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# Punctuational ecological changes rather than global factors drive species diversification and the evolution of wing phenotypes in *Morpho* butterflies

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## ► To cite this version:

Nicolas Chazot, Patrick Blandin, Vincent Debat, Marianne Elias, Fabien L. Condamine. Punctuational ecological changes rather than global factors drive species diversification and the evolution of wing phenotypes in *Morpho* butterflies. *Journal of Evolutionary Biology*, 2021, 10.1111/jeb.13921 . hal-03330520v1

**HAL Id: hal-03330520**

**<https://hal.science/hal-03330520v1>**

Submitted on 1 Sep 2021 (v1), last revised 6 Oct 2021 (v2)

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1 **Article type**

2 Original article

3

4 **Title**

5 Punctuational ecological changes rather than global factors drive species diversification and  
6 the evolution of wing phenotypes in *Morpho* butterflies

7

8 **Short running title**

9 Dynamics of species and wing diversification

10

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25

26 **Acknowledgments**

27 The authors have no conflict of interest to declare. F.L.C. has benefited from an  
28 “Investissements d’Avenir” grant managed by Agence Nationale de la Recherche (CEBA,  
29 ref. ANR-10-LABX-25-01). P.B benefited from the Programme Pluriformation “Etat et  
30 structure phylogénétique de la biodiversité actuelle et fossile”.

31

32 **Abstract**

33 Assessing the relative importance of geographical and ecological drivers of evolution is  
34 paramount to understand the diversification of species and traits at the macroevolutionary  
35 scale. Here, we use an integrative approach, combining phylogenetics, biogeography,  
36 ecology, and quantified phenotypes to investigate the drivers of both species and phenotypic  
37 diversification of the iconic Neotropical butterfly genus *Morpho*. We generated a time-  
38 calibrated phylogeny for all known species and inferred historical biogeography. We fitted  
39 models of time-dependent (accounting for rate heterogeneity across the phylogeny) and  
40 paleoenvironment-dependent diversification (accounting for global effect on the phylogeny).  
41 We used geometric morphometrics to assess variation of wing size and shape across the tree,  
42 and investigated their dynamics of evolution. We found that the diversification of *Morpho* is  
43 best explained when considering variable diversification rates across the tree, possibly  
44 associated with lineages occupying different microhabitat conditions. First, a shift from  
45 understory to canopy was characterized by an increased speciation rate partially coupled with  
46 an increasing rate of wing shape evolution. Second, the occupation of dense bamboo thickets  
47 accompanying a major host-plant shift from dicotyledons towards monocotyledons was  
48 associated with a simultaneous diversification rate shift and an evolutionary “jump” of wing  
49 size. Our study points to a diversification pattern driven by punctuational ecological changes  
50 instead of a global driver or biogeographic history.

51

52 **Keywords**

53 Species diversification, phenotypic diversification, wing size, wing shape, geometric  
54 morphometrics, butterflies, *Morpho*.

## 55 **Introduction**

56 Investigating the rates of phenotypic evolution and the relationships between  
57 phenotypes and species ecology can shed light on the drivers of time and geographic patterns  
58 of diversity. Previous studies have demonstrated that rates of both species and phenotypic  
59 diversification vary widely through time and among clades at all taxonomic scales (e.g.  
60 Venditti *et al.*, 2011; Eastman *et al.*, 2011; Rabosky & Adams, 2012; Rabosky *et al.*, 2013;  
61 Rabosky *et al.*, 2014; Cooney & Thomas, 2020). These variations have resulted in the  
62 striking heterogeneity in species and phenotypic diversity observed across the tree of life.  
63 Such variations may eventually be coupled, indicating an interaction between the processes  
64 of species and phenotypic diversifications. Studies investigating such coupling have yielded  
65 contrasted results. Some of them support an association between specific and phenotypic  
66 diversification (e.g. in salamanders: Rabosky & Adams, 2012; fish: Rabosky *et al.*, 2013;  
67 vertebrates: Cooney & Thomas, 2020), while others found no support for this relationship  
68 (e.g. in lizards: Rabosky *et al.*, 2014; squirrels: Zelditch *et al.*, 2015; reef fishes: Price *et al.*,  
69 2015; snakes: Lee *et al.*, 2016). For example in squirrels, Zelditch *et al.* (2015) suggested that  
70 species diversification was geographically driven while phenotypic diversification was  
71 ecologically driven, resulting in a decoupling of the two dynamics.

72 A correlation between species and phenotypic diversification rates is notably expected  
73 in some specific cases. For example, adaptive radiations – rapid adaptive diversification in a  
74 variety of ecological niches – are expected to produce bursts of diversification and  
75 phenotypic evolution especially during the initial stages of diversification (Schluter, 2000;  
76 Gavrilets & Losos, 2009). Speciation rate increases when a large number of ecological niches  
77 are vacant while phenotypes rapidly evolve in response to the diversity of ecological  
78 opportunities. Strong correlation between speciation rates and phenotypic diversification may  
79 also be found when the focal trait directly drives reproductive isolation. For example, the

80 evolution of male genitalia, involved in mating, may facilitate reproductive isolation between  
81 populations (see Langerhans *et al.*, 2016 for a review). Correlated dynamics leading to a  
82 lower rate of diversification can also be predicted. For example, if extinction probability is  
83 biased with respect to phenotype leading to a non-random loss of variation in a particular  
84 clade, both species and morphological diversity should show a correlated drop down (Foote,  
85 1997). In this study, we assess the role of multiple ecological causes of variations in rates of  
86 species and wing diversification and the extent to which these variations are coupled, by  
87 focusing on the case of the butterfly genus *Morpho* (Nymphalidae).

88         The genus *Morpho* comprises 30 species (Blandin & Purser, 2013), which are  
89 amongst the largest butterflies in the Neotropics and are well known for their blue iridescent  
90 wing coloration. Several ecological factors have already been suggested as potential drivers  
91 of diversification and phenotypic evolution. Previous biogeographic estimations suggested  
92 that *Morpho* butterflies originated and started diversifying in the Andes (Penz *et al.*, 2012,  
93 Blandin & Purser 2013), before spreading across the Neotropics. There is also evidence that  
94 *Morpho* lineages separated early in their history into two microhabitats (DeVries *et al.*, 2010;  
95 Chazot *et al.*, 2016). One clade is composed of species that tend to fly high, often above the  
96 forest canopy, with some species typically harbouring gliding flight behaviour such as *M.*  
97 *cisseis* and *M. hecuba*. The remaining species mostly fly within the first meters above ground  
98 in the understory (DeVries *et al.*, 2010; Chazot *et al.*, 2016). Finally, according to Cassildé *et*  
99 *al.* (2010) and Penz *et al.* (2012), the genus *Morpho* was ancestrally feeding on  
100 monocotyledons, and two major host-plant shifts occurred during its diversification: after the  
101 first divergence event, one of the two clades shifted to dicotyledon host-plants and, within  
102 this clade, a subclade subsequently reversed to the monocotyledons.

103         Here we focus on the wings of *Morpho*, which are at the crossroad of multiple  
104 selective pressures and tightly linked to species diversification. Typically, wing colour

105 patterns can be involved in camouflage, aposematism or courting behaviours (Naisbit *et al.*,  
106 2001; Merrill *et al.*, 2011). Wings also allow flight, enabling dispersal, foraging, predator  
107 escape, mating or host-plant searching (Dudley, 2002). Hence butterfly wings are under  
108 strong natural and/or sexual selection and may be associated with variations of speciation rate  
109 (Ortiz-Acevedo *et al.*, 2020). Both size and shape are important aspects of wing morphology.  
110 They both strongly affect the performance of flight behaviours (Dudley, 2002; Le Roy *et al.*,  
111 2019) and therefore might be closely associated to habitat use, dispersal strategies or host-  
112 plant searching. Besides, fore and hind wings can be functionally differentiated, for example  
113 during flight (Grodnitsky *et al.*, 1994; Le Roy *et al.*, 2020), which may lead to different  
114 patterns of diversification.

115 To investigate whether species and phenotypic diversification dynamics are coupled  
116 and to identify potential drivers of variations, we inferred a time-calibrated molecular  
117 phylogeny of the genus that we combined to a dataset of geographical distributions and  
118 morphometric measurements of wing size and shape. We applied an integrative approach and  
119 addressed the following questions: (1) Have rates of phenotypic diversification varied across  
120 the tree? We investigated potential variations in rate of phenotypic diversification among  
121 clades using phenograms and models of trait evolution to compare evolutionary rates for  
122 wing size and shape. (2) Is species diversification better explained by global processes or  
123 clade-specific (ecological) factors? First, we fitted different models of species diversification  
124 testing for global drivers of diversification, specifically past temperatures and Andean  
125 orogeny. Second, we compared these global drivers to models in which species  
126 diversification varied according to clade-specific ecological factors (microhabitat and major  
127 shifts of host-plants) and/or variations of phenotypic diversification identified in the first step.  
128 (3) Can we explain the variations in diversification rates by historical biogeography? We  
129 performed ancestral areas estimation in order to assess whether variations in phenotypic

130 evolutionary rates or species diversification rates may be associated with specific  
131 biogeographic events.

132

## 133 **Material and methods**

### 134 *Time-calibrated phylogeny*

135 Phylogenetic relationships and divergence time were inferred with Bayesian inference. We  
136 concatenated DNA data for one mitochondrial (COI) and four nuclear genes (CAD, EF-1 $\alpha$ ,  
137 GAPDH and MDH) using published sequences (Cassildé *et al.*, 2012; Penz *et al.*, 2012;  
138 Chazot *et al.*, 2016) retrieved from GenBank, generating a molecular dataset of a total length  
139 of 5001 nucleotides. Our dataset includes all *Morpho* species (i.e. 30 species *sensu* Blandin,  
140 2007). *Morpho helenor*, which harbours many subspecies, is distributed throughout the entire  
141 Neotropical region, resulting in unresolved biogeographic reconstructions in preliminary  
142 analyses. To help resolving the biogeographic inferences, *M. helenor* was represented in the  
143 biogeographic analyses by six subspecies that each occupies a distinct Neotropical area. For  
144 all other analyses, we pruned all subspecies of *M. helenor* but one in order to keep a single  
145 branch for the species. We also included 11 outgroups to root and calibrate the tree (see  
146 Supporting Information S1) on the basis of the most comprehensive nymphalid phylogeny to  
147 date (Wahlberg *et al.*, 2009).

148 To simultaneously estimate the topology and branching times of the phylogeny we  
149 used a Bayesian relaxed-clock approach as implemented in *BEAST* 1.8.2 (Drummond *et al.*,  
150 2012). To choose the best partitioning strategy and the corresponding substitution models, we  
151 ran *PartitionFinder* 1.1.1 (Lanfear *et al.*, 2012) allowing all possible partitions and models  
152 implemented in *BEAST*. Three subsets were defined: the first included position 1 and 2 of all  
153 genes and followed a GTR+I+ $\Gamma$  model, the second included position 3 of all nuclear  
154 fragments and followed a GTR+ $\Gamma$  model, and the third including the position 3 of the

155 mitochondrial fragment and followed a TrN+ $\Gamma$  model. We implemented an uncorrelated  
156 lognormal relaxed clock model. Given the lack of fossils in the focal clade, we relied on  
157 secondary calibrations to calibrate the molecular clock. Penz *et al.* (2012) calibrated the  
158 divergence between *Morpho* and its sister groups using a unique calibration point from  
159 Wahlberg *et al.* (2009), and a normal distribution for the corresponding prior. However,  
160 Sauquet *et al.* (2012) showed that using a single secondary calibration prior could yield  
161 biased estimates. Hence, we used a set of seven calibrations defined by uniform priors  
162 bounded by the 95% credibility intervals (95% CI) estimated by Wahlberg *et al.* (2009) (see  
163 Supporting Information S1). We implemented a Yule process for the tree prior, and we ran  
164 the phylogenetic analyses for 30 million Markov chain Monte Carlo (MCMC) generations.  
165 We checked for chain convergence using *Tracer* 1.6, as indicated by effective sample size  
166 (ESS) values. Finally, we used *TreeAnnotator* 1.8.2 (Drummond *et al.*, 2012) to select the  
167 maximum clade credibility (MCC) tree with median age values calculated from the posterior  
168 distribution of branch lengths, applying a 20% burn-in.

169

### 170 ***Morphological data***

171 Our morphological dataset (published by Chazot *et al.* 2016) consists in the size and shape of  
172 the fore and hind wings, as assessed by morphometric measurements. A total of 911  
173 collection specimens of both sexes and representing all *Morpho* species were photographed.  
174 Wing shape was described using landmarks and semi-landmarks placed at vein intersections  
175 and wing margins, respectively (see Chazot *et al.*, 2016 for details), which were  
176 superimposed with *tpsRelw* (Rohlf, 1993). Wing size was measured using the log-  
177 transformed mean centroid size per species. Importantly, for analyses involving wing shape  
178 we used the residuals of a multivariate regression of species mean Procrustes coordinates on  
179 species mean centroid size (log-transformed), which allows focusing on the non-allometric

180 shape variation. Similar analyses were performed separately on the fore and hind wings. All  
181 analyses were performed on males and females separately. As we found divergent patterns  
182 among sexes, we show the results for males and females separately. No female *M. niepelti*  
183 was available. This species was therefore pruned from the tree for all analyses involving  
184 female data.

