



Trait evolution, resource specialization and vulnerability to plant extinctions among Antillean hummingbirds

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1 Correction to ‘Trait evolution, resource
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3 extinction among Antillean hummingbirds’

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16 Add the following text in the Acknowledgements:

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20

21

22 **Trait evolution, resource specialisation and vulnerability to plant extinctions among Antillean**
23 **hummingbirds**

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43 **Abstract (max 200 words)**

44 Species traits are thought to predict feeding specialisation and the vulnerability of a species to
45 extinctions of interaction partners, but the context in which a species evolved and currently inhabits
46 may also matter. Notably, the predictive power of traits may require that traits evolved to fit
47 interaction partners. Furthermore, local abiotic and biotic conditions may be important. On islands,
48 for instance, specialised and vulnerable species are predicted to be found mainly in mountains,
49 whereas species in lowlands should be generalized and less vulnerable. We evaluated these
50 predictions for hummingbirds and their nectar-food plants on Antillean islands. Our results suggest
51 that the rates of hummingbird trait divergence were higher among ancestral mainland forms before
52 the colonization of the Antilles. In correspondence with the limited trait evolution that occurred
53 within the Antilles, local abiotic and biotic conditions – not species traits – correlate with
54 hummingbird resource specialisation and the vulnerability of hummingbirds to extinctions of their
55 floral resources. Specifically, hummingbirds were more specialised and vulnerable in conditions
56 with high topographical complexity, high rainfall, low temperatures, and high floral resource
57 richness, which characterize the Antillean Mountains. These findings show that resource
58 specialisation and species vulnerability to extinctions of interaction partners are highly context
59 dependent.

60

61 **Keywords: island biology, mountains, mutualistic networks, endemics, specialisation, taxon**
62 **cycles**

63 **1. Introduction**

64 For more than one hundred and fifty years, ecologists have realized that species are entangled in
65 networks of interactions with locally co-occurring species [1, 2]. Species interaction networks can be
66 used to investigate whether species traits influence resource specialisation and species vulnerability
67 to extinctions of their interaction partners [3–5], but how these crucial aspects of species ecology
68 are predicted by local abiotic and biotic conditions is less well known [6–8]. Moreover, although
69 traits may evolve to exploit specific resources and minimize competition [9, 10], it is poorly
70 understood whether the importance of traits in determining resource specialisation and species
71 vulnerability is related to rates of trait evolution. In other words, the context in which a species
72 evolved, and is currently distributed, is often neglected as a determinant of resource specialisation
73 and vulnerability to the extinction of interaction partners.

74 With respect to resource specialisation, island organisms are often found to be more
75 generalized than their mainland counterparts, and sometimes engage in interactions rarely observed
76 on the mainland e.g. pollination by lizards [11–13]. Such generalized behavior may be due to the
77 limited number of species and reduced interspecific competition on islands, resulting in ecological
78 release and the evolution of generalized feeding niches [11]. Colonization history may also matter,
79 as mainland generalists from the lowland should more easily colonize and establish on islands than
80 mainland specialists and mountainous species [14, 15]. However, not all island species have
81 generalized feeding niches, particularly if they undergo sequential phases of range expansion and
82 contraction as predicted by taxon cycle theory. Notably, according to taxon cycle theory, newly
83 colonized species that are in a period of range expansion often have fairly generalized niches and
84 establish in marginal lowland habitats, whereas species at the end of the taxon cycle are endemics
85 specialised to interior mountain abiotic and biotic environments [15–17]. Thus, contrary to the
86 prevailing trend for island species to be generalists, mountain endemics may provide extreme

87 examples of specialisation. One such example is the Purple-throated Carib (*Eulampis jugularis*), an
88 endemic hummingbird specialised to feed on nectar from the flowers of *Heliconia* plants in the
89 Lesser Antillean mountains [9, 18]. On islands, there should therefore be an association between
90 local conditions and the level of resource specialisation: lowland species being generalized and
91 species in mountains being more specialised.

92 In addition to these geographical trends in resource generalization-specialisation,
93 island species are known to be more vulnerable to extinction than mainland species [19, 20]. For
94 example, during the last 400 years, about 90% of all bird extinctions have occurred on islands [19].
95 This is thought to be a consequence of island populations being small – many are endemic to one or
96 a few islands – and because island species have evolved largely in isolation. Thus, species on
97 islands are susceptible to natural disasters, habitat destruction and introduced species [20], such as
98 rats or cats, causing extinctions and threatening endemics across numerous islands throughout the
99 world. The negative consequences of disrupting mutualistic associations are a further potentially
100 important influence upon the extinction risk of island taxa, but these are less well known [21]. Bird
101 pollination provides a good example of how disrupting mutualistic associations can influence
102 reproductive output and population density [22]. Recently, species vulnerability to the extinction of
103 their mutualistic partners has been modelled using networks of interactions between animal and
104 plant communities [5, 7, 23, 24], illustrating that plant extinctions are more likely to cause animal
105 coextinctions than *vice versa* [7]. However, it remains poorly understood how animal vulnerability
106 to plant extinctions is affected by their traits and local abiotic and biotic conditions.

