



1 **High proportion of smaller-ranged hummingbird species coincides with ecological**
2 **specialization across the Americas**

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74

75 **Abstract**

76 Species communities that experience stable conditions have been speculated to preserve more
77 specialized interspecific associations as well as having higher proportions of smaller-ranged
78 species. However, this suggestion remains poorly supported with empirical evidence. Here, we
79 analyzed data for hummingbird resource specialization, range size, contemporary climate and late
80 Quaternary climate stability for 46 hummingbird-plant mutualistic networks distributed across the
81 Americas, representing 130 hummingbird species (ca. 40% of all hummingbird species). We
82 demonstrate a positive relationship between the proportion of smaller-ranged hummingbird species
83 (SRS) and community-level specialization, i.e. the division of the floral niche among coexisting
84 hummingbird species. This relationship remained strong also when accounting for climate.
85 Furthermore, the much stronger statistical effect of SRS on specialization than *vice versa*
86 (standardized coefficient = 0.75 vs. 0.43), suggests that climate largely associates with
87 specialization through species' range-size dynamics. Irrespective of the exact mechanism involved,
88 our results indicate that communities consisting of higher proportions of smaller-ranged species
89 may be vulnerable to disturbance not only because of their small geographic ranges but also
90 because of high degree of specialization.

91

92 **Keywords: biogeography, climate gradients, macroecology, mutualistic networks, range size,**
93 **specialization**

94 **1. Introduction**

95 Ecological specialization may facilitate species coexistence and speciation, and is therefore
96 hypothesized to structure global patterns of biodiversity [1]. Notably, higher degrees of community-
97 level resource specialization, i.e. the division of local resources, may be associated with reduced
98 interspecific competition and greater local richness [2]. It is therefore debated whether high
99 ecological specialization in the tropics may contribute to the observed continental-scale increased
100 species richness toward the tropics [3–10]. Likewise, it is speculated that large-scale geographical
101 differences in ecological specialization coincides with patterns of range-size frequency distributions
102 [11].

103 We address this and the role of extrinsic factors, notably climate, as potential
104 determinants of community-level specialization and range-size distributions. Contemporary climate
105 has been suggested to influence ecological specialization, with communities in productive areas
106 having the highest degree of specialization [12,13]. Similarly, in areas with low contemporary
107 seasonality, where resource availability supposedly is relatively stable throughout the year,
108 communities may have a higher degree of specialization than those found in more seasonal
109 environments [14–16]. Recent studies have also pointed towards historical climate fluctuations as
110 influencing the local degree of specialization, as unstable climatic conditions are hypothesized to
111 disrupt specialized species interactions, either through changes in the phenology of species or
112 through increased dynamics in range-size [6,11,17–19]. Both ecological and historical factors may
113 thus shape geographical patterns of ecological specialization as found for plant-hummingbird
114 networks, which have a higher community-wide specialization in areas with higher precipitation
115 and temperature, lower seasonality and more stable climate conditions since the last glacial
116 maximum [6,20]

117 Contemporary and historical climate may also affect the geographical distribution of
118 species range-sizes [21–23]. For instance, variable climate conditions have traditionally been

119 suggested to select for broad environmental tolerance, which influence the potential geographical
120 range of species and, hence, causes species to have large ranges in seasonal areas [23–27], though
121 see [28,29]. A highly seasonal climate may also force species to migrate in order to track suitable
122 environmental conditions, and as smaller-ranged species have been suggested to have weaker
123 dispersal ability than larger-ranged species [30], they are more likely to be residents in seasonally
124 stable environments. This reasoning may be extended to fluctuations in historical climate, which
125 may have forced species either to adapt to the new conditions, track suitable climatic conditions or
126 to go locally extinct. As smaller-ranged species may track suitable climate conditions more slowly
127 [30], these would suffer from an increased local extinction probability under climate change
128 [27,31]. In accordance with this, late Quaternary climate-change velocity correlates negatively with
129 the global distribution of proportionally smaller-ranged amphibian, mammal and bird species [31].

130 Taken together, numerous studies have pointed towards historical climate stability and
131 contemporary seasonality as being important to support both ecological specialization and high
132 proportions of smaller-ranged species. Thus, areas with disproportionately many smaller-ranged
133 species are expected to coincide geographically with a high degree of community-level ecological
134 specialization, but this remains poorly supported [6,11,19]. We tested this using a database
135 consisting of 46 quantitative hummingbird-plant networks, i.e., studies of all hummingbird species’
136 visitation frequencies on plant species at a given locality. The 46 networks are distributed widely
137 across the American mainland [20; figure 1]. Specifically, we investigate: (i) whether
138 specialization in plant-hummingbird networks is positively related with community-level proportion
139 of smaller-ranged species (hereafter SRS), and (ii) whether contemporary and late Quaternary
140 climate correlates with both specialization and SRS, or whether contemporary and late Quaternary
141 climate are more likely to influence specialization indirectly via SRS (or *vice versa*). Hummingbirds
142 are well-suited for such large-scale comparative studies on the pattern of ecological specialization

143 as they are highly specialized on nectar-feeding, and the hummingbirds and the plants they pollinate
144 are mutually dependent [32–34], i.e. it is ecologically relevant to understand how specialization
145 vary geographically [6] Moreover, hummingbirds are highly successful, being the second most
146 species-rich family of birds and able to thrive in an array of environments across most of the
147 Americas [35], and, finally, hummingbird-plant communities have long served as model system for
148 examining ecological and evolutionary processes as determinants of ecological specialization at the
149 community-level [6,32,33]. Our study advances the current understanding of how geographical
150 patterns of range-size and specialization are shaped, and have additional implications for
151 conservation of species communities engaged in specialized associations.

152

153 **2. Materials and Methods**

154 **(a) Plant-hummingbird network data.**

155 We used a database consisting of 46 plant-hummingbird networks [table S1; see 20 for more
156 detailed information about the network data], from which we constructed weighted interaction
157 networks for the hummingbirds and their associated nectar plants (figure 1). Taking a network
158 approach allow for detailed information about the interaction frequencies between all hummingbird
159 and plant species within a given community to be summarized by easily interpretable metrics. For
160 the present study, networks were presented as P (number of plant species) x H (number of
161 hummingbird species) matrices with entries indicating the strength of each interaction (i.e. the
162 number of visitations recorded for a given hummingbird-plant species pair). Known incidents of
163 nectar robbing, for instance if a hummingbird pierced the flower corolla without contacting the
164 floral reproductive organs, were not considered since they represent antagonistic rather than
165 mutualistic interactions [36]. For a network to be included in the study, it should fulfil certain
166 criteria: i) each study must have a community approach, i.e. aiming to include all hummingbird and

167 hummingbird-pollinated plant species within the given community over the sampled period; (ii)
168 networks need to consist of weighted data, i.e. include frequency of interactions, since binary
169 networks exhibit high sensitivity to sampling effort and species abundance [37]; (iii) moreover,
170 island networks were not included since species from islands are naturally constrained in their
171 geographic distribution by the hard boundaries made up by the sea. Measuring species range size
172 solely as the number of occupied grid cells would therefore contain less biological and mostly
173 geographical information and, hence, is not comparable to the situation on the continent.

174

175 **(b) Measuring hummingbird range-size proportions.**

176 The geographical range-size of each hummingbird species was extracted from an updated database
177 previously presented in Rahbek & Graves [38] – see [39,40] for details on method and data sources.
178 As an estimate of hummingbird geographical range-size, we used the total number of occupied $1^\circ \times$
179 1° latitude-longitude grid cells. Following Jetz and Rahbek [41], we divided the total number of
180 species ($n = 130$) into quartiles according to range size (i.e. the 1st quartile consists of the 25%
181 species with the smallest ranges ($n = 33$) and the 4th quartile consist of the 25% with largest ranges
182 sizes in order to determine the community level proportion of smallest-ranging species (SRS). For
183 each network, we calculated the proportion of 1st quartile species. As larger-ranging species
184 contribute with more records among communities than smaller-ranging species [41], even though
185 the majority of hummingbirds have relatively small ranges (S1). Hence, summary statistics as the
186 mean and median range size for co-occurring species would largely be influenced by large-ranging
187 species. This was confirmed for data set where linear models regressing the local proportion of 25%
188 of species with largest ranges, was strongly correlated with both the mean range size (Pearson
189 correlation = 0.85, $P < 0.001$) and the median range size (Pearson correlation = 0.83, $P < 0.001$). On
190 this basis, we assess the proportional variable SRS to be a more appropriate attribute of the local

191 range-size frequency distribution for determining the variation in presence of smaller-ranged
192 species. In addition, where richness of smaller-ranged species may reflect areas of high stability
193 [42,43], richness of larger-ranged species, which would influence the mean/median calculations,
194 may rather reflect factors related to productivity [41]. Hence, for the reason that the degree of
195 specialization may be higher in climatic more stable areas, we argue that testing for an association
196 to the proportion of smaller-range species is more relevant. However, It should be noted that the
197 range-size-frequency-distribution of our data is somewhat skewed toward larger ranges than the
198 RSFD of all hummingbird species of the world (figure S1). This is why we refer to 1st quartile
199 species as “smaller-ranged” species rather than using the term “restricted-range” species as in Jetz
200 & Rahbek [41] and others using continental data on all species (see also “Sensitivity Analyses”
201 below). This proportional variable was transformed by using arcsine square-root transformation for
202 the further analysis.