185

### 186 ***Dynamics of phenotypic diversification***

187 We investigated whether the evolutionary rates of wing size and shape have varied among  
188 subclades across the phylogeny.

189 *Wing size* – We first visualized the evolution of traits through time using the  
190 *phenogram* function in *PHYTOOLS* 0.5-20 (Revell, 2012), which represents the trait values  
191 inferred at each node along a time axis. Second, we investigated the dynamics of wing size  
192 evolution across lineages using the method implemented in the function *rjcmc.bm* available  
193 in *GEIGER* 2.0.6 (Harmon *et al.*, 2008; Eastman *et al.*, 2011) for univariate traits. This  
194 method uses Bayesian analyses and reversible-jump MCMC to infer the number and the  
195 location of shifts of morphological diversification dynamics. We fitted and compared three  
196 different models of trait evolution: (1) a single-rate Brownian model (BM); (2) a relaxed  
197 model of Brownian evolution in which a trait evolved according to distinct Brownian-motion  
198 models across the tree (rBM); and (3); a model in which trait evolution can also occur at  
199 punctuational “jumps”, i.e. brief periods of rapid evolution at any branch in the phylogeny  
200 (jBM). We ran models on both the MCC and a posterior distribution of trees. For the MCC  
201 tree analysis, we ran for each model one MCMC of 30 million generations, sampling every  
202 3,000 generations. We checked for convergence of each run using *CODA* (Plummer *et al.*  
203 2020), and computed the ESS. We applied a 25% burn-in and compared the three models  
204 using the Akaike's Information Criterion for MCMC samples *aicm* and *aicw* implemented in

205 *GEIGER* (Supporting Information S2). To assess the robustness of the inferences to branch  
206 length uncertainties, we repeated the analysis on a posterior distribution of trees and  
207 summarized the results. We sampled 100 trees with a topology identical to that of the MCC  
208 tree from the posterior distribution. For each tree, we ran the three models but reduced the  
209 MCMC to 10 million generations, calculated the *aicm* score, the mean *aicm* pairwise  
210 differences between models and the position of rate shifts and jumps. We summarized the  
211 results by calculating the frequency of shifts and jumps at nodes across the posterior  
212 distribution. These results are hereafter referred to as shift/jump posterior tree frequencies.

213 *Wing shape* –Some authors have used the scores on the first PC-axis as a univariate  
214 shape measure (e.g. Rabosky *et al.*, 2014; Thacker, 2014) to investigate shifts in evolutionary  
215 rates for multidimensional traits, but this may lead to spurious results (Uyeda *et al.*, 2014).  
216 We rather investigated variations in rates of shape evolution across the phylogeny in a  
217 multivariate way using the function *compare.evol.rate* from *GEOMORPH* (Adams, 2014;  
218 Denton & Adams, 2015). It allows testing whether species assigned to different ecological  
219 factors have significantly different rates of shape evolution, by comparing the ratio between  
220 the rates of each group to a null distribution of ratios obtained through simulation of a unique  
221 neutral evolutionary rate (two or more factors can be tested). When more than two factors are  
222 included, the function performs a global test for the significance of the multiple rates model  
223 compared to a one-rate model, but also assesses the significance of differences among each  
224 pair of factors. We used this factor assignment to define monophyletic subgroups with  
225 potentially divergent evolutionary rate from the background rate. We first tested all models  
226 with one shift, i.e. all species belonging to one subclade (each subclade had a minimum of  
227 three species) are assigned to one group, and the rest of the species assigned to another group.  
228 If two or more subclades were identified as having a rate of evolution significantly different  
229 from that of the background, we identified the subclade with the highest ratio (hence the

230 greatest shift). Then we ran again *compare.evol.rate* on all possible combinations of two  
231 shifting subclades that include the first identified shift. A two-shift model was considered  
232 significant if at least the two shifting subclades showed a significant difference with the  
233 background rate when considering the pairwise comparisons. Given the relatively small size  
234 of our phylogeny, we limited our analysis to two shifts (Supporting Information S3-S4). As  
235 for wing size, we repeated the analysis on both the MCC tree and a posterior distribution of  
236 trees with identical topologies. We summarized the results from the posterior distribution by  
237 calculating the frequency of significant shifts at nodes across the trees, and refer to these as  
238 posterior tree frequencies.

239

#### 240 ***Dynamics of species diversification***

241 We compared two types of species diversification models: (1) diversification rates varying  
242 according to global factors, i.e. factors virtually affecting all lineages, and (2) diversification  
243 rates varying at specific clades characterized by clade-specific ecological factors. For each  
244 type we investigated different factors (see below). All models were compared using their AIC  
245 scores to identify the model that best explains the diversification of the genus *Morpho*.

246 *Global drivers of diversification* – We tested the role of temperature fluctuations and  
247 of the paleo-elevation of the Andes on species diversification by using birth-death models  
248 that allow speciation and extinction rates to vary according to a past environmental variable  
249 itself varying through time (Condamine *et al.*, 2013). For each paleoenvironmental variable,  
250 we designed three models to be tested: (i) the speciation rate varies exponentially with the  
251 environment and the extinction rate is constant, (ii) the speciation rate is constant and the  
252 extinction rate varies exponentially with the environment, and (iii) both speciation and  
253 extinction rates vary exponentially with the environment. We repeated these three models  
254 with a linear dependence to the environmental variable, instead of exponential dependence.

255 For temperature we relied on the well-known Cenozoic temperature dataset published by  
256 Zachos *et al.* (2008). The orogeny of the Andes is a highly complex process, with important  
257 differences in uplift tempo and mode from the south of Central Andes to Northern Andes  
258 (Blandin & Purser, 2013, and references therein). Several general phases have been identified  
259 from the late Eocene to present, but they are difficult to synthesize in a unique model. As  
260 Blandin & Purser (2013) suggested that the early diversification of the *Morpho* occurred  
261 along the proto-Central Andes, we used the model of surface uplift inferred by Leier *et al.*  
262 (2013) for the eastern cordillera of the southern Central Andes to test the possible influence  
263 of Andean orogeny on the diversification of the *Morpho*. We used the R-package *PSPLINE*  
264 1.0-17 to reconstruct smooth lines of the paleo-data for each environmental variable. The  
265 smooth line is introduced in the birth-death model to represent the variation of the  
266 environment through time. Given the dated phylogeny, the model then estimates speciation  
267 and extinction rates, as well as their respective variations according to the environment  
268 (Condamine *et al.*, 2013). These analyses were performed on 200 trees randomly sampled  
269 from the posterior distribution generated by BEAST.

270 *Clade-specific drivers of diversification* – We assessed whether the diversification  
271 rates across the genus *Morpho* have varied among specific clades using models of time-  
272 dependent diversification. To do so we used the method developed by Morlon *et al.* (2011),  
273 which allows partitioning diversification rates into independent dynamics (a backbone and  
274 different subclades). We compared different partitioning schemes according to three events:  
275 (1) the microhabitat change (from understory to canopy), (2) the shift of wing shape  
276 evolutionary rate, and (3) the reverse shift to monocotyledon host-plants (also identified as a  
277 punctuational evolutionary jump of wing size at the stem). Because the evolutionary rate shift  
278 of wing shape is nested within the microhabitat shift (see Results), we could not test both  
279 combined. Instead, each of those shifts was combined to the monocotyledon host-plant shift

280 with a two-shift model of diversification rate. For each subclade and the remaining backbone,  
281 we fitted the following models: (i) constant speciation rate and no extinction, (ii) time-  
282 dependent speciation rate and no extinction, (iii) constant speciation and extinction rates, (iv)  
283 time-dependent speciation rate and constant extinction rate, (v) constant speciation rate and  
284 time-dependent extinction rate, and (vi) time-dependent speciation and extinction rates. Time  
285 dependency was modelled using an exponential function of time. The stem branch of each  
286 subclade was included in the subclades and excluded from the backbones but we kept the  
287 node of the divergence (speciation event) of the subclade within the backbones. The root of  
288 the tree was excluded from the analyses. The analysis was performed on the MCC tree, since  
289 partitioning the tree requires defining clades *a priori*, which entails a fixed topology.

290

### 291 ***Historical biogeography***

292 To assess where and when diversification occurred, we estimated ancestral areas using the  
293 dispersal-extinction-cladogenesis (DEC, Ree and Smith, 2008) model as implemented in the  
294 R-package *BioGeoBEARS* 0.2.1 (Matzke, 2014). The analyses were performed using the  
295 MCC tree (outgroups removed) and included six subspecies of *M. helenor* (each subspecies  
296 was assigned to its current distribution).

297 The distribution of *Morpho* is restricted to South America and Central America (all  
298 Neotropics except the Caribbean Islands). A geographic model was incorporated to include  
299 operational areas, defined as geographic ranges shared by at least two or more species and  
300 delimited by geological, oceanic or landscape features, which may have acted as barriers to  
301 dispersal. The model comprised 7 component areas: (A) Central America, (B) trans-Andean  
302 South-America, (C) slopes of northern Andes, (D) eastern slopes of central Andes, Orinoco-  
303 Amazonian basin north of the Amazon, including the Guyanas, (E) Amazonian basin, south  
304 of the Amazon River, and (F) Atlantic forest.

305 An adjacency matrix was designed whilst taking into account the geological history  
306 and the biological plausibility of combined ranges (Supporting Information S6).  
307 Distributional data were compiled from monographies (Blandin, 2007). We excluded  
308 distribution margins overlapping with adjacent areas. For example, *M. marcus* and *M.*  
309 *eugenia* are mainly found in lowlands but their distributions reach the Andean slopes up to  
310 altitudes of 700-800m. Nevertheless, we did not consider these as species occupying the  
311 Andean biogeographic areas. By contrast, a species such as *M. sulkowskyi*, which occurs  
312 between 1500 and 3500m high in the Andes was considered as an Andean species. We also  
313 set a maximum of 3 areas per node to be constitutive of an ancestral range. We fitted two  
314 different DEC models, one that assumed equal dispersal probabilities among all areas and one  
315 that included time-stratified matrices of varying dispersal probabilities (Supporting  
316 Information S6). We compared the likelihoods of both reconstructions to select the model  
317 best explaining the current pattern of species distribution.

318

## 319 **Results**

### 320 ***Divergence times***

321 We estimated that the genus *Morpho* diverged (stem age) from its sister genus *Caerois* 38.05  
322 Ma (95% CI=35.48-39.20 Ma) and the first event (crown age) of diversification was  
323 recovered at 28.12 Ma (95% CI=25.22-31.24 Ma; Supporting Information S1). These  
324 divergence time estimates are slightly older than those estimated by Penz *et al.* (2012) and  
325 Chazot *et al.* (2019) who found an average divergence from *Caerois* around 32.00 Ma and  
326 29.08 Ma respectively. This difference probably results from prior choices for calibrating the  
327 trees (see Material and Methods).

328

### 329 ***Dynamics of phenotypic diversification***

330 *Wing size* – Both analyses on the MCC and posterior distribution of trees found  
331 similar results. We found no support for any shift in rate of wing size diversification.  
332 However, we found support for an evolutionary jump. For females the model jBM was highly  
333 supported for both wings, with a highly probable evolutionary jump at the root of the clade  
334 including the species *M. absoloni*, *M. aurora*, *M. zephyritis*, *M. rhodopteron*, *M. sulkowskyi*,  
335 *M. lympharis*, *M. aega*, and *M. portis* (subclade *portis*; posterior tree frequency [PF] of 0.99,  
336 Supporting Information S2). Phenograms show that in this subclade, female wings are on  
337 average 34% smaller than in the other *Morpho* species for both fore and hind wings (Fig. 1).  
338 This is all the more striking as the sister clade (including *M. amathonte*, *M. menelaus*, and *M.*  
339 *godartii*) contains some of the largest species of the genus (e.g. *M. amathonte* has a wingspan  
340 of 10–15 cm). For males, the *portis* clade exhibits the same trend, but the support for the  
341 evolutionary jump is lower than for females (PF<sub>forewing</sub>=0.76, PF<sub>hindwing</sub>=0.71, respectively,  
342 Supporting Information S2). Males wings in the *portis* clade were on average 30 and 32%  
343 smaller for fore and hind-wing respectively.