107 Here, we use mutualistic plant-hummingbird networks in the Antillean archipelago to
108 ask how species traits and local abiotic and biotic conditions relate to resource specialisation and
109 hummingbird vulnerability to plant extinctions. Hummingbirds have a long co-evolutionary history
110 with their nectar-food plants, which they are energetically highly dependent on. Likewise, although

111 plants pollinated by hummingbirds may also be pollinated by other animals [18], many are, to a
112 large extent, dependent on hummingbird's pollination services [25, 26]. Notably, large-bodied and
113 long-billed hummingbirds, and those living in wet, cool and topographically heterogeneous
114 environments, seem to establish specialised interactions with their nectar-food plants [9, 18, 27–29].
115 High resource specialisation may reduce competition between hummingbirds, increase the
116 likelihood of pollen transfer among conspecific plants [3, 30], and thus benefit both the
117 hummingbirds and their nectar-food plants. However, high resource specialisation may also make
118 them more vulnerable to extinctions of their mutualistic partners [31, 32]. It is therefore important
119 to understand to what degree resource specialisation and vulnerability to plant extinctions are
120 associated with hummingbird traits and local abiotic and biotic conditions. As the evolution of
121 hummingbird traits, notably bill length and body mass, may be associated with specialisation on
122 specific floral resources that have matching corolla morphologies and nectar-production rates [9], it
123 is relevant to assess the degree of trait evolution among the Lesser Antillean hummingbirds. As
124 such, we expect hummingbird traits to determine specialisation and vulnerability when traits have
125 co-evolved *in situ* to fit their floral partners in the Antilles. Thus we ask: (1) have the rates of
126 hummingbird body size and bill length evolution been highest early or late in the history of
127 Antillean hummingbirds, i.e. did hummingbird body size and bill length evolve primarily among
128 ancestral mainland forms prior to colonizing the islands or more recently on the Antillean islands?
129 (2) within the Antilles, is hummingbird resource specialisation and vulnerability to plant extinctions
130 associated mainly with (a) morphological traits that are important for partitioning floral resources,
131 i.e. hummingbird bill length and body mass, or (b) the abiotic and biotic conditions of the localities
132 in which they occur? As measures of local abiotic conditions we include topographic heterogeneity,
133 precipitation, and temperature, whereas biotic conditions were represented by hummingbird and
134 nectar-food plant richness. These abiotic and biotic factors are hypothesized to influence how

135 hummingbirds partition floral resources. Specifically, species-rich communities and wet, cool
136 mountain environments are hypothesized to support more specialised and vulnerable hummingbird
137 species [18, 27].

138

139 **2. Materials and Methods**

140 **(a) Hummingbird trait evolution**

141 Extant hummingbirds colonised South America ~ 22 Mya, and arrived through multiple
142 colonization events to the Antillean archipelago approximately 5-9 Mya (Figure 1a, [33, 34]). All
143 Antillean hummingbirds are endemic to the archipelago, except the Rufous-breasted Hermit
144 (*Glaucis hirsutus*) which is found both on the South American mainland and on Grenada, the most
145 southern island of the Antilles. We used phylogenetic comparative methods to evaluate changes in
146 the rate of morphological evolution among Antillean hummingbird species through time, and to
147 subsequently assess whether the body size and bill length of Antillean hummingbirds likely evolved
148 on the mainland prior to colonizing the islands, or on the Antillean islands. To achieve this, we used
149 a recent hummingbird phylogeny [33] which represents a highly resolved time-calibrated analysis
150 of molecular data from 284 hummingbird species (~86% of all hummingbird species). The
151 maximum clade credibility tree from this analysis was pruned to contain 13 of the 14 Antillean
152 hummingbird species. Among the Antillean species, only *Mellisuga helenae* is missing from the
153 phylogeny [33]. We analyzed rates of hummingbird morphological diversification using
154 phylogenetic independent contrasts (PICs; [35]) and Blomberg's K in the R packages APE and
155 phytools [36–38]. The absolute values of the contrasts for body mass and bill length were regressed
156 against node age using linear models, which enables assessment of how evolutionary rates change
157 through time. Subsequently, we used Blomberg's K to test for the phylogenetic signal in both body