203

204 **(c) Specialization, richness, environmental variables and sampling intensity.**

205 Following Blütgen, Menzel & Blütgen [44] ecological specialization ($\langle d \rangle$) for each hummingbird
206 community was calculated as the weighted mean of the normalized Kullback-Leibler distance for
207 all coexisting hummingbird species [45]. The estimate is based on frequency data representing the
208 strength of each interaction (i.e. number of visits recorded for each hummingbird-plant partner) in
209 the network, which has been shown to be relatively insensitive to sampling intensity and network
210 size [44,46]. First, species level degree of specialization (d_i) is calculated as a comparison of the
211 distribution of hummingbird interactions with plant partners in relation to the overall partner
212 availability:

$$d_i = \sum_{j=1}^c \left(p'_{ij} \times \ln \frac{p'_{ij}}{q_j} \right)$$

213 Here, p_{ij} is the proportion of interactions with plant j in relation to the summed number of
214 interactions for hummingbird i (A_i), q_j denotes the summed number of interaction for plant j relative
215 to the summed number of interactions in the network (m) and c indicates the plant species richness.
216 Following a normalization procedure, letting d'_i denote the deviation of the empirical frequencies of
217 interaction for hummingbird i from the null expectation that all plants a visited equal to their
218 availability (see [44] for details regarding the normalization procedure), the weighted averaged
219 degree of specialization for the hummingbird assembly is calculated as:

$$\langle d'_i \rangle = \frac{1}{m} \sum_{i=1}^r (d'_i \times A_i)$$

220 Where r denotes the hummingbird species richness. The index ranges between 0 (extreme
221 generalization; i.e. many interactions with many plants shared by other hummingbird species) and 1
222 (extreme specialization; i.e. many interactions with few plants and limited sharing with other
223 hummingbird species). Weighting the averages by the summed number of interactions for each
224 hummingbird gives more accurate measures for comparison as rare interactions are not over-
225 interpreted [44]. Conceptually, the use of $\langle d'_i \rangle$ as a measure of ecological specialization can be
226 translated into the functional attributes specific to the local species community, i.e. the realized
227 Eltonian niche [47]. Estimating ecological specialization based on species interaction networks
228 could potentially be biased by differences in species abundance. This is the reason for weighting the
229 average degree of hummingbird specialization by the marginal sum of interactions, assuming a
230 positive association between abundance and visitation frequency. Although we do not have
231 sufficient independent measurement of abundance to validate this assumption, a study conducted on
232 a network collected in the Brazilian Atlantic Rainforest documented that the frequency of
233 hummingbird interactions was a good surrogate for their abundance [see Table S1 network ID 41
234 48]. On the other hand, for the specialization estimate, we identified potential confounding effects:

235 network size [6], i.e. the richness of hummingbird and plant species in the network (standardized
236 coefficient; *std. coeff.* = -0.495, $P = 0.015$), and network asymmetry [49], i.e. the ratio between the
237 richness of hummingbird and plant species $P = 0.013$). We thus conducted independent analyses
238 using the residuals of linear regressions predicting $\langle d' \rangle$ by respectively network size and network
239 asymmetry, respectively. To assess the confounding influence of differences in sampling effort, we
240 conducted additional linear regressions predicting both SRS and specialization by sampling
241 intensity, which for each network is calculated by dividing the total number of observed interactions
242 (square root transformed) with the richness for plants and hummingbirds [50].

243 The contemporary climate variables hypothesized to predict specialization and SRS,
244 i.e. mean annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality
245 (i.e. standard deviation in annual temperature; TS) and precipitation seasonality (i.e. standard
246 deviation in annual precipitation; PS), were extracted from the WorldClim database in resolution of
247 1 x 1 km [<http://www.worldclim.org>; 51]. We estimated variables reflecting historical climate
248 change as the absolute difference in temperature and precipitation between pre-industrial time and
249 the Last Glacial Maximum (21,000 years ago), i.e. temperature and precipitation anomalies
250 (AnomT and AnomP). To generate projections of climate anomaly, we used the Hadley Centre
251 Model Version 3 (HadCM3) at 3.75 x 2.5 arc degrees resolution and subsequently down scaled to
252 0.1 x 0.1 arc degrees [52]. We included also measures of topographic heterogeneity (i.e. range in
253 elevation; TH), as predictors of both specialization and SRS [53,54]. As an estimate of the
254 interactive effect of historical climate and topography, we included estimates of temperature and
255 precipitation velocity (VelT and VelP), which capture the buffering effect in mountain areas where
256 species can track their original climate zone by migrating a short distance up or down slope [55].
257 For each community, TH and estimates of historical and contemporary climate were calculated as
258 the average of values within a radius of 10 km from the sampled location. Given the large

259 geographical scale of the data, we assume that the regional down scaled climate estimates are good
260 indicators of the variation of local climate among communities. To meet statistical assumptions
261 about normality, mean annual temperature was squared and mean annual precipitation, temperature
262 seasonality, temperature and precipitation velocities and anomalies were log-transformed prior to
263 further analyses. All variables were scaled to zero mean and unit variance.

264

265 **(d) Structural Equation Modeling.**

266 Structural Equation Models (SEMs) are statistical tools used to evaluate multivariate hypotheses.
267 Compared to multiple regression models, the main advantage is that they seek to account for both
268 direct and indirect effects among predictor and response variables while allowing multiple
269 dependent variables to be tested simultaneously. Initially, we constructed two SEM's based on *a*
270 *priori* hypotheses, considering different causal paths among the response variables. The first
271 considered a link from SRS to specialization, corresponding to a scenario where local preservation
272 of higher proportions of smaller-ranged species (e.g. through lowered range size dynamics) affect
273 species possibilities to develop specialized interactions in the local plant community. Secondly we
274 considered an opposite link from specialization to SRS corresponding to a scenario where local
275 opportunities to develop increased ecological specialization provides better conditions for the
276 preservations of smaller ranged species. Due to relatively low sample size ($n = 46$) in comparison to
277 the number of predictor variables, this model was simplified through model selections using the
278 Akaike Information Criterion (AIC). For each response variable, among all model combinations,
279 only predictors present in the better predicting models (determined from having ΔAIC less than 2 in
280 relation to the model with lowest AIC; 50) were included in the initial SEM models (figure S2). The
281 two SEMs were evaluated through the chi-square test, comparative fit index (CFI) and the Root
282 Mean Square Error of Approximation (RMSA) [57]. The chi-square value indicates the divergence

283 between the sample and the fitted structures in the data and was used to evaluate overall model fit
284 where a non-significant result ($P > 0.05$) indicated good model fit. The CFI compares the chi-square
285 of the model with the chi-square value of an independent model assuming no correlation among all
286 variables while accounting for sample size. With a range from 0 to 1, we accepted models with
287 CFIs > 0.09 [58]. Lastly, the RMSA was implemented, but only on the simplified models due to the
288 index's sensitivity to the number of estimated parameters in the model. Here, values below 0.07
289 were used as indication of good model fit [58]. We expected some degree of correlation among the
290 included climate predictors. In order to obtain reliable model fit according to the three above
291 mentioned indices, we identified and added this covariance based on high modification indices and
292 large residual correlations [59,60]. By stepwise refitting, we simplified the SEMs, removing non-
293 significant links conditional on the model fit being satisfied [61,62]. The contribution of each
294 predictor variable was evaluated through the standardized path coefficients. Three additional SEM
295 pairs were constructed to examine if our results were sensitive to the significant positive effects of
296 network size and network asymmetry on specialization (figure S3-S4), and when using climate
297 velocities rather than anomalies (figure S5). All SEMs were constructed and analyzed with the R
298 package lavaan [63].

299 **(e) Spatial auto-correlation.**

300 Using the R package ncf [64], we assessed whether significant positive spatial autocorrelation
301 occurred in linear model residuals by computing correlograms with distance classes of 1000 km.
302 Four linear models were set up similarly to the direct links between climate and specialization and
303 SRS as in figure. 2. None of them contained significantly positive spatial autocorrelation, and we
304 thus conclude that spatial autocorrelation is negligible for the model results.