344 *Wing shape* – We found support for two shifts of evolutionary rate for male hindwing,  
345 in both cases towards lower rate of evolution. These subclades encompass *M. helenor*, *M.*  
346 *achilles*, and *M. granadensis* (Fig. 2, Supporting Information S3) on one side, and *M.*  
347 *godartii*, *M. menelaus*, and *M. amathonte* on the other. This result was supported by the  
348 analyses with the MCC tree. The analyses performed on the posterior tree distribution found  
349 a moderate support for these shifts, with PF of 0.62 and 0.77, respectively. For females and  
350 for both wings the subclade encompassing *M. theseus*, *M. amphitryon*, *M. telemachus* and *M.*  
351 *hercules* exhibited the greatest shift (highest ratio) (Fig. 2, Supporting Information S4). This  
352 shift corresponds to a large increase in rate of evolution (forewing ratio=181.74, hindwing  
353 ratio=184.49 in the MCC analysis), i.e. wing shape evolving faster within this group than the

354 other *Morpho*. This result was strongly supported by posterior distribution analyses, with PF  
355 of 0.96 and 0.99 for fore and hind-wing, respectively.

356

### 357 ***Dynamics of species diversification***

358 *Global drivers of diversification* – In the best model accommodating for Central  
359 Andean paleo-altitudes, speciation rates were negatively dependent on the paleo-altitude and  
360 extinction rates were constant (Table 2a). This model leads to a continuous decrease in  
361 speciation rate towards the present, suggesting that *Morpho* diversification was high during  
362 the early stages of the orogeny but the rise in altitude did not lead to any increased  
363 opportunities for speciation over time. We also found a significant correlation between  
364 *Morpho* diversification and temperature compared to a null model (Table 2b). The best fitting  
365 paleoclimatic model indicates that speciation rate was positively correlated with temperature  
366 variation while extinction remained constant. This means that speciation rate was high during  
367 the initial stages of diversification when the temperatures were warmer but globally  
368 decreased during the last 14 million years as the Earth cooled down (Zachos *et al.*, 2008).

369 *Clade-specific dynamics of diversification* – The best-partitioned models included a  
370 shift of diversification rate for the host-plant shift and for the canopy shift (Table 3,  
371 Supporting Information S5). Under this configuration, the diversification of the clade that  
372 shifted to monocotyledon host-plants was best modelled by a speciation rate decreasing  
373 through time combined with no extinction, and the diversification of the canopy clade was  
374 best modelled by a constant speciation rate with no extinction (Table 3, Fig. 3). For the  
375 remaining backbone lineages the best fitting model was a time-dependent speciation and  
376 extinction. The resulting net diversification rate (speciation minus extinction) of this  
377 backbone was high during the very early stages of diversification but rapidly decreased  
378 through time and became negative *ca.* 25 Ma, implying a declining diversity (Fig. 3). Around

379 22 Ma, the net diversification rate became positive again and reached zero at the present. This  
380 model of partitioned dynamics of diversification outperformed any model involving a global  
381 driver of diversification. Indeed, the multi-rate time-dependent model better fit the  
382 diversification of *Morpho* (AICc=191.69) than the temperature-dependent model  
383 (AICc=197.3,  $\Delta$ AIC=5.61) and the altitude-dependent model (AICc=199.0,  $\Delta$ AIC=7.31).

384

### 385 ***Historical biogeography***

386 The model of biogeographic estimation with user-specified dispersal probabilities yielded a  
387 worse fit than the model with equal dispersal probabilities (likelihood with time-stratified  
388 dispersal multipliers:  $DEC_{strat}=-143.41$ ; likelihood without time-stratified dispersal  
389 multipliers  $DEC_{null}=-140.75$ ) and the ancestral state estimations involved some important  
390 differences. In both reconstructions the root state was highly unresolved. In the  $DEC_{null}$   
391 model (highest likelihood), the area with the highest probability at the root was the southern  
392 part of the Amazonian Basin, *ca.* 28.1 Ma. The early divergence of the clade containing *M.*  
393 *marcus* and *M. eugenia* was accompanied by a colonization of the northern part of the  
394 Amazonian Basin (Fig. 4). The ancestor of the remaining group of *Morpho* occupied the  
395 Central Andes. This lineage then diverged into an Andean and an Amazonian lineage. This  
396 event (21.8 Ma) was also accompanied by a shift in microhabitat use: flight in low forest  
397 strata (understory) for the Andean lineage, and flight high above ground up to the canopy for  
398 the Amazonian lineage. The Andean lineage began a long-term occupation of the Central  
399 Andes with local diversification (12 nodes inferred occupying the Central Andes after the  
400 initial dispersal event). Around 11-12 Ma, cis-Andean (east of the Andes) recolonizations of  
401 Amazonia and the Atlantic Forest happened in three lineages. *M. polyphemus* is an intriguing  
402 case as it diverged 20.8 Ma from an Andean ancestor, but nowadays occupies Central  
403 America, whose connection to South America is often considered to be only completed

404 during the last 4-3 million years. This implies either an earlier dispersal route of emerging  
405 Central America or a more recent dispersal with a joint extinction in the South American  
406 landmass. Overall, Northern Amazonia and the Northern Andes appear to have been  
407 colonized recently, during the last 5 million years (Fig. 4).

408

## 409 **Discussion**

410 In this study we aimed at investigating the large-scale patterns of diversification of the  
411 *Morpho* butterflies by jointly evaluating the dynamics of species and phenotypic  
412 diversification, to assess whether they are coupled or not and to test whether they correlate  
413 with clade-specific factors and/or biogeographic events. Our results show that ecological  
414 idiosyncrasies predominantly explain the pattern of diversification, instead of global (tree  
415 wide) factors. These ecological changes affected to a large extent both species and  
416 phenotypic diversification, leading to the partial coupling of both dynamics. Based on the  
417 amount of information currently available on the ecology of *Morpho* we discuss the potential  
418 role of several ecological and biogeographic events as well as the correlation with phenotypic  
419 diversification in explaining these variations among groups.

420

### 421 *Study limitations*

422 A number of limitations have to be mentioned before discussing our results. Focusing on a  
423 small clade allowed us to combine multiple ecological, morphological and historical  
424 components thereby providing a deep understanding of the *Morpho* history. Although we  
425 sampled all known species for both the molecular phylogeny and morphological traits, our  
426 comparative analyses probably lack power as a result of both the small number of taxa (30  
427 species) and the phylogenetic distribution of the traits of interest. Both microhabitat shift and  
428 host-plant shift (towards monocotyledons) are single events happening at the root of a single

429 clade each and we lack phylogenetically independent similar shifts. Typically, we found an  
430 evolutionary jump in wing size to be associated with a shift from dicotyledons to  
431 monocotyledons host-plants. Further work addressing this pattern at a larger phylogenetic  
432 scale will be necessary to assess the generality of our finding. Furthermore, the reliability of  
433 birth-death models to assess the diversification dynamics from phylogenies of extant taxa is  
434 debated (e.g. Quental & Marshall, 2010; Louca & Pennell, 2020). We thus remain cautious  
435 with our estimation of the diversification dynamics and the interpretation of the different  
436 models tested. In particular, we avoided interpreting the speciation and extinction rates  
437 independently to focus only on the net diversification dynamics. Finally, the timing and  
438 magnitude of the Andean surface uplift is also controversial (see for example Evenstar *et al.*,  
439 2015, and references therein; Fiorella *et al.*, 2015). We based our test on the reconstruction  
440 proposed by Leier *et al.* (2013) that focused only on the eastern cordillera of the Central  
441 Andes where the *Morpho* diversity is the highest, but had a large uncertainty in their paleo-  
442 altitude estimations. The Andean orogeny was spatially and temporally heterogeneous  
443 (Horton, 2018), which makes the use and interpretation of the paleoaltitude-dependent  
444 diversification model difficult (Condamine *et al.*, 2018). Those limitations should thus be  
445 kept in mind throughout the following discussion of the drivers of diversification, and the  
446 signal of declining diversity in particular.

447

#### 448 *Early Andean diversification not directly driven by Andean uplift*

449 The diversification of the genus *Morpho* in the Andes could have happened either  
450 simultaneously with the uplift – a scenario where speciation is driven by the increasing  
451 heterogeneity of ecological conditions with new altitudes (Lagomarsino *et al.*, 2016) – or  
452 decoupled from orogenesis – a scenario where a clade radiates across a range of altitudes  
453 already established through adaptations to ecological conditions (e.g. climate, host-plants,

454 predators). Our results support the second hypothesis. We found that a model of  
455 diversification rate responding to paleo-altitude performed worse than the clade-specific  
456 diversification models (Tables 2 and 3), which means that neither global speciation nor  
457 extinction rate variations are well explained by the paleo-altitudes of the Central Andes. From  
458 a biogeographic point of view, 16 extant species (over 30) are almost restricted to the  
459 lowlands, while only six extant species have a distribution strictly restricted to the Andes.  
460 Yet, from the Oligocene-Miocene boundary to middle Miocene periods (23.5 to 11.6 Ma), 11  
461 nodes out of 14 were inferred to be at least in the Central Andes from our biogeographic  
462 estimation (Fig. 4). Combined to the hypothesis that the *Morpho* probably originated in the  
463 foothills of the proto-Central-Andes, it is undeniable that the Central Andes played an  
464 important role in the early diversification of *Morpho*. During the second half of their  
465 evolutionary history, these lineages dispersed and diversified out of the Central Andes.

466 In contrast with the pattern of Central Andean diversification described above, the  
467 Northern Andes appear to have played only a minor role: while Northern Andean uplift likely  
468 established a barrier in three instances, resulting in cis- and trans-Andean *Morpho* lineages  
469 (Fig. 4), no major diversification was associated with the periods of Northern Andean uplift  
470 (Blandin & Purser, 2013). This absence of local diversification in the Northern Andes is a  
471 major difference compared to other butterflies such as the Ithomiini in which several groups  
472 repeatedly diversified at a high rate in the Northern Andes such as the genera *Napeogenes*  
473 (Elias *et al.*, 2009), *Oleria* (De-Silva *et al.*, 2016), *Hypomenitis* (Chazot *et al.*, 2016) or  
474 *Pteronymia* (De-Silva *et al.*, 2017).

475 Diversification driven by host-plant evolution may be an alternative explanation for  
476 the early diversification of *Morpho*. Penz and DeVries (2002) and Cassildé *et al.* (2010)  
477 suggested that monocotyledons were the ancestral host-plants of the genus *Morpho*, probably  
478 because at the time it was admitted that *M. marcus* larvae feed on monocotyledons

479 (Constantino, 1997). However, we now know that *M. marcus* very probably feeds on  
480 Fabaceae (e.g. *Inga auristellae*; Ramírez-García *et al.*, 2014; Vásquez Bardales *et al.*, 2017),  
481 and *M. eugenia* certainly feed on Caesalpiniaceae (Bénéruz, 2016). Therefore, since groups  
482 closely related to *Morpho*, notably the sister genus *Caerois*, are known to only feed on  
483 monocotyledon host-plants (Beccaloni *et al.*, 2008), it is likely that the divergence of the  
484 *Morpho* was associated with an initial shift to dicotyledons. This host-plant shift at the root of  
485 Morphos created the conditions for an early rapid diversification of the group.

486

#### 487 *A shift towards the canopy driving phenotypic and diversification changes*

488 We found a shift of species diversification associated with a single shift from the understory  
489 to the canopy (DeVries *et al.* 2010; Chazot *et al.* 2016). We also found strong indications that  
490 female wing shape evolution in the canopy clade is different from a neutral evolution. An  
491 increasing rate of shape evolution for both fore- and hind-wings was supported in the  
492 subclade nested in the canopy clade and including *M. theseus*, *M. niepelti*, *M. amphytrion*, *M.*  
493 *telemachus*, and *M. hercules*. Chazot *et al.* (2016) showed that both male and female wing  
494 shapes in the canopy clade are significantly different from wing shapes in understory species.  
495 Here we show that this microhabitat change associated with different vegetation structure,  
496 microclimatic conditions and predator community may have also affected the rate of female  
497 wing shape evolution in addition to shape *per se*. However, we note that the highest rate shift  
498 was not placed at the root of the canopy clade, suggesting that other factors may have caused  
499 this rapid phenotypic evolution. This increased rate of wing shape evolution was not found in  
500 males. Instead, in males we found two significant slowdowns in rate at different small  
501 subclades, only in the case of hindwings. The lack of more precise information on these  
502 species ecology unfortunately prevents speculating on the factors involved in such changes in  
503 wing shape evolutionary rate.