158 mass and bill length. PICs and Blomberg's K represent alternative methods of assessing rates of
159 trait evolution and how these compare to the null expectation under a Brownian motion model of
160 evolution [35–38]. The smallest bird in the world, the Bee Hummingbird (*Mellisuga helenae*), is
161 endemic to Cuba in the Greater Antilles. Although *Mellisuga helenae* is missing from the
162 phylogeny [33], and therefore not included in our analysis, we expect the results presented to be
163 robust to the inclusion of this species given the similarity in body mass and bill length with its
164 congener *Mellisuga minima* (2.2 g versus 2.4 g body mass; 10.8 mm versus 10.5 mm bill length;
165 Table S1).

166 **(b) Hummingbird specialisation on nectar-food plants**

167 To estimate hummingbird specialisation on nectar-food plants in the Antilles, we assembled a
168 database of our own Antillean hummingbird-plant network studies, which recorded mutualistic
169 interactions between assemblages of hummingbirds and their nectar-food plants. Details on the
170 sampling can be found in [18], but here we give a brief overview. The database includes eight
171 networks covering 12 of the 14 hummingbird species in the Antilles, only missing the Jamaican
172 Mango (*Anthracothonax mango*) and Hispaniolan Emerald (*Chlorostilbon swainsonii*). Within the
173 study plots of each network, we surveyed all flowering plant species for hummingbird visitation. In
174 all networks, the link weight of each legitimate plant-hummingbird interaction was reported as the
175 visitation rates of hummingbirds to flowers. Compared to binary networks, which only record
176 whether an interaction occurred or not, weighted networks better reflect the dependencies between
177 species [39]. Additionally, network-derived specialisation indices based on weighted networks are
178 less sensitive to sampling effort than their binary counterparts, making cross-network comparisons
179 more reliable [40–43]. All studies collected hummingbird-plant interactions within the same season
180 (March to July) and approximately the same sampling length (1.5 to 3.5 months; mean 3 months).
181 The size of the study plots were: 200 m x 5 m (Cuba, Puerto Rico, Grenada; 5 plots), 400 m x 5 m

182 (Dominica; 2 plots) and 870 m x 6 m (Jamaica; 1 plot). In every study, we observed all
183 hummingbird species whose range distribution overlapped the study area. The raw quantitative
184 hummingbird-plant networks can be downloaded from Dryad (doi:10.5061/dryad.5770gm7). See
185 Supplementary material Table S1 for details on the local abiotic and biotic conditions of each
186 network: topographic heterogeneity, precipitation, temperature, and richness of hummingbirds and
187 nectar-food plants.

188 To estimate hummingbird specialisation, we used the ‘complementary specialisation’
189 metric, which is a measure of the partitioning of interactions among species in weighted networks
190 [40]. We calculated the species-level version of complementary specialisation d' (Kullback–Leibler
191 divergence), which measures the interaction specialisation of a given species by quantifying the
192 deviation of interaction frequencies from a null expectation that assumes that all partners interact
193 proportionally to their availability, using interaction frequency as a surrogate for abundance [40].
194 Values of d' are scaled to range from 0 to 1 indicating the extremes of generalization and
195 specialisation, respectively. Complementary specialisation d' is conceived to account for differences
196 in species richness among networks [40]. Calculations of hummingbird specialisation d' were
197 conducted in the bipartite package 1.20 in R [38, 44].

198 Next, we used linear mixed effects models to examine how hummingbird
199 specialisation d' associates with local conditions (abiotic: topography, temperature, precipitation;
200 and biotic: richness of hummingbirds and plants, i.e. network size) and hummingbird traits (bill
201 length and body mass). First, however, due to the relatively small sample size ($n = 12$ hummingbird
202 species) and large number of intercorrelated variables (e.g. for hummingbird bill length and body
203 mass: $n = 12$ species, $r = 0.87$, $P < 0.05$), we reduced the number of predictor variables to two using
204 Principal Component Analysis (PCA). To do this, for each of the two groups of predictors (local
205 conditions and species traits), we used PCA and the broken stick method, identifying one PCA axis