305 **(f) Sensitivity analyses of range-size definition.**

306 To evaluate the robustness to the use of different range-size cut-offs, We fitted ten additional linear
307 models using different range-size cut-offs to define a smaller-ranged species (i.e. from 20 to 30% of
308 species having the smallest range sizes; figure S6). In addition, we conducted follow up analyses
309 using a redefined measure of the proportion of smaller-ranged species based on the 1st quartile
310 species of the global pool of mainland hummingbird species (n = 318) as in Jets, Rahbek & Colwell
311 [43] rather than the one in our data set (n = 130). Following this method, a species was assigned to
312 be smaller-ranged if it had a global range-size less than 10 grid cells, as this represent the threshold
313 between 1st and 2nd quartile of the global species pool. For the 130 species occurring in the dataset,
314 this cut-off will include the 13% of species with the smallest range sizes. Du to zero inflation in the
315 corrected SRS variable, we were unable to conduct the above SEMs, which are based on linear
316 model assumptions. Instead, we used a logistic regression including all data points (n = 46) to test
317 the association between specialization on the corrected SRS (figure 3a). We note that a chi-square
318 test applied on the residual deviance and degrees of freedom to assess model fit indicated that SRS
319 was acceptably represented by a binominal distribution (P = 0.06). Considering specialization as
320 response variable, we separated the corrected SRS into two variables: one categorical that simply
321 determines whether communities hold smaller-ranged species or not (n = 46) and one containing
322 only communities having smaller-ranged species according to the corrected threshold (n = 10). The
323 association between the corrected SRS and specialization was fitted using ANOVA and simple
324 univariate linear models, respectively (figure 3b and c).

325 In addition to the threshold used to define smaller-ranged species, the latitudinal
326 variation in continental or biome narrowness may constitute hard boundaries to the range size of
327 species [28,65], which could also influence the association between SRS and specialization. To
328 account for this, we used dispersion fields to construct a null model, which generates SRS values
329 for each community from a similarity-weighted species source pool [66]. The null model integrates

330 data of the presence-absence of all 318 hummingbird species across mainland Americas at $1^\circ \times 1^\circ$
331 latitude-longitude resolution. The concept of the biogeographical source pool is based on dispersal
332 of species to most likely occur within their biogeographical region [66,67]. Thus, we determined the
333 regional source pool of a community using the rationale that species living in communities with
334 species compositions more similar the focal are more likely to constitute its source pool. Across
335 1000 iterations of each community containing n species, the null model algorithm randomly
336 samples n grid cells probabilistically weighted by the number of shared species with the focal
337 community. From these, n species were randomly assembled weighted by their frequency of
338 occurrence in the n sampled grid cells. For these, the null values of SRS were then calculated.
339 Deviations between the observed SRS values and the normal curve of the null generated SRS values
340 were standardized as the z-score: $SRS_z = (SRS_{\text{observed}} - \overline{SRS_{\text{null}}})/sd(SRS_{\text{null}})$.

341

342 **3. Results**

343 We found a positive correlation between specialization and SRS (coefficient; *coef.* = 0.394, $R^2 =$
344 0.349, $P < 0.001$, $n = 46$). For the SEM containing a hypothesized direct link from specialization to
345 SRS was considered, a positive association was found between the two (*std coeff.* = 0.43, figure.
346 2a). Here, we found that SRS was negatively associated with temperature seasonality (TS; *std coeff.*
347 = -0.42) and positively associated with topographical heterogeneity (TH; *std coeff.* = 0.42) and
348 temperature anomaly (AnomT; *std coeff.* = 0.23), whereas specialization was negatively related to
349 temperature anomaly (AnomT; *std coeff.* = -0.37) and positively related to both mean annual
350 precipitation (MAP; *std coeff.* = 0.31) and precipitation anomaly (AnomP; *std coeff.* = 0.35). In the
351 SEM having SRS as a predictor of specialization (figure 2b), there was a similarly strong positive
352 link from SRS to specialization (*std coeff.* = 0.75). In comparison to the above SEM, we here found

353 additional links between specialization and mean annual temperature (MAT; *std coeff.* = 0.29), TS
354 (*std coeff.* = 0.31) and a positive influence of AnomP on SRS instead of specialization.

355 Linear regressions testing the influence of sampling intensity on specialization and
356 SRS showed no significant associations (*coef.* = -0.01, $R^2 = 0.07$, $P = 0.07$, $n = 46$; *coef.* = -0.02, R^2
357 = 0.08, $P = 0.06$, $n = 46$ respectively). Similarly, the strong association between SRS and
358 specialization was insensitive to specialization estimates when correcting for network richness
359 (figure S3) and network asymmetry (figure S4). The results from the SEM pairs considering the
360 interactive effect of topographic heterogeneity and historical climate through estimates of climate-
361 change velocity also showed similar results (figure S5).

362 Linear regression including SRS variables calculated using different range-size cut-
363 offs to define smaller-ranged species (ranging from 20% to 30% of species having the smallest
364 range sizes) documented a robust association between the degree of specialization and SRS (figure
365 S6). When using the first quartile of the global mainland species pool of hummingbirds rather than
366 the first quartile of our dataset as a threshold to define smaller-ranged species (figure 3): (i) a
367 logistic regression confirmed that the association between specialization and SRS remained
368 significantly positive ($R^2 = 0.345$, $P < 0.001$, $n = 46$; figure 3a); (ii) a one-way ANOVA test
369 showed significantly higher degree of specialization in communities with smaller-ranged species
370 present ($F = 6.719$, $P = 0.013$, $n = 46$; figure 3b) and; (iii) a linear regression conducted only for
371 communities containing smaller-ranged species showed similar trend towards increased
372 specialization in communities with higher proportion of smaller-ranged species ($F = 6.739$, $P =$
373 0.032 , $n = 10$, $R^2 = 0.457$; figure 3c). Finally, null model corrected SRS remained significantly
374 positively associated to specialization ($R^2 = 0.357$, $P < 0.001$, $n = 46$; figure 4), indicating that the
375 influence of biome or continental narrowness on the range size of species is negligible in respect to
376 the association between SRS and specialization.

377 **4. Discussion**

378 For hummingbird–plant networks across mainland Americas, we found that communities with high
379 proportions of smaller-ranged species (SRS) also have a high degree of ecological specialization
380 (figure 1-2). The association between SRS and specialization was insensitive to the definition used
381 for smaller-ranged species (figure 3; S6), to the influence of biome or continental narrowness as
382 accounted for by null models (figure 4), to the influence of species richness and network asymmetry
383 on specialization (figure S3-S4) as well as how historical climate stability is summarised (figure
384 S5). Although contemporary and historical climate was important in predicting both SRS and
385 specialization, it did not affect the strong association between specialization and SRS. Notably,
386 current precipitation was strongly correlated with hummingbird specialization, possibly explained
387 by either increased productivity and thus greater opportunities for specialization or lower
388 importance of insects in comparison to hummingbirds as pollinators in more rainy conditions,
389 thereby favouring hummingbird–plant specialization [5,68,69]. Interestingly, we found a strong
390 consistent negative link from temperature seasonality to SRS (figure. 2) and, when accounting for
391 the indirect effects of climate on specialization via SRS, a direct positive association of temperature
392 seasonality on specialization appeared (figure 2*b*). This positive association has likewise been
393 observed for frugivorous bird-plant networks, which could be explained by non-overlapping
394 interactions arising from higher annual turnover in species composition in more seasonal
395 environments [50]. A synthesis of the effects of topography and climate together with the much
396 stronger effect of SRS on specialization than *vice versa* (*std coeff.* = 0.75 vs. *std coeff.* = 0.43), is in
397 accordance with the hypothesis that climate may increase specialization through reduced annual
398 species range dynamics [30,42], facilitating adaptation to local foraging niches. However, the direct
399 association between niche breadth and climatically induced population dynamics still lacks
400 sufficient support by empirical evidence [70]. In accordance with the contrary hypothesis, that less
401 specific adaptations to local food resources may extend the range over which a species can occur

402 resulting in fewer smaller-ranged species in the more generalized communities, a positive direct
403 link from specialization to SRS remained present in all SEM models. Thus, although we are able to
404 confirm the hypothesised interrelatedness between SRS and specialization, we are with the present
405 data unable to firmly identify the underlying mechanism causing this association or their causal
406 relationships.

407 In addition to contemporary climate, we found correlations with the estimates of
408 historical climate anomaly. However, their effects were less consistent in the follow-up analyses
409 (figure S3-S5) than those of contemporary climate, which in our models showed higher and
410 consistent importance in predicting the interrelatedness of SRS and specialization. This indicates
411 that late Quaternary temperature stability may play a role, but a minor one compared to
412 contemporary climate. Contradicting the suggested high importance of historical climate changes
413 for species range dynamics [11,31], our results could indicate that annual-scale climate stability also
414 has a considerable influence for the preservation of smaller-ranged species through time [42]. The
415 observed positive link from precipitation anomaly to specialization could derive from historical
416 increases in productivity ultimately facilitating specialization. In contrast, the positive association to
417 SRS could be explained by recent speciation events following the onset of glacial cycles during the
418 Late Pleistocene, where species repeatedly disperse and become isolated in a heterogeneous
419 environment – e.g. on mountain tops [71] – see Garcia-Moreno *et al.* for an explicit example with
420 hummingbirds [72]. Mechanisms, as the latter, related to the evolutionary history of species also
421 operates on time scales beyond the last glacial maximum [11,42], and may influence the
422 intercorrelation of richness of smaller-ranged species, high levels of specialization and high local
423 speciation-low extinction. Therefore, in order to understand what causes communities consisting of
424 mainly smaller-ranged species to be more specialized, one could test the hypothesis that specialized
425 hummingbirds and their nectar-food plants have concerted demographic trends in more stable

426 environments, ranking from current seasonality to climates at deep-time evolutionary time-scales
427 [73]. This could potentially identify the main mechanism and temporal scale facilitating
428 specialization in communities consisting of mainly smaller-ranged species, which have lower
429 dispersal ability and thus may depend more on nectar-food plants from the local flora.

