitson, 1855)	The molecular data place *andromica+annette* as a clade sister to *Pseudoscada*, a topology consistent with morphological data (Willmott & Freitas 2006), and they are here treated as a distinct genus, given the differences in size and habitat elevation in comparison with *Pseudoscada*. However, detailed morphological study is needed to determine whether this clade has any morphological synapomorphies and what its relationships are to other *Greta* not included in this study, to decide on the most appropriate taxonomic treatment
Genus2 *annette*	*Greta annette*	*Greta annette* (Guérin-Méneville, 1844)	See above under *Greta andromica*
Greta is restricted to *G. clavijoi*, *G. morgane*		*Greta clavijoi* (Neild, 2008), *Greta morgane* (Geyer, 1837)	Based on morphology (Willmott & Freitas 2006), the type species of *Greta* Hemming (1934), *G. diaphanus* (Drury, 1773), is sister to *G. morgane* (*G. clavijoi* was not included in Willmott & Freitas 2006). We thus apply the name *Greta* in this study to the clade *G. morgane*+*G. clavijoi*
Heterosais nephele	*Heterosais giulia nephele*	*Heterosais nephele* (Bates, 1862) rev. stat., *H. nephele gedera* (Hewitson, 1869) rev. stat.	Molecular data show that transandean and Amazonian *Heterosais* are strongly distinct and possibly not even sister taxa, consistent with differences in male androconial scales between taxa from the two regions. Transandean taxa (*H. g. giulia* (Hewitson, 1855), *H. g. pallidula* Haensch, 1903, *H. g. cadra* (Godman & Salvin, 1878)) have a much smaller distal patch of hair-like androconial scales on the dorsal hindwing, not extending basally past the base of vein Cu1, whereas in Amazonian taxa (*H. n. nephele*, *H. n. gedera*) the scale patch extends about halfway between the bases of veins Cu2 and Cu1
Hypoleria alema	*Hypoleria lavinia* ssp. (east of Andes)	*Hypoleria lavinia* (Hewitson, 1855) is restricted to taxa occurring west of the Andes, and *Hypoleria alema* (Hewitson, 1857) becomes the oldest name for the Amazonian taxa formerly included in *H. alema* and *H. lavinia*. In addition to *Hypoleria*	Molecular data indicate that the taxa east and west of the Andes that were included within *Hypoleria lavinia* in Lamas (2004) are strongly divergent. In addition, the east Ecuadorian Andes foothill taxon *ina*, hitherto regarded as conspecific with Colombian *H. alema*, was not differentiated from Amazonian *H. lavinia chrysodonia*. The data suggest that *H. lavinia* should be split into distinct species east and west of the Andes, and that *ina* (and presumably *alema*) should be regarded as subspecies of the eastern species. Morphological data are consistent with this hypothesis. The male genitalic valva is more

Appendix 1 *Continued*

Classification in this study	Lamas (2004) classification	Resulting formal classification	Explanation
		alema ina (Hewitson, 1859), *Hypoleria alema* thus includes the following as subspecies, all n. stat.: *H. alema asellia* (Hopffer, 1874), *H. a. cajona* Haensch, 1905, *H. a. chrysodonia* (Bates, 1862), *H. a. consimilis* (Talbot, 1928), *H. a. garleppi* (Haensch, 1905), *H. a. indecora* (Haensch, 1905), *H. a. karschi* (Haensch, 1903), *H. a. meridana* (Fox, 1948), *H. a. oreas* (Weymer, 1899), *H. a. proxima* (Weymer, 1899)	elongated with a less strongly produced dorso-posterior projection in *H. lavinia* specimens dissected from Ecuador and southeastern Peru and in *H. alema ina* and *H. alema alema*, in comparison with examined *H. lavinia* specimens from western Ecuador, Panama and Mexico. A long series of highly variable specimens phenotypically intermediate between *H. lavinia chrysodonia* and east Ecuadorian *H. alema*, collected by P. Boyer (personal communication) at an elevational contact zone, supports the conspecificity of these taxa
Hypoleria lavinia	*Hypoleria lavinia* ssp. (west of Andes)	*H. lavinia lavinia*, *H. l. cassotis* (Bates, 1864), *H. l. libera* (Godman & Salvin, 1879), *H. l. rhene* (Godman & Salvin, 1878), *H. l. riffarthi* (Haensch, 1905), *H. l. vanilia* (Herrich-Schäffer, 1865), *H. l. vaniliana* (Kaye, 1919)	See Discussion above
Hypoleria mulviana	*Hypoleria lavinia mulviana*	*Hypoleria mulviana* (d'Almeida, 1958) rev. stat.	*Hypoleria mulviana* was treated as a subspecies of *H. lavinia* by Lamas (2004). However, there is limited evidence (potentially unreliably labelled specimens) to suggest sympatry in the central Amazon, and the male genitalia are quite distinct from other *H. lavinia* and *H. alema* (see above); the ventral posterior projection on the valva is narrow and posteriorly (rather than inwardly) directed, the aedeagus is approximately twice as long and the tegumen is raised up higher above the valvae
Pseudoscada timna 'costarica'	*Pseudoscada timna*	*Pseudoscada timna pusio* (Godman & Salvin, 1877)	The molecular data showed that divergence between *P. timna* from Costa Rica, western Ecuador and the Amazon is similar to that between other species in this genus, and that Amazonian *P. timna* are sister to Brazilian *P. acilla*. We treat these three clades of *P. timna* as three species in the analysis here, but further molecular and morphological research is required. In particular, the relationships of northwest South American *P. timna* taxa (*P. t. saturata* (Staudinger, 1885) and *P. t. troetschi* (Staudinger, 1884)) to Costa Rican *P. t. pusio* and the undescribed west Ecuadorian taxon need to be determined before the classification can be revised
Pseudoscada timna 'eastern'	*Pseudoscada timna*	*Pseudoscada timna timna* (Hewitson, 1855)	See above
Pseudoscada timna 'western'	*Pseudoscada timna*	*Pseudoscada timna* (Hewitson, 1855) n. ssp.	See above