206 each for local conditions (explaining 69% of the total variation; loading: temperature = -0.607,
207 precipitation = 0.832, topography = 0.941, network size = 0.894) and species traits (95%; loading:
208 bill length = 0.975, body mass = 0.975). We note that the data are suitable for PCA analysis, being
209 approximately linear, homoscedastic and normally distributed ($-1.0 < \text{skewness} < 1.1$ [45]). The
210 resulting PCA axes were likewise suitable for linear mixed effects modelling and were not
211 correlated ($r = 0.174$; $p > 0.05$), i.e. there was no association between the local conditions and
212 hummingbird traits. We then ran two linear mixed effects models, one for each of the PCA axes as
213 fixed effects, to predict hummingbird specialisation d' . We used linear mixed effects models
214 because three hummingbird species were observed in more than one network (Table S1) and,
215 therefore, we included hummingbird species identity as a random factor to account for the non-
216 independence of the observations of the same species occurring in different networks [6, 46]. We
217 also ran a full model including both PCA axes (local conditions and hummingbird traits) as
218 predictors of hummingbird specialisation d' . Finally, we performed a set of supplementary models,
219 analyzing the association between hummingbird specialisation d' and the three components of local
220 conditions: 1) local abiotic conditions, 2) local floral resource richness, and 3) local hummingbird
221 richness (the latter two factors representing local biotic conditions). To do this, we first used PCA
222 and the broken stick method for the local abiotic conditions, identifying one PCA axis (explaining
223 68% of the total variation; loading: temperature = -0.681, precipitation = 0.849, topography =
224 0.920). This axis was strongly positively correlated with local resource plant richness ($r = 0.721$; p
225 < 0.05), indicating that in the Antilles there are more hummingbird-visited plant species in
226 topographically complex, high precipitation and low temperature localities than in topographically
227 simple, drier and warmer areas [18, 47]. There was no association between the size of the study
228 plots, the length of the sampling period and the floral resource richness within each site (study plot
229 size: $n = 8$ sites, Pearson's $r = -0.141$; $p = 0.74$; sampling period: $n = 8$ sites, Pearson's $r = 0.187$; $p =$

230 0.66), or with hummingbird specialisation (study plots: R^2 marginal = 0.01, R^2 conditional = 0.01; p
231 = 0.68; sampling period: R^2 marginal = 0.12, R^2 conditional = 0.12; p = 0.16). Thus neither the
232 different sizes of the study plots nor differences in the sampling periods influence our results. For
233 all linear mixed effects models, we report AIC_c, marginal R^2 , and conditional R^2 values to evaluate
234 model performance. To evaluate the performance of each predictor variable, we report coefficient
235 estimates and corresponding P-values, standard errors and 95% confidence intervals. The PCA
236 analyses were conducted in SAM 4.0 [48] and the linear mixed models in SPSS 22 [49].(c)

237 **Hummingbird vulnerability to plant extinctions**

238 We assessed the vulnerability of hummingbird species to iterative plant extinctions in the networks
239 using the recently developed Stochastic Coextinction Model (SCM), full details of which can be
240 found in [50]; here we give a brief overview. In the model, $P_{ij} = R_i d_{ij}$ is the probability of species i
241 going extinct following the extinction of its partner species j . R_i is a species-level property between
242 0 and 1 that reflects the intrinsic demographic dependence of i on the pollination mutualism. In this
243 study, where species i is a plant, R_i reflects the plant's dependence on hummingbird pollination.
244 Where species i is an animal, R_i reflects hummingbird dependence on floral nectar. d_{ij} is the
245 dependence of i on j , defined as the interaction strength between i and j divided by the total
246 interaction strength between i and all its mutualistic partners. In the SCM, let A and B be the two
247 sets of species in the network, with A representing plant species and B representing hummingbird
248 species. Simulations start with the extinction of a single plant species in A. Next, all hummingbird
249 species in B have a probability of extinction following the equation $P_{ij} = R_i d_{ij}$. For each extinction
250 in B, if any, all species in A have a probability of extinction, and so on. This process continues until
251 there are no extinctions and equilibrium is reached. In this way, the SCM allows for complex
252 coextinction cascades: a plant extinction can lead to a pollinator extinction, which in turn can lead
253 to a plant extinction, and so forth. A pervasive phenomenon in nature is the ability for pollinators to

254 rewire, i.e. compensate for the loss of a partner plant species by reallocating lost interactions to
255 other species in the community [51]. In this respect, it is also important to note that, in the SCM, a
256 given species may survive even if all of its partners become extinct, reflecting that hummingbirds
257 may be able to switch to other food resources and plants may not only be pollinated by
258 hummingbirds [18]. Therefore, simulating species vulnerability to extinction using mutualistic
259 networks may not reflect real extinctions in nature, but should reflect reduction in fitness. It is thus
260 an appropriate tool to understand which species are most vulnerable to extinction of their
261 mutualistic partners [24].