430 Irrespective of the exact mechanism involved, the detected relationship between SRS
431 and specialization has relevance for ecological and evolutionary theory regarding their respective
432 geographical patterns. Specifically, it illustrates that interspecific interactions are of great
433 importance to consider when studying biogeographical patterns on large geographical scales, at
434 least for highly specialized systems such as hummingbird–plant communities. Our results also have
435 implications for conservation of species engaged in mutualistic associations, especially as
436 anthropogenic activity may impact mutualistic interactions [74], and cause pollinator and linked
437 plant extinctions [75,76]. For instance, the strong link between SRS and specialization indicate that
438 some communities may be fragile in multiple ways, both by having smaller-ranged species slow in
439 tracking ongoing climate changes and by having species less prone in switching their interactions
440 and at higher risk of secondary extinctions [30,31,77]

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461

462 **Author contribution**

463 JS wrote the manuscript, carried out all statistical analyses, participated in the design and
464 coordination of the study; AMMG assembled the plant-hummingbird database; JVB and PKM
465 collected field data and participated in the design of the study and drafted the manuscript; BS and
466 MSc advised the statistical analyses; ACA, FPA, SMA, ACB, PCA, TTI, GK, CA, FMGLC, AOM,
467 CGM, MAM, ACM, DNB, GMO, PEO, JFO, LCR, LRL, AMR, MS, AT, IGV, ZW, SW collected
468 data; JF participated in the design of the study and made the painted illustrations, JCS and CR
469 participated in the design of the study and helped draft the manuscript; BD participated in the
470 design and coordination of the study and helped draft the manuscript. All authors critically revised
471 and approved the manuscript.

472 **Data accessibility**

473 Location, network characteristics and SRS (the proportion of smaller-ranged species) values of each
474 hummingbird-plant network is presented at table S1. Same dataset has also been used and described
475 for the analyses in Martín González et al. [20]

476 **References**

- 477 1. Bascompte, J. & Jordano, P. 2007 Plant-animal mutualistic networks: The architecture of
478 biodiversity. *Annu. Rev. Ecol. Syst.* **38**, 567–593.
479 (doi:10.1146/annurev.ecolsys.38.091206.095818)
- 480 2. Miller, T. E., Burns, J. H., Munguia, P., Walters, E. L., Kneitel, J. M., Richards, P. M.,
481 Mouquet, N. & Buckley, H. L. 2005 A critical review of twenty years' use of the resource-
482 ratio theory. *Am. Nat.* **165**, 439–448. (doi:10.1086/428681)
- 483 3. Schemske, D. W., Mittelbach, G. G., Cornell, H. V, Sobel, J. M. & Roy, K. 2009 Is there a
484 latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Evol. Syst.* **40**,
485 245–269. (doi:10.1146/annurev.ecolsys.39.110707.173430)
- 486 4. Dyer, L. A. et al. 2007 Host specificity of Lepidoptera in tropical and temperate forests.
487 *Nature* **448**, 696–699. (doi:10.1038/nature05884)
- 488 5. Schleuning, M. et al. 2012 Specialization of mutualistic interaction networks decreases
489 toward tropical latitudes. *Curr. Biol.* **22**, 1925–1931. (doi:10.1016/j.cub.2012.08.015)
- 490 6. Dalsgaard, B. et al. 2011 Specialization in plant-hummingbird networks is associated with
491 species richness, contemporary precipitation and quaternary climate-change velocity. *PLoS*
492 *One* **6**, e25891. (doi:10.1371/journal.pone.0025891)
- 493 7. Olesen, J. M. & Jordano, P. 2002 Geographic patterns in plant-pollinator mutualistic
494 networks. *Ecology* **83**, 2416–2424. (doi:10.1890/0012-9658)
- 495 8. Ollerton, J. & Cranmer, L. 2002 Latitudinal trends in plant-pollinator interactions: are
496 tropical plants more specialised? *Oikos* **98**, 340–350. (doi:10.1034/j.1600-
497 0706.2002.980215.x)
- 498 9. Dobzhansky, T. 1950 Evolution in the tropics. *Am. Sci.* **38**, 209–221.
- 499 10. MacArthur, R. H. 1969 Patterns of communities in the tropics. *Biol. J. Linn. 350 Soc.* **1**, 19–
500 13.

- 501 11. Dynesius, M. & Jansson, R. 2000 Evolutionary consequences of changes in species'
502 geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl. Acad. Sci.*
503 **97**, 9115–9120. (doi:10.1073/pnas.97.16.9115)
- 504 12. Schemske, D. W. 2002 *Ecological and evolutionary perspectives on the origins of tropical*
505 *diversity*.
- 506 13. Srivastava, D. S. & Lawton, J. H. 1998 Why more productive sites have more species: An
507 experimental test of theory using tree-hole communities. *Am. Nat.* **152**, 510–529.
508 (doi:10.1086/286187)
- 509 14. Janzen, D. H. 1967 Why Mountain Passes are Higher in the Tropics. *Am. Nat.* **101**, 233–249.
510 (doi:10.2307/2458977)
- 511 15. Abrahamczyk, S. & Kessler, M. 2010 Hummingbird diversity, food niche characters, and
512 assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. *J.*
513 *Ornithol.* **151**, 615–625. (doi:10.1007/s10336-010-0496-x)
- 514 16. Maruyama, P. K., Oliveira, G. M., Ferreira, C., Dalsgaard, B. & Oliveira, P. E. 2013
515 Pollination syndromes ignored: importance of non-ornithophilous flowers to neotropical
516 savanna hummingbirds. *Naturwissenschaften* **100**, 1061–1068. (doi:10.1007/s00114-013-
517 1111-9)
- 518 17. Tylianakis, J. M., Didham, R. K., Bascompte, J. & Wardle, D. A. 2008 Global change and
519 species interactions in terrestrial ecosystems. *Ecol. Lett.* **11**, 1351–1363. (doi:10.1111/j.1461-
520 0248.2008.01250.x)
- 521 18. Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W. & Holt, R. D. 2010 A
522 framework for community interactions under climate change. *Trends Ecol. Evol.* **25**, 325–
523 331. (doi:10.1016/j.tree.2010.03.002)
- 524 19. Dalsgaard, B. et al. 2013 Historical climate-change influences modularity and nestedness of
525 pollination networks. *Ecography* (doi:10.1111/j.1600-0587.2013.00201.x)
- 526 20. Martín González, A. M., Dalsgaard, B., Nogués-Bravo, D., Graham, C. H., Schleuning, M.,
527 Abrahamczyk, S., Alarcón, R., Araujo, A. C. & Al., E. 2015 The macroecology of
528 phylogenetically structured hummingbird-plant networks. *Glob. Ecol. Biogeogr.* **in press**.
529 (doi:10.1111/geb.12355)
- 530 21. Svenning, J.-C. 2003 Deterministic Plio-Pleistocene extinctions in the European cool-
531 temperate tree flora. *Ecol. Lett.* **6**, 646–653. (doi:10.1046/j.1461-0248.2003.00477.x)
- 532 22. Araújo, M. B., Nogués-Bravo, D., Diniz-Filho, J. A. F., Haywood, A. M., Valdes, P. J. &
533 Rahbek, C. 2008 Quaternary climate changes explain diversity among reptiles and
534 amphibians. *Ecography* **31**, 8–15. (doi:10.1111/j.2007.0906-7590.05318.x)
- 535 23. Araújo, M. B. & Pearson, R. G. 2005 Equilibrium of species' distributions with climate.
536 *Ecography* **28**, 693–695. (doi:10.1111/j.2005.0906-7590.04253.x)