Appendix 1 *Continued*

Classification in this study	Lamas (2004) classification	Resulting formal classification	Explanation
Veladyris cytharista	*Veladyris pardalis cytharista*	*Veladyris cytharista* (Salvin, 1869) rev. stat.	The Ecuadorian to north Peruvian taxa *Veladyris pardalis aurea* Lamas, 1980, *V. p. pardalis* (Hewitson, 1855) and *V. p. totumbra* (Kaye, 1919) formed a clade distinct from the Peruvian *V. p. cytharista*, which clustered with *Veladyris electrea* (Brabant, 2004). In addition, *V. p. christina* Lamas, 1980, seems to be sympatric in north Peru (Amazonas) with an undescribed taxon which we regard as conspecific with *V. p. cytharista*; *V. p. christina* shares a distinctive white spot on the ventral hindwing in cell Sc+R1-Rs with the Ecuadorian *Veladyris pardalis* taxa, and we thus retain all four of these taxa in *V. pardalis*, and treat *V. cytharista* rev. stat. as a distinct species. A revision of the genus is in preparation by KRW, GL and others
Velamysta nsp1			This is an undescribed species recently discovered in western Ecuador by T. Kell (Kell, Willmott & Lamas, unpublished data)
Hypomenitis spp.	*Greta* spp.	We reinstate *Hypomenitis* to include the following species (and their subspecies and synonyms as listed in Lamas 2004), all **rev. stat.**: *H. alphesiboea* (Hewitson, 1869), *H. depauperata* (Boisduval, 1870), *H. dercetis* (Doubleday, 1847), *H. enigma* (Haensch, 1905), *H. esula* (Hewitson, 1855), *H. gardneri* (Weeks, 1901), *H. hermana* (Haensch, 1903), *H. libethris* (C. & R. Felder, 1865), *H. lojana* (Vitale & Bollino, 2001), *H. lydia* (Weymer, 1899), *H. ochretis* (Haensch, 1903), *H. oneidodes* (Kaye, 1918), *H. ortygia* (Weymer, 1890), *H. polissena* (Hewitson, 1863), *H. theudelinda* (Hewitson, 1861)	The majority of the montane species treated in *Greta* by Lamas (2004) form a well-supported clade, including *Ithomia theudelinda* Hewitson, the type species for *Hypomenitis* (Fox, 1945), that is significantly separated from that containing *G. morgane* (and presumably the type species of *Greta*, *G. diaphanus*, see Discussion above). Although Willmott & Freitas (2006) found no morphological synapomorphy for the two representative species of *Hypomenitis*, *H. ortygia*+*H. theudelinda*, support for the topology of this part of the tree was very weak, and the shared mid- to high elevation cloud forest habitats of all species included here in *Hypomenitis* is consistent with the monophyly indicated by the molecular data

Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1 List of specimens used with Genbank accession codes.

Appendix S2 Primers used for PCR.

Appendix S3 Phylogenetic tree of 206 individuals based on the concatenation of COI-tRNA-COII-EFI-Tektin gene fragments inferred with MrBayes.

Appendix S4 Maximum Likelihood tree inferred using IQ-tree software. We performed 1000 ultra-fast bootstrap iterations to get node supports (Minh *et al*. 2013).

Appendix S5 Secondary calibration points used with uniform distribution between the lower and upper bound, corresponding to the 95% credibility interval reported in Wahlberg *et al*. (2009).

Appendix S6 Time-calibrated maximum clade credibility tree. Median of node ages are shown at the nodes. Bars show the 95% credibility interval of node ages.

Appendix S7 Time-calibrated maximum clade credibility tree. Bayesian posterior probabilities are shown at the nodes.

Appendix S8 Matrices of dispersal probabilities for four time slices as used in the Dispersal-Extinction-Cladogenesis model of BiogeoBears.