262 We ran two groups of simulations. In the first group ('random plant R values'), R
263 values for plants were sampled from a uniform distribution between 0 and 1, with all plant species
264 being assigned the same R value in each model run [50]. In the second group ('expert-assigned
265 plant R values'), R values for plants were assigned based on expert opinion using fieldwork
266 knowledge on floral phenotype and known insect visitation, which may contribute to pollination of
267 hummingbird-visited flowers [18]. Each plant species was assigned low (0 – 0.33), medium (0.33 –
268 0.66) or high (0.66 – 1) R values, or values spanning two or more of these categories. Plants
269 assigned as 'low' have flowers pollinated by both hummingbirds and insects; plants scored as
270 'medium' were plants with intermediate dependence on pollination by hummingbirds; 'high'
271 categorized plants have ornithophilous syndrome flowers rarely visited by insects (for details, see
272 Supplementary Table S2). In each run, all 'low' species were assigned the same randomly sampled
273 value in the 'low' range, all 'medium' species were assigned the same randomly sampled value in
274 the 'medium' range etc. In both group of simulations, as hummingbirds are highly dependent on
275 floral nectar, R values for hummingbirds were assigned as 'high' (0.66 – 1). In each run, all
276 hummingbird species were assigned the same randomly sampled value in the 'high' range. For both
277 groups of model runs (random plant R values and expert-assigned plant R values), we carried out

278 three sets of simulations, corresponding to three different plant extinction sequences [5, 24]. In the
279 first set of simulations, we iteratively removed the lowest degree plant species, i.e. those plant
280 species with fewest hummingbird pollinators. This represents a ‘realistic extinction scenario’ as
281 specialist species tend to be more vulnerable to extinction [24, 31, 32]. In the second set of
282 simulations, we iteratively removed the highest degree species. This quantifies the ‘attack tolerance’
283 of the network; a ‘worst case scenario’ where high degree nodes are lost first [52, 53]. Finally, we
284 simulated the loss of plants in a random order: this represents the null expectation between the two
285 systematic removal orders discussed above [24]. All simulations were run 10,000 times.

286 From these six simulations (two methods of assigning plant R values and three plant
287 extinction sequences), we calculated three measures of hummingbird vulnerability to plant
288 extinctions: (i) the probability of extinction, PE , defined as the proportion of the 10,000 runs in
289 which the species went extinct; (ii) the average proportion of plant species which had to be removed
290 for a given hummingbird species to go extinct across the 10,000 runs (excluding model runs when it
291 survived), representing the speed of extinction, SE ; and (iii) a novel index of vulnerability of
292 extinction, VE , where $VE = PE (1 - SE)$. This index captures two components of vulnerability, such
293 that species are considered more vulnerable when they have a higher probability of extinction (PE)
294 and when, on average, their extinction occurs early in an extinction sequence (when $1 - SE$ is high).
295 The R-codes for calculating the three measures of vulnerability can be downloaded from Dryad
296 (doi:10.5061/dryad.5770gm7).

297 We examined the association between the three measures of hummingbird
298 vulnerability (PE , SE , and VE) and local conditions (temperature, precipitation, topography, and
299 network size, i.e. species richness of hummingbirds and plants) and hummingbird traits (bill length
300 and body mass) using linear mixed effects models. In all cases, the calculations were performed for
301 all three extinction scenarios (iteratively removing species with the lowest degree; iteratively

302 removing species with the highest degree, removing species at random), and for both methods of
303 assigning plant R values: random (Tables 2, S4, S7) and expert assigned dependency values based
304 on floral phenotype and insect visitation (Tables S5-S6). The linear mixed effects modelling
305 approach was identical to the one for hummingbird specialisation d' , including the use of PCA axes,
306 except in this instance we used hummingbird vulnerability as the response variable. We report the
307 results both for the 'Index of vulnerability', VE , (Tables 2, S5 and S7), and 'the speed of
308 extinction', calculated as $1 - SE$, (Tables S4 and S6). As we forced the networks to collapse
309 completely in terms of simulating the removal of all plant species (see above), the probability of
310 hummingbird extinction PE was very high for nearly all species ($0.83 < PE < 0.98$), thus PE
311 showed no association to either local conditions or to hummingbird traits (results not shown).