- 537 24. Stevens, G. 1989 The latitudinal gradient in geographical range: how so many species coexist
538 in the tropics. *Am. Nat.*
- 539 25. Sunday, J. M., Bates, A. E. & Dulvy, N. K. 2011 Global analysis of thermal tolerance and
540 latitude in ectotherms. *Proc. R. Soc. B Biol. Sci.* **278**, 1823–1830.
541 (doi:10.1098/rspb.2010.1295)
- 542 26. Addo-Bediako, A., Chown, S. L. & Gaston, K. J. 2000 Thermal tolerance, climatic
543 variability and latitude. *Proc. R. Soc. London. Ser. B Biol. Sci.* **267**, 739–745.
544 (doi:10.1098/rspb.2000.1065)
- 545 27. Lande, R. 1993 Risks of population extinction from demographic and environmental
546 stochasticity and random catastrophes. *Am. Nat.* , 911–927.
- 547 28. Colwell, R. K. & Hurtt, G. C. 1994 Nonbiological gradients in species richness and a
548 spurious rapoport effect. *Am. Nat.* **144**, 570–595. (doi:10.2307/2462939)
- 549 29. Gaston, K. J., Blackburn, T. M. & Spicer, J. I. 1998 Rapoport’s rule: time for an epitaph?
550 *Trends Ecol. Evol.* **13**, 70–74. (doi:10.1016/S0169-5347(97)01236-6)
- 551 30. Laube, I., Korntheuer, H., Schwager, M., Trautmann, S., Rahbek, C. & Böhning-Gaese, K.
552 2013 Towards a more mechanistic understanding of traits and range sizes. *Glob. Ecol.*
553 *Biogeogr.* **22**, 233–241. (doi:10.1111/j.1466-8238.2012.00798.x)
- 554 31. Sandel, B., Arge, L., Dalsgaard, B., Davies, R. G., Gaston, K. J., Sutherland, W. J. &
555 Svenning, J.-C. 2011 The influence of Late Quaternary climate-change velocity on species
556 endemism. *Science* **334**, 660–664. (doi:10.1126/science.1210173)
- 557 32. Stiles, F. G. 1981 Geographical aspects of bird-flower coevolution, with particular reference
558 to Central America. *Ann. Missouri Bot. Gard.* **68**, 323–351. (doi:10.2307/2398801)
- 559 33. Stiles, F. G. 1978 Ecological and evolutionary implications of bird pollination. *Am. Zool.* **18**,
560 715–727. (doi:10.2307/3882531)
- 561 34. Temeles, E. J. & Kress, W. J. 2003 Adaptation in a Plant-Hummingbird Association. *Science*
562 **300**, 630–633. (doi:10.1126/science.1080003)
- 563 35. McGuire, J. A., Witt, C. C., Remsen Jr, J. V, Corl, A., Rabosky, D. L., Altshuler, D. L. &
564 Dudley, R. 2014 Molecular phylogenetics and the diversification of hummingbirds. *Curr.*
565 *Biol.* **24**, 910–916. (doi:10.1016/j.cub.2014.03.016)
- 566 36. Maruyama, P., Vizenin-Bugoni, J., Dalsgaard, B., Sazima, I. & Sazima, M. 2015 Nectar
567 robbery by a hermit hummingbird: association to floral phenotype and its influence on
568 flowers and network structure. *Oecologia* (doi:10.1007/s00442-015-3275-9)
- 569 37. Banašek-Richter, C., Cattin, M. F. & Bersier, L. F. 2004 Sampling effects and the robustness
570 of quantitative and qualitative food-web descriptors. *J. Theor. Biol.* **226**, 23–32.
571 (doi:10.1016/S0022-5193(03)00305-9)

- 572 38. Rahbek, C. & Graves, G. R. 2000 Detection of macro-ecological patterns in South American
573 hummingbirds is affected by spatial scale. *Proc. Biol. Sci.* **267**, 2259–2265.
574 (doi:10.2307/2665820)
- 575 39. Rahbek, C., Gotelli, N. J., Colwell, R. K., Entsminger, G. L., Rangel, T. F. L. V. B. &
576 Graves, G. R. 2007 Predicting continental-scale patterns of bird species richness with
577 spatially explicit models. *Proc. R. Soc. B Biol. Sci.* **274**, 165–174.
578 (doi:10.1098/rspb.2006.3700)
- 579 40. Holt, B. G. et al. 2013 An update of Wallace’s zoogeographic regions of the world. *Science*
580 **339**, 74–78. (doi:10.1126/science.1228282)
- 581 41. Jetz, W. & Rahbek, C. 2002 Geographic range size and determinants of avian species
582 richness. *Science* **297**, 1548–1551. (doi:10.1126/science.1072779)
- 583 42. Fjeldså, J., Lambin, E. & Mertens, B. 1999 Correlation between endemism and local
584 ecoclimatic stability documented by comparing Andean bird distributions and remotely
585 sensed land surface data. *Ecography* **22**, 63–78. (doi:10.2307/3683208)
- 586 43. Jetz, W., Rahbek, C. & Colwell, R. K. 2004 The coincidence of rarity and richness and the
587 potential signature of history in centres of endemism. *Ecol. Lett.* **7**, 1180–1191.
588 (doi:10.1111/j.1461-0248.2004.00678.x)
- 589 44. Blüthgen, N., Menzel, F. & Blüthgen, N. 2006 Measuring specialization in species
590 interaction networks. *BMC Ecol.* **6**, 9. (doi:10.1038/nature03450)
- 591 45. Dormann, C., Gruber, B. & Fründ, J. 2008 Introducing the bipartite package: analysing
592 ecological networks. *R news* **8**, 8–11.
- 593 46. Fründ, J., McCann, K. S. & Williams, N. M. 2015 Sampling bias is a challenge for
594 quantifying specialization and network structure: lessons from a quantitative niche model.
595 *Oikos*, n/a–n/a. (doi:10.1111/oik.02256)
- 596 47. Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P.,
597 Villéger, S. & Mouquet, N. 2010 Defining and measuring ecological specialization. *J. Appl.*
598 *Ecol.* **47**, 15–25. (doi:10.1111/j.1365-2664.2009.01744.x)
- 599 48. Vizenin-Bugoni, J., Maruyama, P. K. & Sazima, M. 2014 Processes entangling interactions
600 in communities: forbidden links are more important than abundance in a hummingbird-plant
601 network. *Proc. R. Soc. B Biol. Sci.* **281**, 20132397–20132397. (doi:10.1098/rspb.2013.2397)
- 602 49. Blüthgen, N., Menzel, F., Hovestadt, T., Fiala, B. & Blüthgen, N. 2007 Specialization,
603 constraints, and conflicting interests in mutualistic networks. *Curr. Biol.* **17**, 341–346.
604 (doi:10.1016/j.cub.2006.12.039)
- 605 50. Schleuning, M. et al. 2014 Ecological, historical and evolutionary determinants of modularity
606 in weighted seed-dispersal networks. *Ecol. Lett.* **17**, 454–463. (doi:10.1111/ele.12245)

- 607 51. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. 2005 Very high
608 resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978.
609 (doi:10.1002/joc.1276)
- 610 52. Singarayer, J. S. & Valdes, P. J. 2010 High-latitude climate sensitivity to ice-sheet forcing
611 over the last 120kyr. *Quat. Sci. Rev.* **29**, 43–55. (doi:10.1016/j.quascirev.2009.10.011)
- 612 53. Terborgh, J. 1971 Distribution on Environmental Gradients: Theory and a Preliminary
613 Interpretation of Distributional Patterns in the Avifauna of the Cordillera Vilcabamba, Peru.
614 *Ecology* **52**, 23–40. (doi:10.2307/1934735)
- 615 54. Feinsinger, P., Colwell, R., Terborgh, J. & Chaplin, S. 1979 Elevation and the morphology,
616 flight energetics, and foraging ecology of tropical hummingbirds. *Am. Nat.*
- 617 55. Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B. & Ackerly, D. D. 2009
618 The velocity of climate change. *Nature* **462**, 1052–U111. (doi:10.1038/nature08649)
- 619 56. Burnham, K. & Anderson, D. 2002 Model selection and multimodel inference: a practical
620 information-theoretic approach.
- 621 57. Shipley, B. 2002 *Cause and correlation in biology: a user's guide to path analysis,*
622 *structural equations and causal inference*. Cambridge University Press.
- 623 58. Hooper, D., Coughlan, J. & Mullen, M. 2008 Structural equation modelling: guidelines for
624 determining model fit. *Articles* , 2.
- 625 59. Grace, J. B., Schoolmaster, D. R., Guntenspergen, G. R., Little, A. M., Mitchell, B. R.,
626 Miller, K. M. & Schweiger, E. W. 2012 Guidelines for a graph-theoretic implementation of
627 structural equation modeling. *Ecosphere* **3**, art73. (doi:10.1890/ES12-00048.1)
- 628 60. Sandom, C., Dalby, L., Fløjgaard, C., Kissling, W. D., Lenoir, J., Sandel, B., Trøjelsgaard,
629 K., Ejrnæs, R. & Svenning, J.-C. 2013 Mammal predator and prey species richness are
630 strongly linked at macroscales. *Ecology* **94**, 1112–1122. (doi:10.1890/12-1342.1)
- 631 61. Zhang, J., Kissling, W. D. & He, F. 2013 Local forest structure, climate and human
632 disturbance determine regional distribution of boreal bird species richness in Alberta,
633 Canada. *J. Biogeogr.* **40**, 1131–1142. (doi:10.1111/jbi.12063)
- 634 62. Ferger, S. W., Schleuning, M., Hemp, A., Howell, K. M. & Böhning-Gaese, K. 2014 Food
635 resources and vegetation structure mediate climatic effects on species richness of birds. *Glob.*
636 *Ecol. Biogeogr.* **23**, 541–549. (doi:10.1111/geb.12151)
- 637 63. Rosseel, Y. 2012 lavaan: An R Package for structural Equation Modeling . **48**, 1–36.
- 638 64. Bjornstad, O. N. 2013 ncf: spatial nonparametric covariance functions.