504

505 *A second change in microhabitat conditions associated with a host-plant, phenotypical and*  
506 *diversification shifts*

507 Published information in the *portis* clade (Heredia & Alvarez, 2007; Beccaloni *et al.*,  
508 2008; Montero Abril & Ortiz Perez, 2010) indicate that four *Morpho* species (*M. portis*, *M.*  
509 *aega*, *M. sulkowskyi* and *M. rhodopteron*) feed on Neotropical woody bamboos (Poaceae,  
510 tribe Bambuseae), notably on *Chusquea* species (subtribe Chusqueinae), in particular  
511 *Chusquea* aff. *scandens* for *M. sulkowskyi* that occurs at cloud forest elevations (Heredia &  
512 Alvarez, 2007). Recent observations indicate that *M. zephyritis* also feeds on woody  
513 bamboos (Roberto Maravi, pers. comm.). For the other species of the *portis* clade, there are  
514 only field observations indicating that they live in areas with important bamboo vegetation  
515 (Purser & Lacomme, 2016; pers. obs. in Peru, Daniel Lacomme pers. com.).

516 If, as observations indicate, the *portis* clade diversified after an initial shift back to  
517 monocotyledon host-plants, this reversal evolutionary event is a strong support for the  
518 “oscillation hypothesis” (Janz *et al.*, 2006). This hypothesis was proposed to explain the  
519 pattern of nymphalid butterflies with respect to host-plant use (Janz *et al.*, 2006) and states  
520 that the ability to recolonize “lost” hosts should be conserved over long evolutionary times,  
521 leading to recurrent recolonization events. Compared to the speciation rate of the backbone,  
522 species diversification within the *portis* clade proceeded at a higher rate, and rapidly  
523 decreased through time to reach almost zero at present. Adaptive radiations, here following a  
524 major host-plant shift, predict this rapid dampening of speciation rate as a result of niche  
525 filling (Schluter, 2000; Gavrilets & Losos, 2009).

526 Interestingly, we found that an evolutionary jump – a fast punctuational event of  
527 evolution – toward smaller wing sizes also coincided with the host-plant shift. Chazot *et al.*  
528 (2016) did not identify any driver of this wing size evolution. To our knowledge, there is no

529 clear expectation or evidence supporting a specific relationship between body size and  
530 monocot *versus* dicot feeders but this question has rarely been addressed (but see Garcia-  
531 Barros 2000). The jump toward smaller sizes also cannot be associated with any altitudinal  
532 change because some species of the clade only occur at low to mid altitudes (200-1500 m),  
533 while others occur at higher altitudes (1500-3500 m) (Blandin, 2007; Gayman *et al.*, 2016).

534 Therefore, other hypotheses need to be explored, in particular that of a second  
535 possible change of microhabitat conditions. Many Bambusinae, in particular *Chusquea*  
536 species, form dense thickets, twigs and leaves creating inextricable tangles as a result from  
537 abundant vegetative branching at each node (Fisher, 2011; Fisher *et al.*, 2014). Observational  
538 data on the behaviour of the bamboo feeding *Morpho* is scarce, but observations on *M.*  
539 *rhodopteron* (Montero Abril and Ortiz Perez, 2010; Purser and Lacomme, 2016), *M.*  
540 *sulkowskyi* (Heredia and Alvarez-Lopez 2007), and *M. aega* (Otero & Marigo, 1990) suggest  
541 that females are more often resting inside the *Chusquea* thickets while males are flying  
542 around (males, when resting, also stand in the vegetation). Moreover, Heredia & Alvarez-  
543 Lopez (2007) noted that *M. sulkowskyi* females having light and dark alternating stripes on  
544 wings ventral side are difficult to detect inside *Chusquea* thickets. More or less contrasted  
545 similar patterns exist in males and females of other species, except in *M. absoloni*. Therefore,  
546 we hypothesize that size reduction, associated to a more or less striped appearance of the  
547 ventral side, could be an adaptation to the microhabitat structure of dense woody bamboo  
548 thickets, highlighting once again the importance of the microhabitat conditions on species  
549 and trait evolution.

550

#### 551 *Declining diversity in the Neotropical Morpho*

552 When accounting for heterogeneity in diversification rates (isolating the two shifting  
553 subclades), the diversification dynamics for the remaining lineages was characterized by a

554 negative net diversification rate, indicative of a declining diversity, mainly during the  
555 Miocene. Whether diversity decline can be accurately estimated only from phylogenies of  
556 extant species is a matter of debate (e.g. Quental & Marshall, 2010; but see Morlon *et al.*,  
557 2011). In the case of *Morpho*, this pattern may explain why some branches in the tree (such  
558 as the stem branch of *M. marcus* and *M. eugenia* or the branches leading to *M.anaxibia*, *M.*  
559 *deidamia*, or *M. polyphemus*) are surprisingly long. Extinct lineages may also explain why *M.*  
560 *polyphemus*, which diverged from its sister clade 20 Ma, is found in Central America, while  
561 colonization of Central America is often expected to be much more recent (but see Montes *et*  
562 *al.*, 2015, Farris *et al.*, 2011). Major landscape transformations during the Miocene in western  
563 Amazonia may explain this decline. Between 23-10 Ma, Western Amazonia transformed into  
564 a large wetland of lakes, swamps and shallow water, called the Pebas System (Wesselingh  
565 *et al.*, 2001; Hoorn *et al.*, 2010). The exact nature of the Pebas System is still under  
566 discussion but it was most likely unsuitable for terrestrial fauna (Salas-Gismondi *et al.*,  
567 2015). Evidence of extinction has been found from a west Amazonian fossil record, in  
568 particular with a major decrease of mammalian diversity at the transition between the  
569 Oligocene and the Miocene (Antoine *et al.*, 2016), which is in line with the beginning of the  
570 diversity decline in *Morpho* (Fig. 3).

571

## 572 *Conclusion*

573 Our results support a prevailing ecological basis for both species and phenotypic  
574 diversification in *Morpho* butterflies: (1) a major host-plant shift, which affected wing size  
575 evolution and greatly affected species diversification dynamics (pattern of adaptive  
576 radiation), and (2) a microhabitat shift affecting species diversification and partially wing  
577 shape diversification. Therefore, to a large extent, the dynamics of species diversification and  
578 phenotypic diversification are coupled in *Morpho*, most likely as a result of two major

579 ecological events. More importantly, we show that both species and phenotypic  
580 diversification in *Morpho* butterflies are better explained by multiple clade-specific factors  
581 instead of global abiotic drivers. Current methods for identifying drivers of diversification,  
582 based on model comparisons, are unable to test for potential interactions between drivers.  
583 Hence, our results do not exclude the possibility that the Andes played a role in  
584 diversification, but rather suggest that their effect on the shape of the phylogenetic tree was  
585 less significant than other factors. Nevertheless, the extent to which the effects of these  
586 ecological drivers can be generalised is unknown given the scale of our dataset. In particular  
587 future work at a larger phylogenetic scale should shed light on the importance of major host-  
588 plant transitions on the evolution of body size and the dynamics of diversification. Our study  
589 also highlights that both phenotypic and ecological information are of key relevance for  
590 understanding macroevolutionary patterns of diversification.

591

592

593 **Table 1.** Summary results obtained from fitting three models of trait evolution on 100 trees,  
594 using the *rjmc.mcmc* function as implemented in the R package GEIGER on a) males and b)  
595 females. *bm*=single Brownian rate, *rbm*=relaxed Brownian rates, *jbm*=jumps of Brownian  
596 rates. AIC<sub>bm</sub>, AIC<sub>rbm</sub>, AIC<sub>jbm</sub> = mean AIC score across the 100 trees for all three models.  
597  $\Delta$ AIC<sub>bm-rbm</sub>,  $\Delta$ AIC<sub>bm-jbm</sub>,  $\Delta$ AIC<sub>rbm-jbm</sub> = pairwise AIC differences between models for each  
598 tree.

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**a) Males**

	AIC <sub>bm</sub>	AIC <sub>rbm</sub>	AIC <sub>jbm</sub>	$\Delta$ AIC <sub>bm-rbm</sub>	$\Delta$ AIC <sub>bm-jbm</sub>	$\Delta$ AIC <sub>rbm-jbm</sub>
Forewing	-23.92 (18.72)	-27.78 (10.33)	13.41 (26.32)	3.85 (21.70)	-37.34 (34.54)	-41.20 (30.02)
Hindwing	-14.43 (20.28)	-18.62 (14.58)	14.94 (24.28)	4.18 (24.02)	-29.37 (29.76)	-33.56 (28.21)

601  
602

**b) Females**

	AIC <sub>bm</sub>	AIC <sub>rbm</sub>	AIC <sub>jbm</sub>	$\Delta$ AIC <sub>bm-rbm</sub>	$\Delta$ AIC <sub>bm-jbm</sub>	$\Delta$ AIC <sub>rbm-jbm</sub>
Forewing	-22.36 (10.44)	-17.74 (9.40)	-34.70 (1.60)	-4.61 (15.73)	12.33 (10.98)	16.95 (9.56)
Hindwing	-15.44 (17.06)	-13.30 (22.83)	-32.80 (1.17)	-2.14 (29.62)	17.36 (16.88)	19.50 (23.01)

603 **Table 2.** Paleoenvironmental-dependent diversification analyses using paleoaltitude (a) and  
604 Cenozoic temperature (b) data. Mean parameter and standard error estimates are presented  
605 for each model. Best-fitting model, as determined via a combination of the lowest AIC and  
606  $\Delta$ AIC (see main text) highlighted in bold. In our best-fit paleoaltitude-dependent model,  
607 speciation is negatively correlated to Andean orogeny over time (adding extinction as a  
608 parameter did not improve the model fit). Likewise, speciation is positively correlated to  
609 temperature variation over time (allowing extinction to vary with temperature did not  
610 improve the likelihood).  $\lambda$  = speciation rate (in events/Myr/lineage);  $\mu$  = extinction rate (in  
611 events/Myr/lineage);  $\alpha$  = rate of variation of the speciation according to the relevant  
612 paleoenvironmental variable;  $\beta$  = rate of variation of the extinction according to the  
613 paleoenvironmental variable; NP = number of parameters in each model.

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**a) Paleoaltitude models**

Models	Dependency	NP	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
$\lambda$ Alti. and no $\mu$	Linear	2	-97.50 $\pm 0.085$	199.00 $\pm 0.171$	0.00	0.190 $\pm 0.004$	-3.60E-05 $\pm 1.39E-06$	-	-
$\lambda$ Alti. and no $\mu$	Exponential	2	-97.68 $\pm 0.083$	199.37 $\pm 0.166$	0.37	0.210 $\pm 0.004$	-3.06E-04 $\pm 5.76E-06$	-	-
$\lambda$ Alti. and $\mu$ constant.	Linear	3	-97.49 $\pm 0.085$	200.99 $\pm 0.170$	1.99	0.190 $\pm 0.0003$	-3.47E-05 $\pm 8.75E-07$	5.15E-04 $\pm 4.17E-04$	-
$\lambda$ Alti. and $\mu$ constant	Exponential	3	-97.69 $\pm 0.083$	201.37 $\pm 0.166$	2.37	0.220 $\pm 0.004$	-3.11E-04 $\pm 5.68E-06$	9.09E-07 $\pm 7.91E-07$	-
$\lambda$ constant and $\mu$ Alti	Exponential	3	-97.75 $\pm 0.104$	201.51 $\pm 0.207$	2.51	0.080 $\pm 3.16E-04$	-	42038.92 $\pm 11873.33$	-7.48E-03 $\pm 2.62E-04$
$\lambda$ Alti. and $\mu$ Alti	Exponential	4	-96.94 $\pm 0.094$	201.87 $\pm 0.187$	2.87	0.880 $\pm 0.160$	-5.00E-04 $\pm 2.00E-05$	6.820 $\pm 1.159$	-1.89E-03 $\pm 4.72E-05$
$\lambda$ Alti. and $\mu$ Alti.	Linear	4	-97.42 $\pm 0.086$	202.83 $\pm 0.171$	3.84	0.210 $\pm 0.004$	-3.83E-05 $\pm 1.18E-06$	0.070 $\pm 0.007$	-2.38E-05 $\pm 2.32E-06$
$\lambda$ constant and $\mu$ Alti.	Linear	3	-98.56 $\pm 0.099$	203.12 $\pm 0.198$	4.12	0.080 $\pm 0.001$	-	0.030 $\pm 0.005$	-1.14E-05 $\pm 1.76E-06$