312

313 **3. Results**

314 **(a) Hummingbird trait evolution**

315 The absolute contrast values of bill length showed a significant negative correlation with distance
316 from the root of the phylogeny (Figure 1b; $r = -0.87$, $P < 0.001$), indicating higher rates of
317 morphological evolution early in the history of Antillean hummingbirds, which has subsequently
318 slowed towards the present day. Differences in hummingbird bill length appear to have accumulated
319 mainly before the colonization of the Antilles 5-9 Mya (Figure 1b). Blomberg's K indicated a
320 greater amount of evolution in bill length than expected under Brownian motion ($K = 1.65$; $P =$
321 0.001) and thus species that share recent evolutionary history are more similar in bill length than
322 expected by chance. Conversely, body mass contrasts were positively but non-significantly
323 correlated with distance from the root of the tree (Figure 1c; $r=0.28$, $P= 0.38$). Blomberg's K
324 suggested body mass to be more divergent than expected under Brownian motion, however, this
325 phylogenetic signal was also non-significant upon performing a randomization test ($K = 0.41$, $P =$

326 0.21). These results suggest the lack of a general trend in the evolution of body mass through time
327 among Antillean hummingbirds; however, we note a large recent contrast among congeners of the
328 genus *Eulampis*, which is endemic to the Antilles (Figure 1c).

329 **(b) Hummingbird specialisation on nectar-food plants**

330 The specialisation of hummingbirds on their nectar plants was not significantly associated with
331 hummingbird body mass or bill length (Table 1). Instead, hummingbird specialisation was strongly
332 associated to the local conditions (Table 1), with specialisation increasing as a factor of the local
333 abiotic conditions (high topographic complexity, high precipitation, and low temperature promoting
334 specialisation; Table S3, Figure 2a) and hummingbird and floral resource richness (Table S3, Figure
335 2b).

336 **(c) Hummingbird vulnerability to plant extinctions**

337 The vulnerability of hummingbirds to plant extinctions VE was not associated with the
338 morphological traits analysed: small and large bodied/billed hummingbirds were equally vulnerable
339 (Table 2, S5). Instead, when removing plant species in a ‘realistic extinction scenario’ (iteratively
340 removing lowest degree plant species) and at random, hummingbird vulnerability was strongly
341 associated to the local conditions (Table 2): hummingbirds were most vulnerable in conditions
342 characterized by high topographic complexity, high precipitation, low temperature, and high floral
343 resource richness (Figure 2c, d). The ‘attack tolerance’ of the network (iteratively removing highest
344 degree plant species) showed no association to either hummingbird traits or local conditions. The
345 results were qualitatively similar when vulnerability was modelled using the speed of hummingbird
346 extinctions $1 - SE$ (Tables S4, S6). All results were also qualitatively consistent irrespective of
347 whether plant dependencies on hummingbird pollination, R , were assigned randomly or by expert
348 opinion (Tables 2, S4-S6).

349

350 **4. Discussion**

351 Our results suggest that high rates of divergence in hummingbird bill length primarily occurred
352 before lineages colonised the Antilles approximately 5-9 Mya, while the evolution of body mass
353 differences were more constant through time (Fig. 1). In correspondence with the limited trait
354 evolution occurring within the Antilles, especially bill length that have often been shown to
355 determine floral niche partitioning [420, 542], we found that hummingbird specialisation on floral
356 resources and their corresponding vulnerability to plant extinctions were not predicted by their bill
357 length and body mass. Instead, hummingbird resource specialisation and vulnerability to plant
358 extinctions were strongly associated with high topographical complexity, more rainfall, cooler
359 temperatures, and greater richness of flowers utilised by hummingbirds (Fig. 2), conditions which
360 characterize the Antillean Mountains [18, 47].

361 These findings fit well with expectations of taxon cycle theory, which predicts that
362 endemic species found in interior mountains are specialised and vulnerable species, whereas species
363 in the lowlands are more generalized and resilient [15, 16]. The repeated structuring of Antillean
364 hummingbird communities into lowland and highland communities – each consisting of one small
365 and one large bodied/billed species – has been suggested to be a consequence of competition,
366 possibly for floral resources [14, 55]. Similar patterns have been observed for other pollination
367 systems, such as coexisting bumblebees that differ in proboscis length to minimize competition
368 [56]. For Antillean hummingbirds, there is also recent evidence of competitive exclusion, as the
369 Lesser Antillean species *Orthorhyncus cristatus* and *Eulampis holosericeus* have expanded north in
370 recent years displacing the Greater Antillean species *Anthracothonax dominicus* from many of the
371 Virgin Islands and northeastern Puerto Rico [14, 57]. Combined with the apparently limited trait