- 639 65. Colwell, R. K. & Lees, D. C. 2000 The mid-domain effect: geometric constraints on the
640 geography of species richness. *Trends Ecol. Evol.* **15**, 70–76. (doi:10.1016/S0169-
641 5347(99)01767-X)
- 642 66. Lessard, J.-P., Borregaard, M. K., Fordyce, J. A., Rahbek, C., Weiser, M. D., Dunn, R. R. &
643 Sanders, N. J. 2012 Strong influence of regional species pools on continent-wide structuring
644 of local communities. *Proc. R. Soc. B Biol. Sci.* **279**, 266–274. (doi:10.1098/rspb.2011.0552)
- 645 67. Carstensen, D. W., Lessard, J.-P., Holt, B. G. & Borregaard, M. K. 2013 Introducing the
646 biogeographic species pool. *Ecography* **36**, 1–9.
- 647 68. Dalsgaard, B., González, A. M. M., Olesen, J. M., Ollerton, J., Timmermann, A., Andersen,
648 L. H. & Tossas, A. G. 2009 Plant-hummingbird interactions in the West Indies: floral
649 specialisation gradients associated with environment and hummingbird size. *Oecologia* **159**,
650 757–766. (doi:10.2307/40309943)
- 651 69. Cruden, R. W. 1972 Pollinators in high-elevation ecosystems: relative effectiveness of birds
652 and bees. *Science* **176**, 1439–1440. (doi:10.2307/1734592)
- 653 70. Vázquez, D. P. & Stevens, R. D. 2004 The latitudinal gradient in niche breadth: concepts and
654 evidence. *Am. Nat.* **164**, E1–E19.
- 655 71. Weir, J. T. 2006 Divergent timing and patterns of species accumulation in lowland and
656 highland neotropical birds. *Evolution* **60**, 842–855. (doi:10.1554/05-272.1)
- 657 72. Garcia-Moreno, J., Arctander, P. & Fjeldså, J. 1999 Strong diversification at the treeline
658 among *Metallura* hummingbirds. *Auk*, 702–711.
- 659 73. Marske, K. A., Rahbek, C., Nogués-Bravo, D. & Nogués-Bravo, D. 2013 Phylogeography:
660 spanning the ecology-evolution continuum. *Ecography* **36**, 1169–1181. (doi:10.1111/j.1600-
661 0587.2013.00244.x)
- 662 74. Sebastián-González, E., Dalsgaard, B., Sandel, B. & Guimarães, P. R. 2015 Macroecological
663 trends in nestedness and modularity of seed-dispersal networks: human impact matters. *Glob.*
664 *Ecol. Biogeogr.* **24**, 293–303. (doi:10.1111/geb.12270)
- 665 75. Biesmeijer, J. C. et al. 2006 Parallel declines in pollinators and insect-pollinated plants in
666 Britain and the Netherlands. *Science* **313**, 351–354. (doi:10.1126/science.1127863)
- 667 76. Ollerton, J., Erenler, H., Edwards, M. & Crockett, R. 2014 Extinctions of aculeate pollinators
668 in Britain and the role of large-scale agricultural changes. *Science* **346**, 1360–1362.
669 (doi:10.1126/science.1257259)
- 670 77. Blüthgen, N. 2010 Why network analysis is often disconnected from community ecology: A
671 critique and an ecologist's guide. *Basic Appl. Ecol.* **11**, 185–195.
672 (doi:10.1016/j.baae.2010.01.001)

673 **Figures and tables**

674

675 **Figure 1.** Geographical pattern of specialization and the proportion of smaller-ranged species (SRS)

676 for 46 hummingbird communities across mainland Americas. The coloration of each circle on the

677 map indicates the degree of specialization in relation to the proportion of smaller-ranged species

678 (SRS); black indicates both high SRS and specialization, white conversely indicates both low SRS

679 and degree of specialization. Orange and blue indicate poorer correlation through either high SRS

680 or specialization, respectively. Note that some points have been slightly moved to avoid overlap.

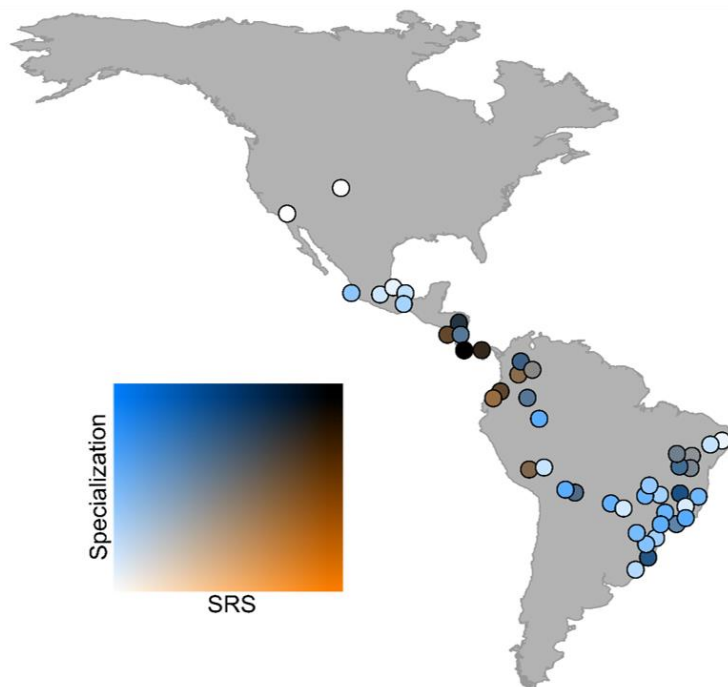
681 SRS was arcsin square-root transformed to improve normality. Painted illustration shows three

682 hummingbird species from the Costa Rican highlands, where the network with the highest degree of

683 specialization and SRS is found in the data set (specialization = 0.782, SRS = 0.6). From above:

684 Volcano Hummingbird (*Selasphorus flammula*), White-bellied Mountain-gem (*Lampornis*

685 *hemileucus*) and Fiery-throated Hummingbird (*Panterpe insignis*). Painting by Jon Fjeldså.



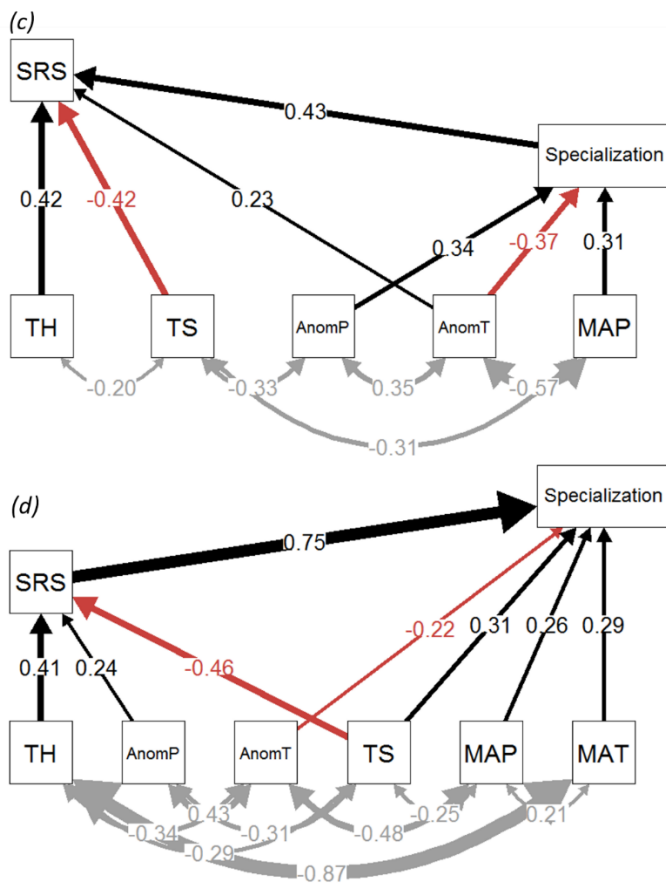
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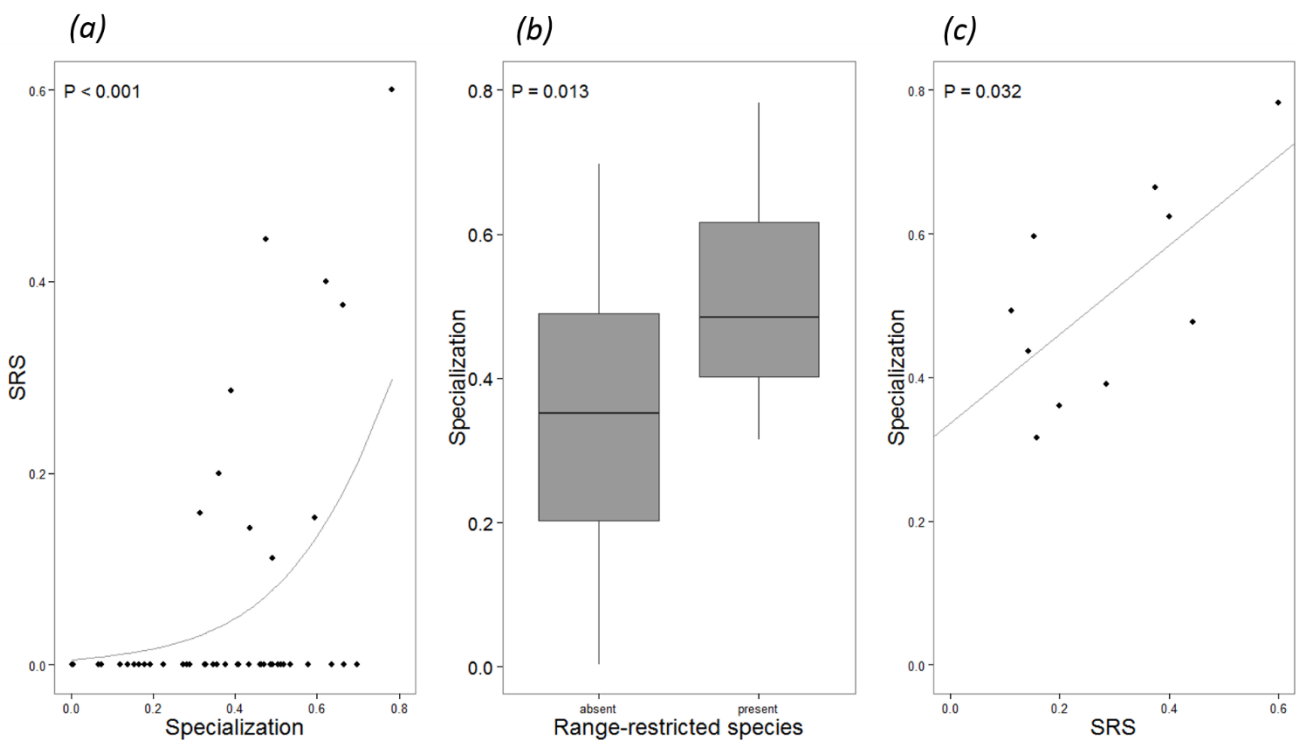
689 **Figure 2.** Results from two reduced structural equation models showing the direct and indirect links
 690 of contemporary climate and Quaternary climate velocity on specialization and the proportion of
 691 smaller-ranged species (SRS; $n = 46$). (a) the path structure when specialization is hypothesized to
 692 predict of SRS. (b) the paths for the possible opposite scenario where SRS is hypothesized to
 693 predict specialization. Black arrows indicate positive relationships, red arrows indicate negative
 694 relationships; the thickness of each arrow illustrates the strength. The double headed grey arrows
 695 indicate covariance links. Other abbreviations are: MAT, mean annual temperature; MAP, mean
 696 annual precipitation; TS, temperature seasonality, PS, precipitation seasonality; AnomT,
 697 temperature anomaly; AnomP, precipitation anomaly; TH, topographic heterogeneity.