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**b) Paleoclimate models**

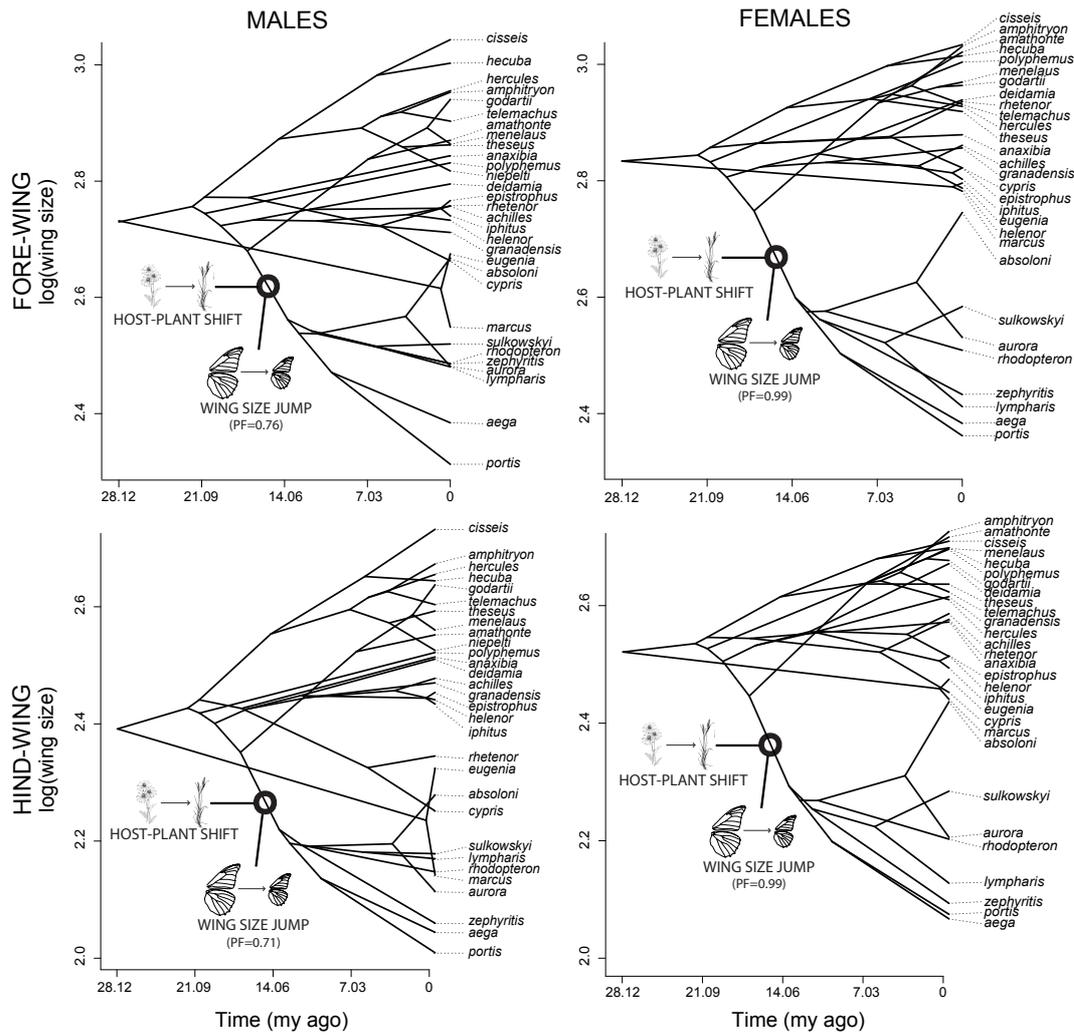
Models	Dependency	NP	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
$\lambda$ Temp. and no $\mu$	Exponential	2	-96.65 $\pm 0.095$	197.30 $\pm 0.189$	0.00	0.030 $\pm 4.13E-04$	0.179 $\pm 1.91E-03$	-	-
$\lambda$ Temp. and no $\mu$	Linear	2	-96.72 $\pm 0.097$	197.44 $\pm 0.195$	0.13	0.015 $\pm 5.50E-04$	0.013 $\pm 1.17E-04$	-	-
$\lambda$ Temp. and $\mu$ constant	Exponential	3	-96.58 $\pm 0.092$	199.15 $\pm 0.184$	1.85	0.030 $\pm 3.93E-04$	0.210 $\pm 3.62E-03$	0.043 $\pm 0.004$	-
$\lambda$ Temp. and $\mu$ constant	Linear	3	-96.67 $\pm 0.097$	199.33 $\pm 0.195$	2.03	0.023 $\pm 1.48E-03$	0.021 $\pm 1.34E-03$	0.046 $\pm 0.007$	-
$\lambda$ Temp. and $\mu$ Temp.	Linear	4	-96.42 $\pm 0.095$	200.85 $\pm 0.189$	3.54	0.017 $\pm 1.11E-03$	0.027 $\pm 8.07E-04$	0.290 $\pm 0.012$	-0.037 $\pm 0.002$
$\lambda$ Temp. and $\mu$ Temp.	Exponential	4	-96.55 $\pm 0.092$	201.10 $\pm 0.183$	3.80	0.032 $\pm 7.99E-04$	0.205 $\pm 4.57E-03$	0.156 $\pm 0.040$	-0.164 $\pm 0.019$
$\lambda$ constant and $\mu$ Temp.	Exponential	3	-98.57 $\pm 0.103$	203.14 $\pm 0.205$	5.84	0.081 $\pm 2.96E-04$	-	4.47E-08 $\pm 3.08E-09$	0.004 $\pm 2.19E-04$
$\lambda$ constant and $\mu$ Temp.	Linear	3	-98.57 $\pm 0.103$	203.14 $\pm 0.205$	5.84	0.081 $\pm 2.97E-04$	-	1.09E-04 $\pm 1.08E-04$	-1.37E-05 $\pm 1.37E-05$

622

623 **Table 3.** Results of model comparison for the five time-dependent diversification analyses  
624 presented, with mean parameter estimates for each model.  $\lambda$  = speciation rate (in  
625 events/Myr/lineage);  $\alpha$  = parameter of rate variation for speciation;  $\mu$  = extinction rate (in  
626 events/Myr/lineage);  $\beta$  = parameter of rate variation for extinction; NP = number of  
627 parameters in each model; AICc = corrected Akaike information criterion; logL = log-  
628 likelihood.

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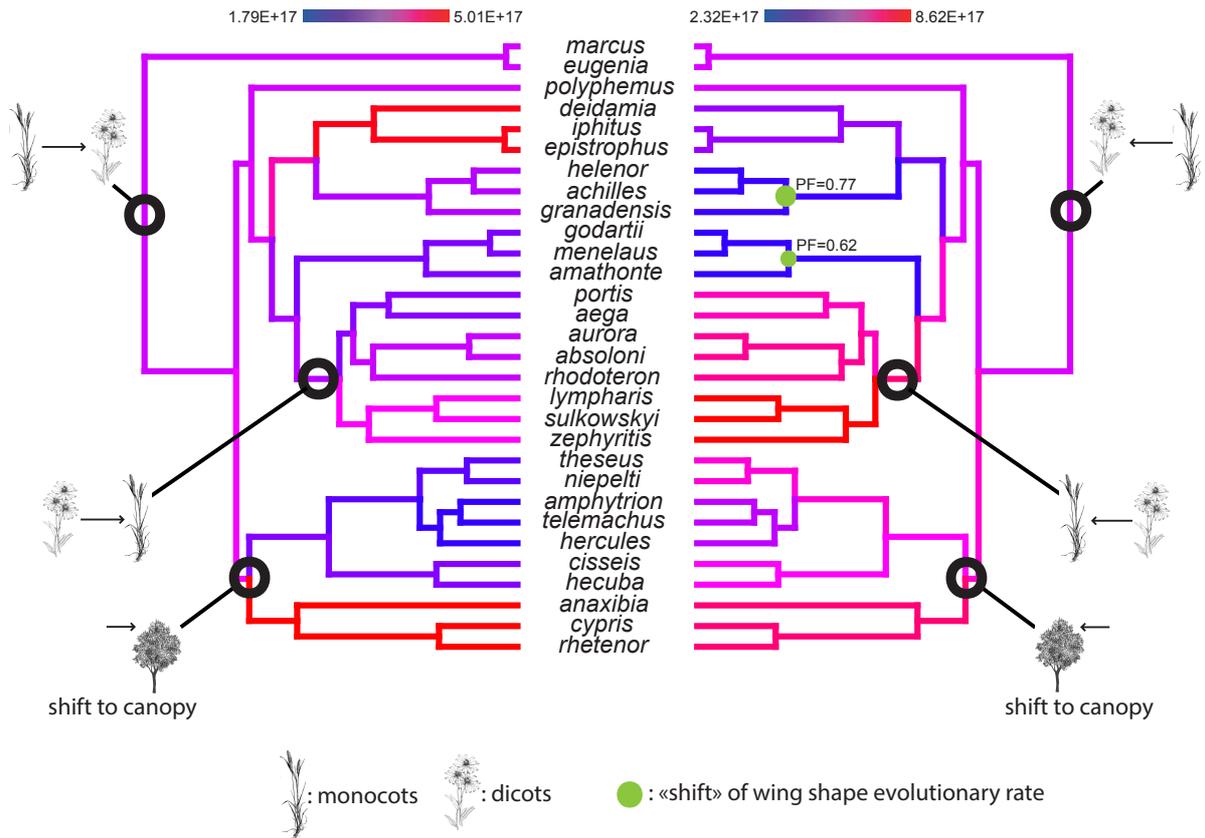
Clade partition	Models	NP	logL	AIC	$\lambda$	$\alpha$	$\mu$	$\beta$	Joint logL	Joint AIC
background	BVAR DVAR	4	-35.68	79.36	0.063	0.237	0.079	0.228		
monocots	BVAR	2	-21.78	47.55	0.014	0.213	-	-	-88.84	191.69
canopy	BCST	1	-31.39	64.77	0.083	-	-	-		
background	BCST	1	-50.91	103.83	0.072	-	-	-		
monocots	BVAR	2	-21.78	47.55	0.014	0.213	-	-	-92.83	193.66
shape shift	BCST	1	-20.14	42.28	0.095	-	-	-		
background	BCST	1	-73.75	149.49	0.081	-	-	-	-95.52	197.05
monocots	BVAR	2	-21.78	47.55	0.014	0.213	-	-		
whole	BCST	1	-98.40	198.81	0.081	-	-	-	-98.40	198.81
background	BCST	1	-78.18	158.36	0.078	-	-	-	-98.32	200.63
shape shift	BCST	1	-20.14	42.28	0.095	-	-	-		
background	BCST	1	-67.01	136.03	0.080	-	-	-	-98.40	200.80
canopy	BCST	1	-31.39	64.77	0.083	-	-	-		



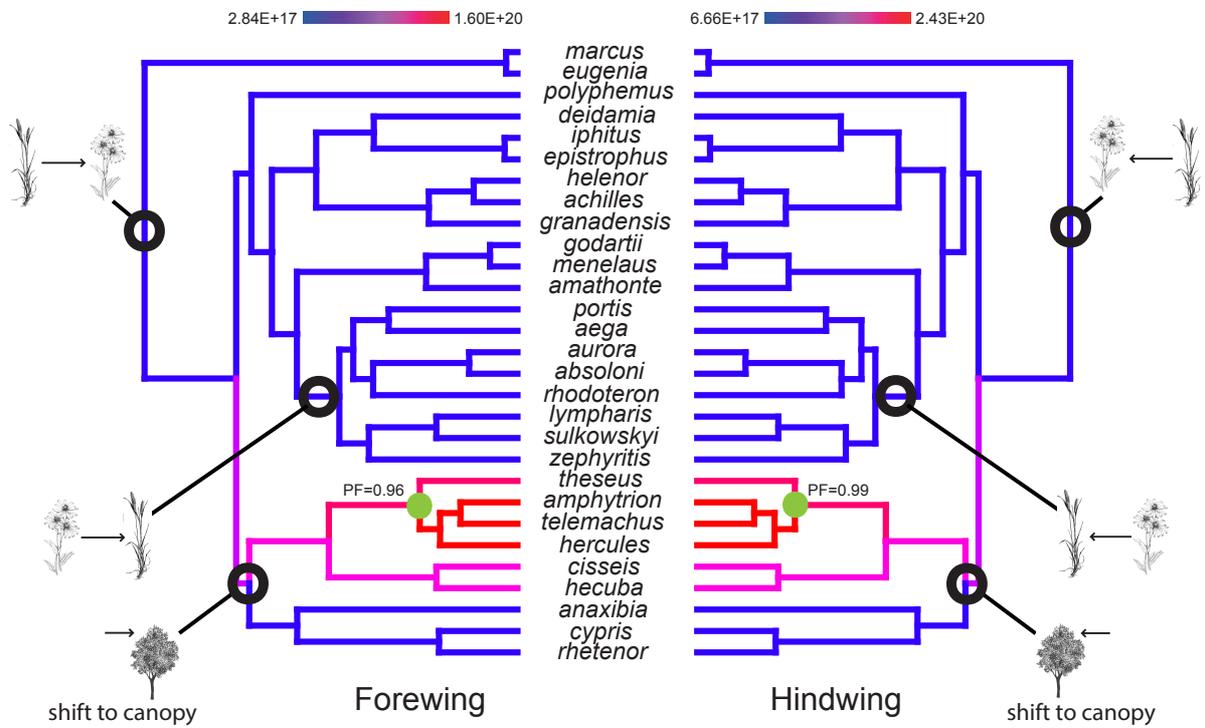
630  
 631 **Figure 1.** Phenograms for wing size (log scale) for males (left panels) and females (right  
 632 panels). The top panels are the forewings, and the bottom panels are the hindwings. Wing  
 633 size values are reconstructed at the nodes and plotted on a time scale. Phylogenetic  
 634 relationships are projected into the phenogram. The position (branch) where the main host-  
 635 plant shift and significant wing size jump happened is also shown. PF values indicate the  
 636 frequency at which each jump was found across the posterior distribution of trees.