372 evolution that occurred in the Antilles (Fig. 1), this suggests that the structuring of hummingbird
373 communities largely reflects an assembly process, possibly driven by competition for the limited
374 nectar-food plant richness observed in the Antilles. The competition for floral resources may have
375 allowed hummingbirds already differentiated in size, i.e. only one small and one large bodied/billed
376 hummingbird species, to enter a given community, thereby resulting in minor evolutionary changes
377 in bill length and body mass among the constituent Antillean hummingbird species. This idea is
378 similar to Janzen's 'ecological fitting' hypothesis, whereby species utilize niches based on the traits
379 they carried with them but which evolved somewhere else [58, 59]. The main exception to this
380 general trend was a large divergence in body mass between the members of the genus *Eulampis*
381 (Fig. 1c). We suggest this most likely reflects evolutionary increases in the mass of *Eulampis*
382 *jugularis*, a large and highly dimorphic mountain endemic that is highly specialised on *Heliconia*
383 flowers [9, 18]. Conversely, *E. holosericeus* is a smaller and less dimorphic species feeding on an
384 array of flowers throughout the Lesser Antillean lowlands [18]. This would further underline that
385 the Antillean mountains has provided optimal conditions for specialised associations between
386 hummingbirds and their nectar-food plants.

387 Taken together, our results indicate that mountain environments, and the
388 corresponding high richness of flowering plants attracting hummingbird pollinators, have
389 influenced the evolution and maintenance of a highly specialised and vulnerable endemic
390 hummingbird fauna in the Antillean Mountains. These results have implications for the
391 conservation of species engaged in mutualistic associations. Notably, as climate change and
392 anthropogenic activity disrupt mutualistic associations, and cause pollinator and plant extinctions
393 [7, 60, 61], the montane biota of the Antilles is more susceptible to extinction of mutualistic
394 partners than the biota in the lowlands. The role of mountain environments in sustaining a highly
395 specialised and vulnerable endemic fauna may be a general phenomenon also occurring in other

396 taxa and in a mainland context [29, 62]. This underlines that resource specialisation and
397 vulnerability is highly context dependent, and that the local abiotic and biotic conditions should be
398 more integrated into studies predicting resource specialisation and vulnerability to extinctions of
399 interaction partners.

400

401 **Data accessibility**

402 The raw quantitative hummingbird-plant networks, morphological and phylogenetic data can be
403 downloaded at Dryad (doi:10.5061/dryad.5770gm7). For each hummingbird-plant network, details
404 on the local abiotic and biotic conditions, i.e. temperature, precipitation, topography, and richness
405 of hummingbirds and their nectar-food plants, is presented in the electronic supplementary material,
406 table S1. In table S1, for each hummingbird species, we also give its body mass, bill length, and
407 network-derived estimates of resource specialization d' and vulnerability VE . Assigned R values for
408 plants based on expert opinion, using knowledge on floral phenotype and known insect visitation
409 [18], are available in Table S2.

410

411 **Authors' contributions**

412 B.D. designed the study, conducted the mixed models analysis, and wrote the manuscript. J. K.
413 conducted the phylogenetic analysis. B.I.S conducted the plant extinction analysis. A.M.M.G
414 conducted the network analysis. A.C.B, A.M.M.G. and A.T. contributed plant-hummingbird
415 networks. All authors contributed to interpretation of the data and manuscript writing.

416

417 **Competing interests**

418 We have no competing interests.

419

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430

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589 Table 1. Linear mixed models, analyzing the association between hummingbird resource
 590 specialisation d' and two types of predictor models: 1) species traits, and 2) local conditions. We
 591 also performed a full model including both predictors. In all models we used species identity as a
 592 random factor, as for three species the degree of specialisation d' was estimated in more than one
 593 network. Note that hummingbird specialisation d' is only associated to the local conditions. See
 594 Table S3 for similar calculations analyzing if the importance of local conditions is mainly due to
 595 local abiotic or biotic conditions.

Model	AIC_c	coefficient	Std Error	CI 95%, lower	CI 95%, upper	R² marginal	R² conditional
Species traits	12.033	+0.048 ^{NS}	+0.044	-0.045	+0.140	0.07	0.07
Local conditions	-3.211	+0.12**	+0.022	+0.074	+0.168	0.64	0.73
Full model	1.709					0.66	0.71
species traits		+0.019 ^{NS}	+0.029	-0.046	+0.084		
local conditions		+0.118**	+0.023	+0.069	+0.167		