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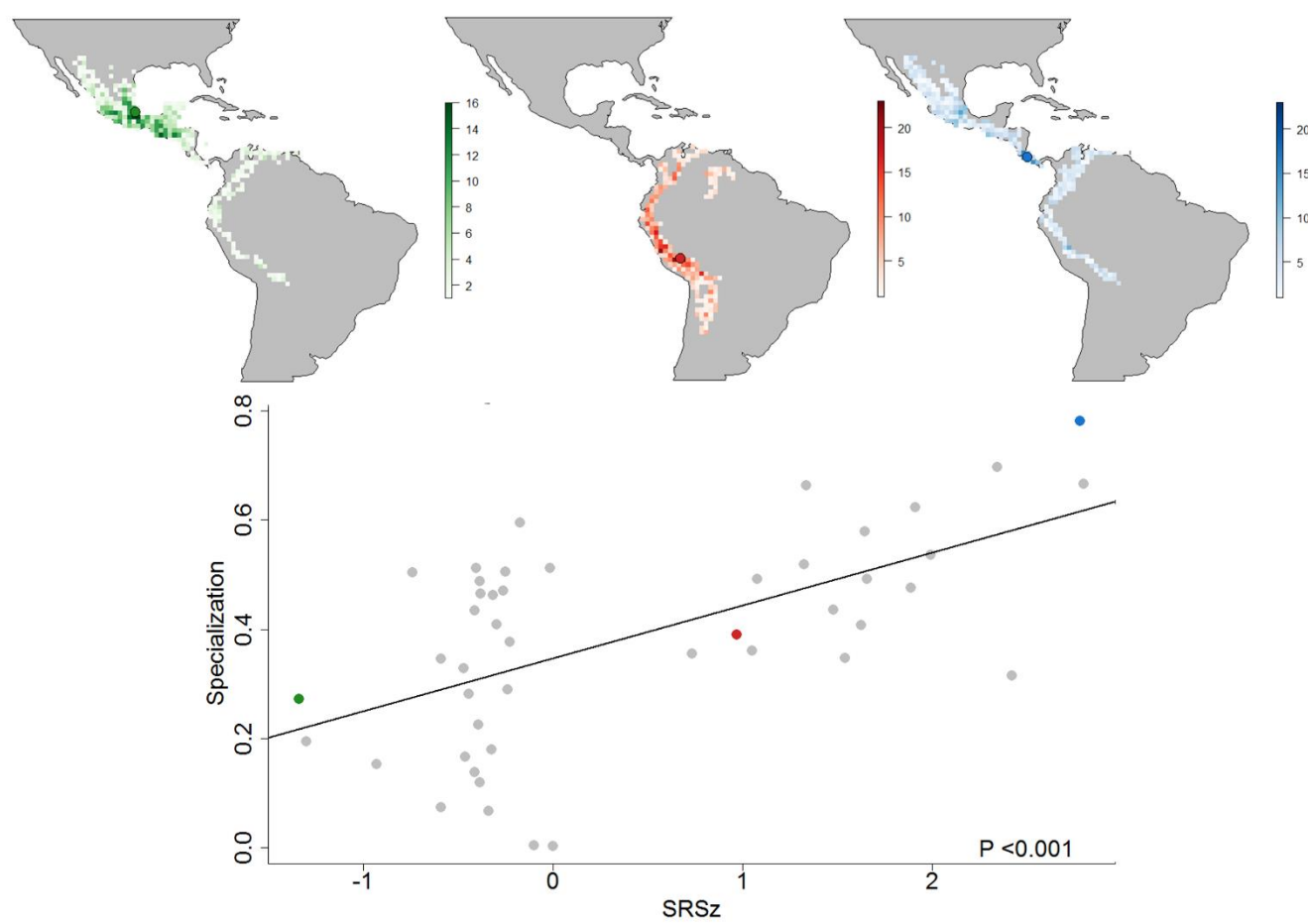
704 **Figure 3.** Three models constructed to test the relationship between specialization and a redefined
705 measurement of the proportion of smaller-ranged species calculated based on the 1st quartile of the
706 range-size frequency distribution for the global mainland species pool of hummingbirds ($n = 318$),
707 rather than for the 130 species occurring in our data set. (a) Logistic regression testing the
708 association between specialization and SRS when treating SRS as a binary variable ($n = 46$). (b)
709 One-way ANOVA testing for difference in specialization among communities with smaller-ranged
710 species either present or absent. (c) A linear regression testing the linear association between the
711 proportion of smaller-ranged species (SRS) and specialization for communities with smaller-ranged
712 species present ($n = 10$).