637

a) Males

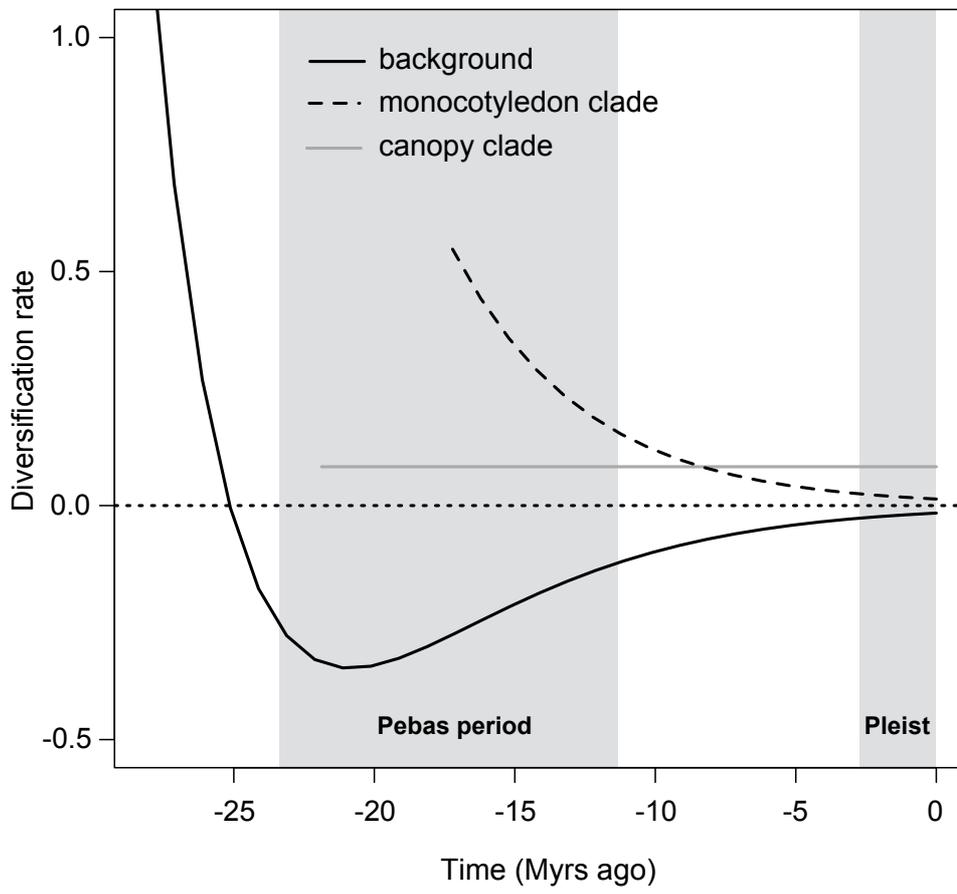


b) Females

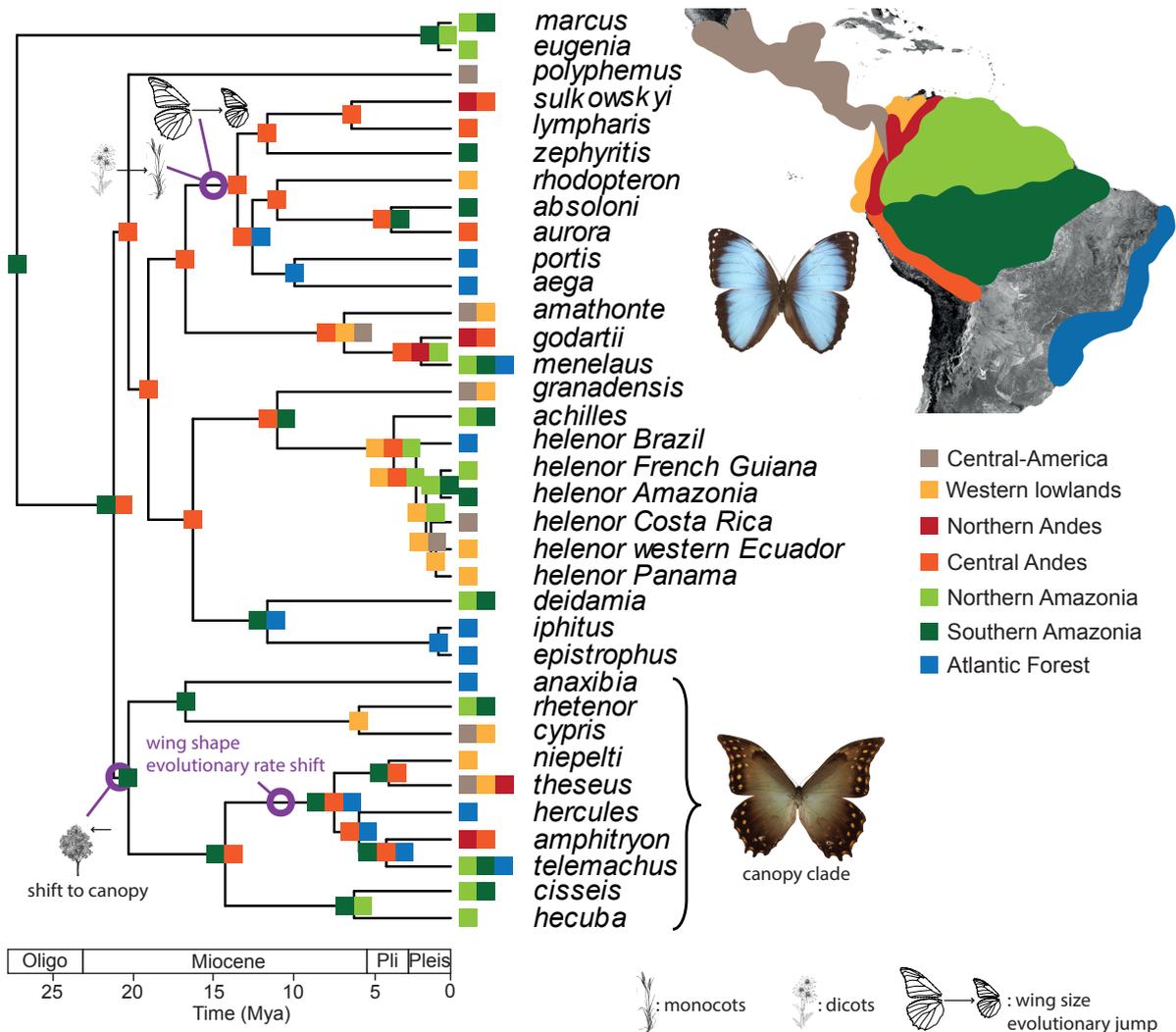


639 **Figure 2.** Rate of wing shape diversification for a) males and b) females. Branches of the  
640 phylogenies are coloured according to the evolutionary rate inferred at the nodes using the R  
641 package GEOMORPH. Green points indicate the changes in the rate of wing shape evolution  
642 and black points the evolutionary jumps of wing size. Only shifts with a posterior tree  
643 frequency higher than 0.5 are shown. PF values indicate the frequency at which each shift  
644 was found across the posterior distribution of trees. On these phylogenies some major  
645 evolutionary events including important host-plant shifts and microhabitat shifts are also  
646 indicated.





650 **Figure 3.** Estimation of the temporal dynamics of diversification for the genus *Morpho*.  
651 Diversification rates (speciation minus extinction) for the best models identified for the  
652 different subclades (canopy and monocotyledon) and the remaining lineages (background).  
653 The early background diversification is elevated and decreases through time until it becomes  
654 negative in the early Miocene. The canopy clade has constant rates of diversification, while  
655 the monocotyledon clade conforms to an early-burst pattern with high rates that decrease  
656 toward the present.  
657



658

659

**Figure 4.** Historical biogeography inferred for the genus *Morpho*. The most likely states are

660

indicated at the nodes. The different clade-specific ecological factors are also indicated on the

661

tree. The two pictures of *Morpho* depict the typical wing shapes associated with each

662

microhabitat – top: short rounded wings characteristic of the understory species, bottom:

663

elongated wings toward the apex characteristic of the canopy clade.

664

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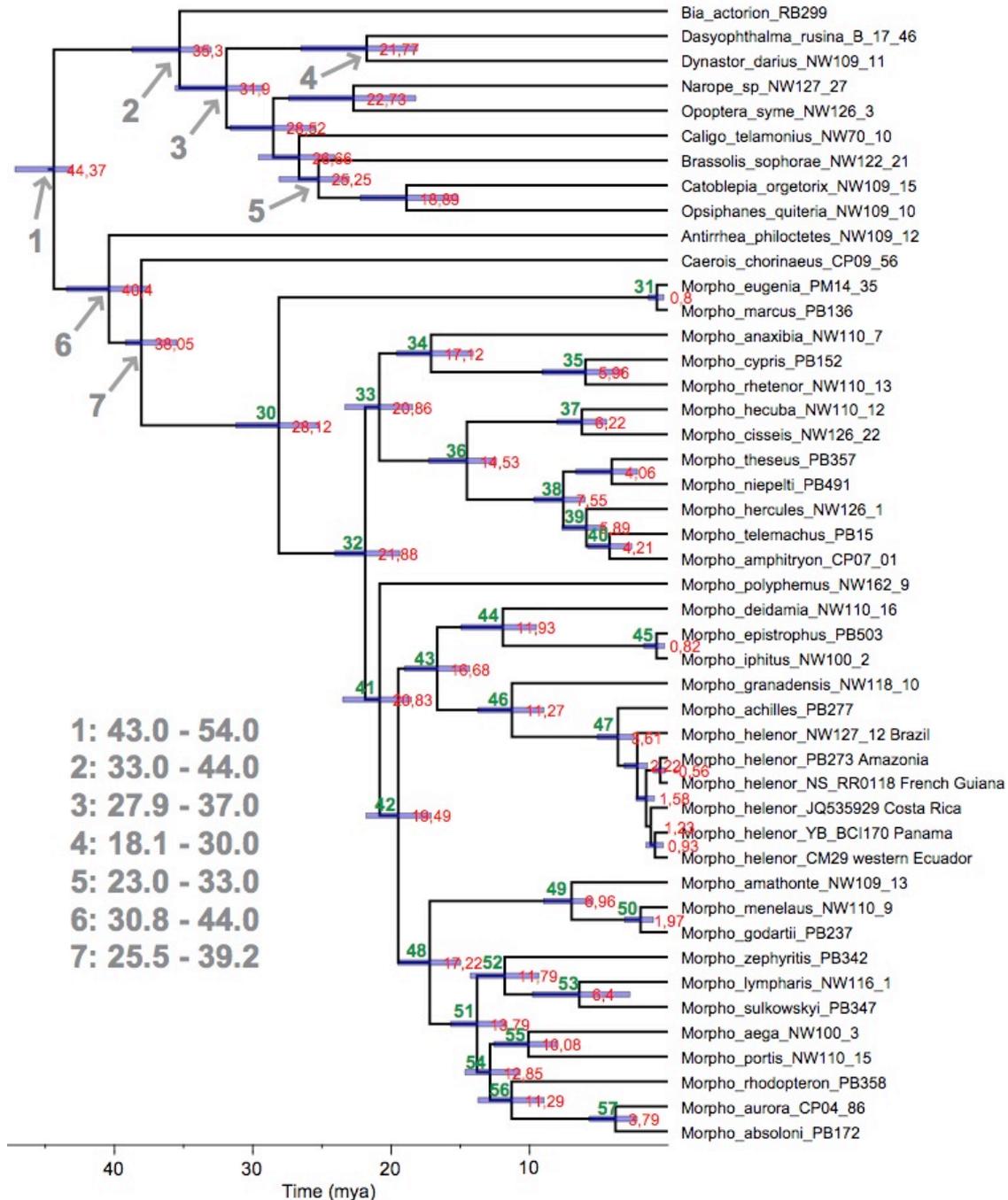
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842

843 Supporting Information S1: Tree reconstructed and time-calibrated using BEAST. Node ages  
 844 in red and the 95% HPD bars are indicated at the nodes. Grey numbers from 1 to 7 are the  
 845 positions of the different time-constraints used. We used uniform distributions bounded by  
 846 the 95% HPD inferred by Wahlberg et al. (2009). Upper and lower boundaries are indicated.  
 847 In green are the node numbers corresponding to the tests for different wing shape  
 848 evolutionary rates.  
 849



850  
 851  
 852

853 Supporting Information S2. Model comparison for wing size evolution for males and females  
854 for the analyses performed on the MCC tree.