596 **P<0.001, *p < 0.05, ^{NS} P > 0.05

597

598

599 Table 2. Linear mixed models, analyzing the association between hummingbird vulnerability of
600 extinction and two types of predictor models: 1) species traits and 2) local conditions. We also
601 performed a full model including both predictors. In all models we used species identity as a
602 random factor, as for three species the degree of specialisation d' was estimated in more than one
603 network. Hummingbird and plant dependencies R on mutualism were assigned at random, and
604 hummingbird vulnerabilities to plant extinction, VE , were calculated as $VE = PE (1 - SE)$. This
605 index captures two components of vulnerability, such that hummingbird species are considered
606 more vulnerable to iterative plant extinctions when they have a higher probability of extinction (PE)
607 and when, on average, their extinction occurs early in an extinction sequence ($1 - SE$). We
608 modelled plant extinctions in three orders of deletion: iteratively removing the lowest degree plant
609 species, iteratively removing the highest degree plant species, and at random. Note that
610 hummingbird vulnerability to plant extinction is only associated to the local conditions. See Table
611 S7 for similar calculations analyzing if the importance of local conditions is mainly due to abiotic or
612 biotic conditions. See ‘Methods’ for details on the modelling, and Table S4 for similar calculations
613 but with the speed of extinction $1 - SE$ as the estimate of species vulnerability. Finally, see Table
614 S5-S6 for similar calculations but assigning plant species dependencies R based on their floral
615 phenotype and known insect-pollination visitors.

Model	AIC _c	coefficient	Std Error	CI 95%, lower	CI 95%, upper	R ² marginal	R ² conditional
Order of deletion: removing species with lowest degree							
Species traits	-10.716	+0.024 ^{NS}	+0.027	-0.035	+0.083	0.01	0.79
Local conditions	-19.800	+0.05*	+0.012	+0.022	+0.075	0.46	0.89
Full model	-13.987					0.44	0.90
species traits		+0.008 ^{NS}	+0.021	-0.041	+0.056		
local conditions		+0.048*	+0.013	+0.020	+0.076		
Order of deletion: removing species with highest degree							
Species traits	-16.367	-0.008 ^{NS}	+0.022	-0.056	+0.040	0.01	0.74
Local conditions	-16.007	-0.016 ^{NS}	+0.014	-0.041	+0.020	0.04	0.70
Full model	-10.156					0.03	0.73

species traits		-0.004 ^{NS}	+0.022	-0.055	+0.046		
local conditions		-0.010 ^{NS}	+0.015	-0.042	+0.023		
Order of deletion: random removal of species							
Species traits	-46.526	+0.009 ^{NS}	+0.007	-0.010	+0.027	0.09	0.20
Local conditions	-57.175	+0.018**	+0.004	+0.010	+0.026	0.47	0.86
Full model	-48.917					0.49	0.87
species traits		+0.002 ^{NS}	+0.007	-0.013	+0.016		
local conditions		+0.018**	+0.004	+0.009	+0.026		

616 **P<0.001, *p < 0.05, ^{NS} P > 0.05

617

618

619 **Fig. 1.** (a) Map of the Caribbean Sea, with the Antillean archipelago shown in black and
620 surrounding islands and the American mainland in light grey. The major colonization routes of
621 Antillean hummingbirds are indicated by dark grey arrows, following Abrahamczyk et al. (2015).
622 We show the rate of morphological evolution of hummingbird (b) bill length and (c) body mass
623 through evolutionary time assessed with phylogenetically independent contrasts. The regression line
624 and +/- 95% confidence intervals derived from repeating the analyses across 1,000 post burn-in
625 phylogenies are shown with the solid and dashed lines, respectively. The dark grey shadings reflect
626 the estimated time of hummingbird colonization to the Antilles some 5-9 Mya, following
627 Abrahamczyk et al. (2015). Note that high rates of divergence in hummingbird bill length primarily
628 occurred early in the evolutionary history, before the colonization of the Antilles, while the
629 evolution of body mass differences were more constant through time. The main exception to this
630 general trend was a large recent divergence in body mass between the members of the genus
631 *Eulampis*. The drawing illustrates *Eulampis jugularis* (credit: Pedro Lorenzo).

632

633 **Fig. 2.** The association between hummingbird specialisation d' (a, b) and hummingbird
634 vulnerability to plant extinctions VE (c, d) with the two main components of 'local conditions', i.e.
635 local abiotic conditions (topography, precipitation and temperature) and local biotic conditions
636 (nectar-food plant richness). High values of the PCA axis 'local environment' reflect topographic
637 complex, high precipitation, and low temperature localities, i.e. Antillean Mountains [18]. The
638 regression line and +/- 95% confidence intervals are shown. Note that some of the data points
639 represent the same hummingbird species observed in several localities; hence we conducted linear
640 mixed models with species identity as a random factor (Table 1, 2).