855

856 a) Males

857

	Models	AIC	$\Delta$ AIC
Forewing	bm	126.833	0
	rbm	128.402	1.568
	jbm	153.859	27.025
Hindwing	bm	113.605	0
	rbm	115.105	1.5
	jbm	124.984	11.379

858

859 b) Females

860

	Models	AIC	$\Delta$ AIC
Forewing	jbm	122.68	0
	bm	154.069	31.389
	rbm	197.752	75.072
Hindwing	jbm	107.923	0
	rbm	117.123	9.2
	bm	197.547	89.624

861

862 Supporting Information S3. A. Results of models with shifts in rates of wing shape evolution  
 863 for males on the MCC tree.

864

865 a) One-shift models

Wing	Node	Ingroup rate	Background rate	Ratio	p-value	
Forewing	33	3.11E+17	3.70E+17	1.18	0.962	866
	34	5.01E+17	3.34E+17	1.50	0.927	867
	36	2.30E+17	3.87E+17	1.68	0.505	868
	38	2.05E+17	3.80E+17	1.85	0.228	869
	39	1.79E+17	3.70E+17	2.06	0.294	870
	42	2.92E+17	4.38E+17	1.49	0.452	871
	43	3.03E+17	4.13E+17	1.36	0.451	872
	44	2.62E+17	4.02E+17	1.53	0.846	873
	45	2.77E+17	3.77E+17	1.36	0.978	874
	46	3.19E+17	3.54E+17	1.11	0.985	875
	48	2.52E+17	3.70E+17	1.47	0.918	876
	49	2.93E+17	3.57E+17	1.21	0.933	877
	52	2.22E+17	3.65E+17	1.64	0.332	878
	54	3.78E+17	3.44E+17	1.09	0.912	879
	55	2.69E+17	3.60E+17	1.33	0.414	880
57	4.87E+17	3.35E+17	1.45	0.672	881	
Hindwing	33	5.6627E+17	5.4632E+17	1.03	0.994	882
	34	7.0283E+17	5.3632E+17	1.31	0.974	883
	36	5.0774E+17	5.6674E+17	1.11	0.93	884
	38	5.5832E+17	5.519E+17	1.01	0.984	885
	39	4.2922E+17	5.6672E+17	1.32	0.751	886
	42	4.7833E+17	6.6492E+17	1.39	0.536	887
	43	4.9549E+17	6.2814E+17	1.26	0.577	888
	44	5.9163E+17	5.3059E+17	1.11	0.991	889
	45	7.2644E+17	4.8989E+17	1.48	0.965	890
	46	8.6181E+17	5.1865E+17	1.66	0.852	891
	48	6.4522E+17	5.3452E+17	1.20	0.987	892
	49	7.0738E+17	5.3581E+17	1.32	0.892	893
	52	2.3213E+17	5.8862E+17	2.53	0.059	894
	54	3.1922E+17	6.1141E+17	1.91	0.229	895
	<b>55</b>	<b>2.522E+17</b>	<b>5.8639E+17</b>	<b>2.32</b>	<b>0.02</b>	896
57	3.8624E+17	5.7149E+17	1.47	0.658	897	

904

905 *Node = node tested for a shift (see Supporting Information S1). Ingroup rate = rate of*  
 906 *evolution estimated in the putative shifting clade. Background rate = rate of evolution for the*  
 907 *remaining phylogeny outside of the putative shifting clade. Ratio = ratio between the ingroup*  
 908 *and the background rate. p-value = significance value of the ratio. Bold p-values indicate*  
 909 *cases where the p-value was below the significance threshold of 0.05.*

910

911

912 b) Two-shifts models - hindwing  
 913

Model	Structure	Rate	Pairwise comparison	Pairwise ratio	Pairwise p-value
1	55	2.52E+17	1_2	2.25	0.29
	33	5.66E+17	1_B	2.37	0.02
	background	5.98E+17	2_B	1.06	0.99
2	55	2.52E+17	1_2	2.79	0.44
	34	7.02E+17	1_B	2.27	0.02
	background	5.71E+17	2_B	1.23	0.97
3	55	2.52E+17	1_2	2.01	0.29
	36	5.07E+17	1_B	2.43	0.02
	background	6.13E+17	2_B	1.21	0.88
4	55	2.52E+17	1_2	2.21	0.15
	38	5.58E+17	1_B	2.35	0.02
	background	5.92E+17	2_B	1.06	0.92
5	55	2.52E+17	1_2	1.70	0.48
	39	4.29E+17	1_B	2.40	0.02
	background	6.06E+17	2_B	1.41	0.67
6	55	2.52E+17	1_2	2.35	0.26
	44	5.91E+17	1_B	2.31	0.03
	background	5.82E+17	2_B	1.02	1.00
7	55	2.52E+17	1_2	2.88	0.24
	45	7.26E+17	1_B	2.09	0.06
	background	5.27E+17	2_B	1.38	0.99
8	55	2.52E+17	1_2	3.42	0.22
	46	8.61E+17	1_B	2.19	0.02
	background	5.51E+17	2_B	1.56	0.86
9	55	2.52E+17	1_2	2.56	0.39
	48	6.45E+17	1_B	2.27	0.01
	background	5.73E+17	2_B	1.13	0.99
10	55	2.52E+17	1_2	2.80	0.23
	49	7.07E+17	1_B	2.27	0.03
	background	5.71E+17	2_B	1.24	0.91
11	55	2.52E+17	1_2	1.09	0.89
	52	2.32E+17	<b>1_B</b>	<b>2.50</b>	<b>0.01</b>
	background	6.30E+17	<b>2_B</b>	<b>2.72</b>	<b>0.04</b>
12	55	2.52E+17	1_2	1.53	0.57
	57	3.86E+17	1_B	2.42	0.02
	background	6.11E+17	2_B	1.58	0.62

914  
 915 *Structure* = structure of the model, i.e. the node number of the two putative shifts tested and  
 916 remaining phylogeny outside from the putative shifting clade (“background”). In each case  
 917 the first node indicated is the node retained in the one-shift model comparisons. Rate = rate  
 918 of evolution of each part of the model, i.e. two ingroup rates and one background rate.  
 919 *Pairwise comparison* = pairs considered in the following pairwise comparison (1-2=ingroup

920 *1 and ingroup 2, 1-B=ingroup 1 and background, 2-B=ingroup 2 and background). Pairwise*  
921 *ratios = ratio between the two rates considered in the pairwise comparison. Pairwise p-value*  
922 *= significance value of the pairwise ratio. Bold p-values indicate the case for which both*  
923 *subclades were significantly different than the background rate.*  
924  
925

926 Supporting Information S4.

927 A. Results of models with shifts in rates of wing shape evolution for females on the MCC  
 928 tree.

929

930 a) One-shift models

Wing	Node	Ingroup rate	Background rate	Ratio	p-value	931 932
Forewing	32	5.49E+19	5.40E+17	101.55	0.001	933
	33	5.58E+17	1.93E+19	34.67	0.001	934
	35	8.20E+19	5.43E+17	151.17	0.001	935
	<b>37</b>	<b>1.22E+20</b>	<b>6.18E+17</b>	<b>197.98</b>	<b>0.001</b>	936
	38	1.60E+20	9.45E+17	169.38	0.001	937
	40	5.18E+17	4.50E+19	86.97	0.001	938
	41	5.04E+17	4.13E+19	82.09	0.001	939
	42	6.09E+17	2.77E+19	45.45	0.001	940
	43	5.96E+17	2.38E+19	39.97	0.001	941
	44	6.17E+17	1.93E+19	31.35	0.001	942
	46	5.83E+17	2.09E+19	35.87	0.001	943
	47	5.78E+17	1.93E+19	33.48	0.001	944
	50	6.44E+17	1.93E+19	30.03	0.001	945
	52	3.11E+17	2.19E+19	70.32	0.001	946
	55	2.84E+17	1.94E+19	68.29	0.001	947
Hindwing	32	8.32E+19	8.50E+17	97.89	0.001	948
	33	7.17E+17	2.93E+19	40.99	0.001	949
	35	1.25E+20	8.33E+17	149.48	0.001	950
	<b>37</b>	<b>1.86E+20</b>	<b>9.29E+17</b>	<b>199.94</b>	<b>0.001</b>	951
	38	2.43E+20	1.47E+18	164.93	0.001	952
	40	8.57E+17	6.82E+19	79.66	0.001	953
	41	8.56E+17	6.26E+19	73.13	0.001	954
	42	9.60E+17	4.19E+19	43.71	0.001	955
	43	1.00E+18	3.61E+19	36.09	0.001	956
	44	9.08E+17	2.93E+19	32.31	0.001	957
	46	1.05E+18	3.17E+19	30.04	0.001	958
	47	1.01E+18	2.93E+19	28.79	0.001	959
50	8.54E+17	2.93E+19	34.39	0.001	960	
52	6.66E+17	3.32E+19	49.75	0.001	961	
55	8.44E+17	2.93E+19	34.79	0.001	962	

955 *Structure* = structure of the model, i.e. the node number of the two putative shifts tested and  
 956 remaining phylogeny outside from the putative shifting clade (“background”). In each case  
 957 the first node indicated is the node retained in the one-shift model comparisons. Rate = rate  
 958 of evolution of each part of the model, i.e. two subclade rates and one background rate.  
 959 Pairwise comparison = pairs considered in the following pairwise comparison ( $1_2$  =  
 960 subclade 1 and subclade 2,  $1_B$  = subclade 1 and background,  $2_B$  = subclade 2 and  
 961 background). Pairwise ratios = ratio between the two rates considered in the pairwise

962 *comparison. Pairwise p-value = significance value of the pairwise ratio. Bold p-values*  
963 *indicate the case for which both subclades were significantly different than the background*  
964 *rate.*  
965

Model	Structure	Rate	Pairwise comparison	Pairwise ratio	Pairwise p-value
1	37	1.22E+20	1_2	219.22	0.001 <sup>967</sup>
	33	5.57E+17	1_B	195.40	0.001 <sup>968</sup>
	background	6.25E+17	2_B	1.12	0.95 <sup>969</sup>
2	37	1.22E+20	1_2	236.21	0.001 <sup>971</sup>
	40	5.17E+17	1_B	139.80	0.001 <sup>972</sup>
	background	8.74E+17	2_B	1.68	0.521 <sup>973</sup>
3	37	1.22E+20	1_2	242.87	0.001 <sup>974</sup>
	41	5.03E+17	1_B	142.15	0.001 <sup>975</sup>
	background	8.60E+17	2_B	1.70	0.468 <sup>976</sup>
4	37	1.22E+20	1_2	200.93	0.001 <sup>977</sup>
	42	6.08E+17	1_B	195.72	0.001 <sup>978</sup>
	background	6.24E+17	2_B	1.02	0.99 <sup>979</sup>
5	37	1.22E+20	1_2	205.38	0.001 <sup>980</sup>
	43	5.95E+17	1_B	194.68	0.001 <sup>981</sup>
	background	6.28E+17	2_B	1.05	0.983 <sup>982</sup>
6	37	1.22E+20	1_2	198.28	0.001 <sup>983</sup>
	44	6.16E+17	1_B	197.94	0.001 <sup>984</sup>
	background	6.17E+17	2_B	1.00	1 <sup>985</sup>
7	37	1.22E+20	1_2	209.89	0.001 <sup>986</sup>
	46	5.82E+17	1_B	195.21	0.001 <sup>987</sup>
	background	6.26E+17	2_B	1.07	0.964 <sup>988</sup>
8	37	1.22E+20	1_2	211.71	0.001 <sup>989</sup>
	47	5.77E+17	1_B	196.25	0.001 <sup>990</sup>
	background	6.23E+17	2_B	1.07	0.942 <sup>991</sup>
9	37	1.22E+20	1_2	189.97	0.001 <sup>992</sup>
	50	6.43E+17	1_B	199.13	0.001 <sup>993</sup>
	background	6.14E+17	2_B	1.04	0.96 <sup>994</sup>
10	37	1.22E+20	1_2	393.42	0.001 <sup>995</sup>
	52	3.10E+17	1_B	171.13	0.001 <sup>996</sup>
	background	7.14E+17	2_B	2.29	0.231 <sup>997</sup>
11	37	1.22E+20	1_2	361.82	0.001 <sup>998</sup>
	53	3.38E+17	1_B	186.47	0.001 <sup>999</sup>
	background	6.55E+17	2_B	1.94	0.328 <sup>1000</sup>
12	37	1.22E+20	1_2	431.07	0.001 <sup>1001</sup>
	55	2.83E+17	1_B	184.39	0.001 <sup>1002</sup>
	background	6.63E+17	2_B	2.33	0.333 <sup>1003</sup>

998 *Structure* = structure of the model, i.e. the node number of the two putative shifts tested and  
 999 remaining phylogeny outside from the putative shifting clade (“background”). In each case  
 1000 the first node indicated is the node retained in the one-shift model comparisons. Rate = rate  
 1001 of evolution of each part of the model, i.e. two subclade rates and one background rate.  
 1002 Pairwise comparison = pairs considered in the following pairwise comparison (1\_2 =  
 1003 subclade 1 and subclade 2, 1\_B = subclade 1 and background, 2\_B = subclade 2 and

1004 *background). Pairwise ratios = ratio between the two rates considered in the pairwise*  
1005 *comparison. Pairwise p-value = significance value of the pairwise ratio. Bold p-values*  
1006 *indicate the case for which both subclades were significantly different than the background*  
1007 *rate.*  
1008

1009 c) Two-shifts models - hindwing

Model	Structure	Rate	Pairwise comparison	Pairwise ratio	Pairwise p-value
1	37	1.86E+20	1_2	259.14	0.001012
	33	7.17E+17	1_B	193.90	0.001013
	background	9.58E+17	2_B	1.33	0.8921014
2	37	1.86E+20	1_2	216.81	0.001016
	40	8.57E+17	1_B	166.60	0.001017
	background	1.11E+18	2_B	1.30	0.7471018
3	37	1.86E+20	1_2	216.87	0.001019
	41	8.56E+17	1_B	171.49	0.001020
	background	1.08E+18	2_B	1.26	0.7331021
4	37	1.86E+20	1_2	193.41	0.001022
	42	9.60E+17	1_B	205.38	0.001023
	background	9.04E+17	2_B	1.06	0.9771024
5	37	1.86E+20	1_2	185.70	0.001026
	43	1.00E+18	1_B	207.42	0.001027
	background	8.95E+17	2_B	1.11	0.9641028
6	37	1.86E+20	1_2	204.42	0.001029
	44	9.08E+17	1_B	199.34	0.001030
	background	9.32E+17	2_B	1.02	0.9881031
7	37	1.86E+20	1_2	176.03	0.001032
	46	1.05E+18	1_B	206.96	0.001033
	background	8.97E+17	2_B	1.17	0.9281034
8	37	1.86E+20	1_2	182.23	0.001035
	47	1.01E+18	1_B	202.62	0.001036
	background	9.17E+17	2_B	1.11	0.9461037
9	37	1.86E+20	1_2	217.50	0.001039
	50	8.54E+17	1_B	197.76	0.001040
	background	9.39E+17	2_B	1.09	0.9361041
10	37	1.86E+20	1_2	278.86	0.001042
	52	6.66E+17	1_B	183.53	0.001043
	background	1.01E+18	2_B	1.51	0.5361044
11	37	1.86E+20	1_2	380.70	0.001045
	53	4.88E+17	1_B	187.78	0.001046
	background	9.89E+17	2_B	2.02	0.3361047
12	37	1.86E+20	1_2	220.01	0.001049
	55	8.44E+17	1_B	197.48	0.001050
	background	9.40E+17	2_B	1.11	0.8821051

1052

1053

1054

1055 *Structure* = structure of the model, i.e. the node number of the two putative shifts tested and

1056 remaining phylogeny outside from the putative shifting clade (“background”). In each case

1057 the first node indicated is the node retained in the one-shift model comparisons. Rate = rate

1058 of evolution of each part of the model, i.e. two subclade rates and one background rate.

1059 *Pairwise comparison = pairs considered in the following pairwise comparison (1\_2 =*  
1060 *subclade 1 and subclade 2, 1\_B = subclade 1 and background, 2\_B = subclade 2 and*  
1061 *background). Pairwise ratios = ratio between the two rates considered in the pairwise*  
1062 *comparison. Pairwise p-value = significance value of the pairwise ratio. Bold p-values*  
1063 *indicate the case for which both subclades were significantly different than the background*  
1064 *rate.*

1065 Supporting Information S5. Results of all time-dependent diversification models fitted on the  
 1066 *Morpho*, the different subscales tested (canopy, monocots, shape shift) and the corresponding  
 1067 backbone trees. *Model* indicates the shape of speciation and extinction rate functions:  
 1068 BCST=constant speciation, BVAR=time-dependent speciation, DCST=constant extinction,  
 1069 DVAR=time-dependent extinction. Par=number of parameters in the model. logL=likelihood  
 1070 of the model. AIC=Akaike Information Criterion.  $\lambda$  =speciation rate at present,  $\alpha$ =coefficient  
 1071 of time variation of the speciation rate,  $\mu$  =extinction rate at present,  $\beta$  =coefficient of time  
 1072 variation of the extinction rate.

1073

**Whole tree**

Model	Par	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
BVAR	2	-96.97	197.95	0.00	0.053	0.047		
BCST	1	-98.40	198.81	0.86	0.081			
BVARDCST	3	-96.97	199.95	2.00	0.053	0.047	0.000	
BCSTDCST	2	-98.40	200.81	2.86	0.081		0.000	
BVARDVAR	4	-96.97	201.95	4.00	0.053	0.047	0.000	0.019
BCSTDVAR	3	-98.40	202.81	4.86	0.081		0.000	0.014

**Background without canopy**

Model	Par	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
BCST	1	-67.01	136.03	0.00	0.080			
BVAR	2	-66.10	136.20	0.18	0.053	0.044		
BCSTDCST	2	-67.01	138.03	2.00	0.080		0.000	
BVARDCST	3	-66.04	138.09	2.06	0.060	0.049	0.034	
BVARDVAR	4	-65.75	139.50	3.47	0.144	0.006	1.048	-0.691
BCSTDVAR	3	-67.01	140.03	4.00	0.080		0.000	0.002

**Background without monocots**

Model	Par	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
BCST	1	-73.75	149.49	0.00	0.081			
BVAR	2	-73.24	150.48	0.98	0.060	0.031		
BVARDVAR	4	-71.58	151.16	1.66	0.034	0.205	0.039	0.201
BCSTDCST	2	-73.75	151.49	2.00	0.081		0.000	
BVARDCST	3	-72.83	151.65	2.16	0.081	0.051	0.101	
BCSTDVAR	3	-73.75	153.49	4.00	0.081		0.000	-0.039

**Background without shape shift**

Model	Par	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
BVAR	2	-76.57	157.13	0.00	0.045	0.054		
BCST	1	-78.18	158.36	1.22	0.078			
BVARDCST	3	-76.52	159.04	1.91	0.051	0.059	0.028	

BCSTDCST	2	-78.18	160.36	3.22	0.078		0.000	
BWARDVAR	4	-76.45	160.89	3.76	0.061	0.047	0.146	-0.287
BCSTDVAR	3	-78.18	162.36	5.22	0.078		0.000	-0.008

**Background without monocots and canopy**

Model	Par	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
BWARDVAR	4	-35.68	79.36	0.00	0.063	0.237	0.079	0.228
BCST	1	-39.78	81.57	2.20	0.073			
BCSTDCST	2	-39.39	82.78	3.41	0.119		0.089	
BCSTDVAR	3	-38.70	83.39	4.03	0.180		0.493	-0.154
BWARDCST	3	-39.47	84.94	5.57	0.183	0.045	0.330	
BVAR	2	-42.22	88.43	9.07	0.064	0.020		

**Background without monocots and shape shift**

Model	Par	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
BCST	1	-50.91	103.83	0.00	0.072			
BWARDVAR	4	-48.05	104.11	0.28	0.046	0.215	0.061	0.205
BCSTDVAR	3	-49.56	105.13	1.30	0.177		0.668	-0.242
BCSTDCST	2	-50.90	105.80	1.97	0.078		0.013	
BWARDCST	3	-50.72	107.45	3.62	0.124	0.057	0.246	
BVAR	2	-52.90	109.80	5.97	0.050	0.039		

**Canopy**

Model	Par	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
BCST	1	-31.39	64.77	0.00	0.083			
BVAR	2	-30.81	65.62	0.84	0.050	0.059		
BCSTDCST	2	-31.39	66.77	2.00	0.083		0.000	
BWARDCST	3	-30.81	67.62	2.84	0.050	0.059	0.000	
BCSTDVAR	3	-31.39	68.77	4.00	0.083		0.000	0.014
BWARDVAR	4	-30.81	69.62	4.84	0.050	0.059	0.000	0.020

**Monocots**

Model	Par	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
BVAR	2	-21.78	47.55	0.00	0.014	0.213		
BWARDCST	3	-21.78	49.55	2.00	0.014	0.213	0.000	
BCST	1	-24.66	51.31	3.76	0.080			
BWARDVAR	4	-21.78	51.55	4.00	0.014	0.213	0.000	0.010
BCSTDCST	2	-24.66	53.31	5.76	0.080		0.000	
BCSTDVAR	3	-24.66	55.31	7.76	0.080		0.000	0.010

**Shape shift**

Model	Par	logL	AIC	$\Delta$ AIC	$\lambda$	$\alpha$	$\mu$	$\beta$
BCST	1	-20.14	42.28	0.00	0.095			

BVAR	2	-20.09	44.18	1.91	0.081	0.023		
BCSTDCST	2	-20.14	44.28	2.00	0.095		0.000	
BVARDCST	3	-20.09	46.18	3.91	0.081	0.023	0.000	
BCSTDVAR	3	-20.14	46.28	4.00	0.095		0.000	0.029
BWARDVAR	4	-20.09	48.18	5.91	0.081	0.023	0.000	0.037

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1074 Supporting Information S6. Adjacency matrix and dispersal matrices time-stratified used for  
 1075 the BioGeoBEARS ancestral state reconstruction. CA=Central America, SN=Sierra Nevada  
 1076 de Santa Maria, W=lowland western Andes, N=Northern Andes, S=Central Andes,  
 1077 NAz=Northern Amazonia, SAz=Southern Amazonia, AF=Atlantic Forest.

1078

1079 a) Adjacency matrix

	CA	SN	W	N	S	NAz	SAz	AF
CA	1	0	1	1	0	0	0	0
SN	0	1	1	0	0	0	0	0
W	1	1	1	1	1	1	0	0
N	1	1	1	1	1	1	0	0
S	0	1	1	1	0	0	1	1
NAz	0	1	1	0	1	1	1	0
SAz	0	0	0	1	1	1	1	1
AF	0	0	0	1	0	0	1	1

1080

1081 b) Dispersal multipliers matrix

1082

1083 **0-5 mya**

	CA	SN	W	N	S	NAz	SAz	AF
CA	1	0	1	0	0	0	0	0
SN	0	1	0	0	0	0	0	0
W	1	0	1	0	0	0	0	0
N	0	0	0	1	1	1	1	0
S	0	0	0	1	1	0.1	1	0.5
NAz	0	0	0	1	0.1	1	0.1	0
SAz	0	0	0	1	1	0.1	1	0
AF	0	0	0	0	0.5	0	0	1

**5-10 mya**

	CA	SN	W	N	S	NAz	SAz	AF
CA	1	0	0	0	0	0	0	0
SN	0	1	0	0	0	0	0	0
W	0	0	1	0.5	0.5	0.25	0	0
N	0	0	0.5	1	0.5	0.5	0.5	0
S	0	0	0.5	0.5	1	0.1	1	0.5
NAz	0	0	0.25	0.5	0.1	1	0.1	0
SAz	0	0	0	0.5	1	0.1	1	0
AF	0	0	0	0	0.5	0	0	1

**10-15 mya**

	CA	SN	W	N	S	NAz	SAz	AF
CA	1	0	0	0	0	0	0	0
SN	0	1	0.5	0.25	0	0	0	0
W	0	0.5	1	0.5	0.5	0	0	0
N	0	0.25	0.5	1	0	0	0	0
S	0	0	0.5	0	1	1	1	0.5
NAz	0	0	0	0	1	1	1	0
SAz	0	0	0	0	1	1	1	0
AF	0	0	0	0	0.5	0	0	1

**15-23 mya**

	CA	SN	W	N	S	NAz	SAz	AF
CA	1	0	0.5	0	0	0	0	0
SN	0	1	0.5	0.5	0	0	0	0
W	0.5	0.5	1	1	0.5	0	0	0
N	0	0.5	1	1	0	0	0	0
S	0	0	0.5	0	1	1	1	0.5
NAz	0	0	0	0	1	1	1	0
SAz	0	0	0	0	1	1	1	0
AF	0	0	0	0	0.5	0	0	1

**23-30 mya**

	CA	SN	W	N	S	NAz	SAz	AF
CA	1	0	0	0	0	0	0	0
SN	0	1	0.5	0.5	0	0	0	0
W	0	0.5	1	1	0.5	0	0	0
N	0	0.5	1	1	0.5	0	0.5	0
S	0	0	0.5	0.5	1	1	1	0.5
NAz	0	0	0	0	1	1	1	0.5
SAz	0	0	0	0.5	1	1	1	0.5
AF	0	0	0	0	0.5	0.5	0.5	1

1084  
1085