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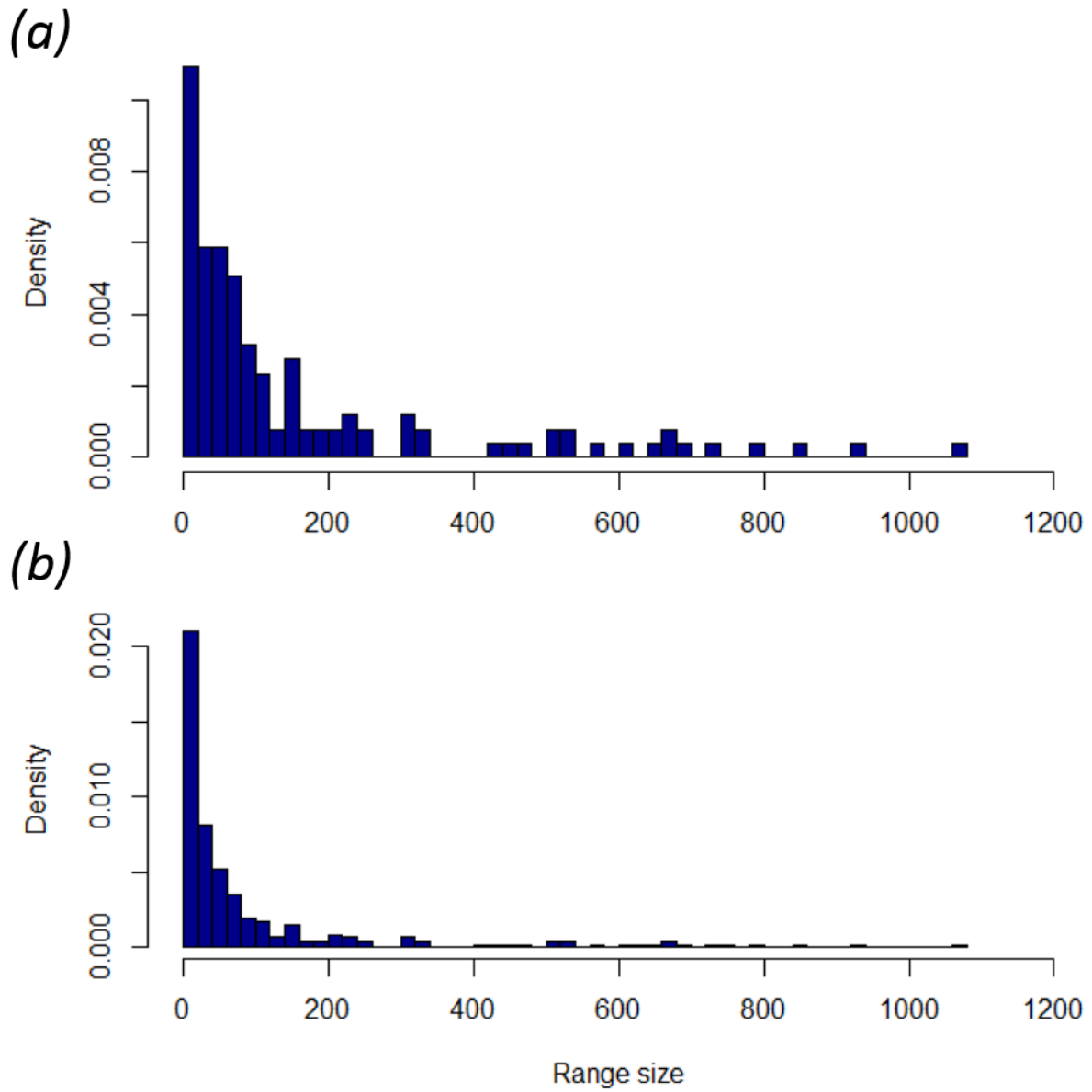
722 **Figure 4.** Scatterplot showing the correlation between specialization and a geographic null model
723 correction of SRS. The source pool for each community was assembled using the rationale that
724 species living in areas, which are compositionally more similar with the focal community, are more
725 likely to be included (see Materials and Methods for details). Deviations between the observed SRS
726 values and the normal curve of the null generated SRS values were standardized as the z-score.
727 Maps show examples of the sampling frequency of grid cells for 1000 randomization within the
728 hummingbird dispersion fields associated with each of the coloured example networks spanning the
729 spectra of SRSz-scores.



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735 **Supplementary Material**

736 **Figure S1.** Range size frequency distributions (RSFD) of all continental hummingbird species ($n =$
737 318; *a*) in comparison to the RSFS for continental hummingbird species occurring in the sampled
738 communities ($n = 130$; *b*). The density indicate that all columns sum to one.

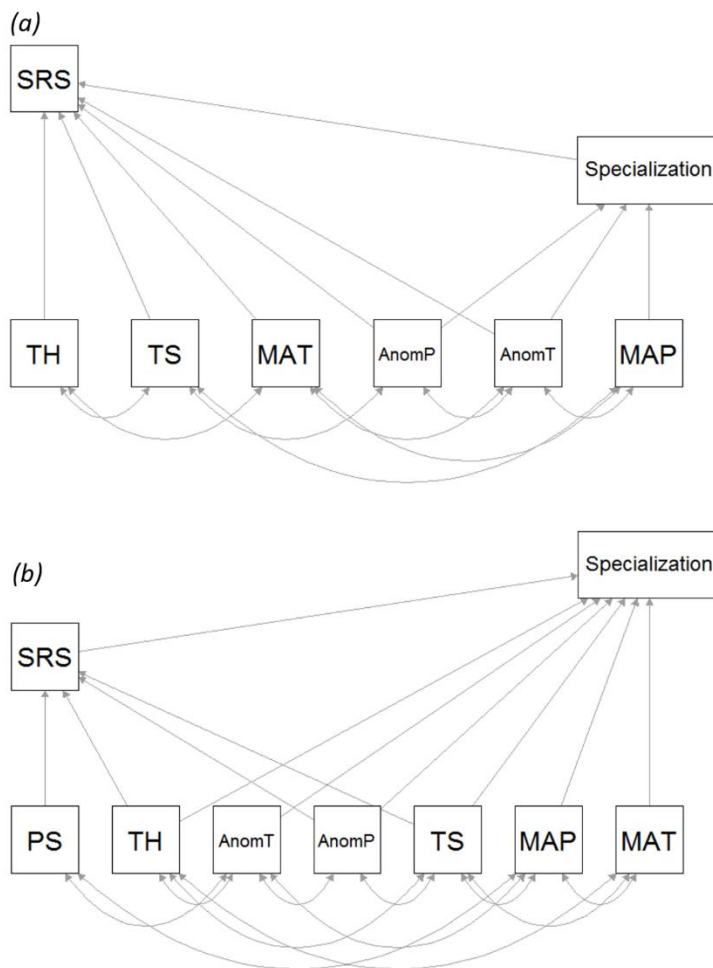


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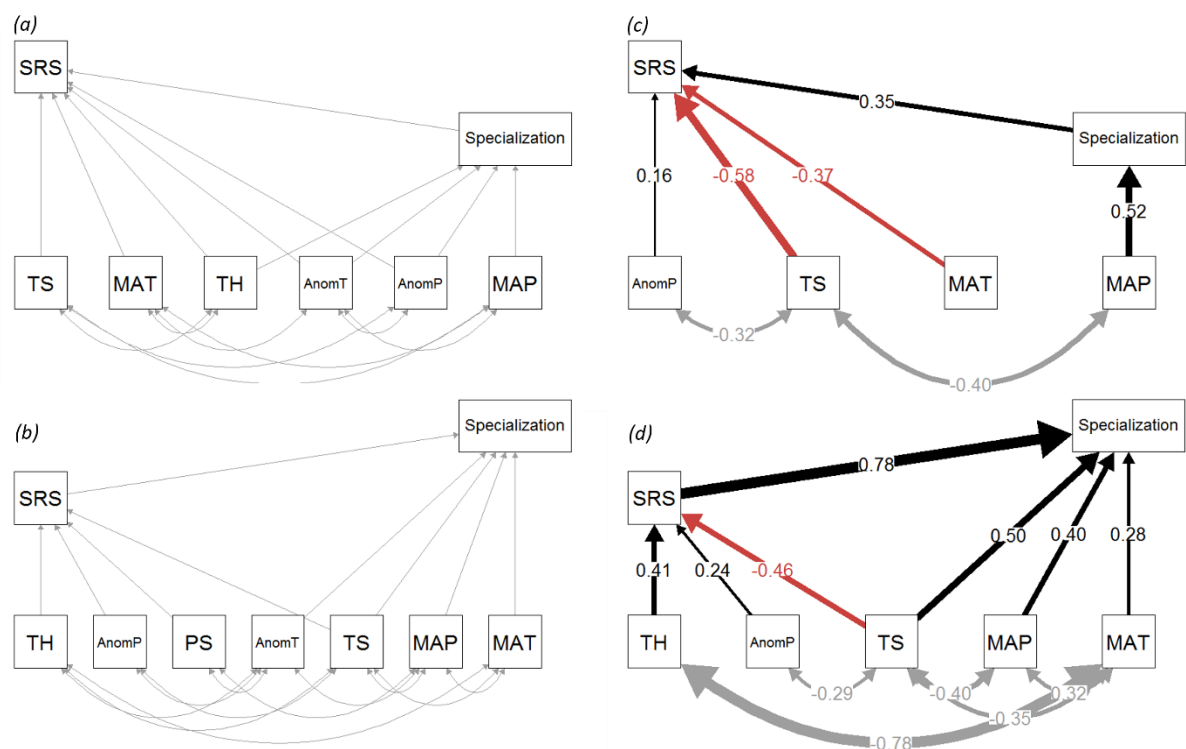
742 **Figure S2.** Initial structural equation models (SEMs) showing all direct and indirect effects of
 743 contemporary climate and Quaternary climate velocity on specialization and the proportion of
 744 smaller-ranged species (SRS; $n = 46$). *A* and *b* show initial SEMs including all predictors present in
 745 the best linear models (i.e. showing $\Delta AIC < 2$ in comparison to the model with lowest AIC). (*a*) a
 746 SEM predicting SRS through specialization and (*b*) *vice versa*. Error covariances were added to
 747 obtain appropriate fit (*see Materials and Methods*). Final SEMs with removed non-significant paths
 748 are presented in figure 2. Other abbreviations are: MAT, mean annual temperature; MAP, mean
 749 annual precipitation; TS, temperature seasonality, PS, precipitation seasonality; AnomT,
 750 temperature anomaly; AnomP, precipitation anomaly; TH, topographic heterogeneity.



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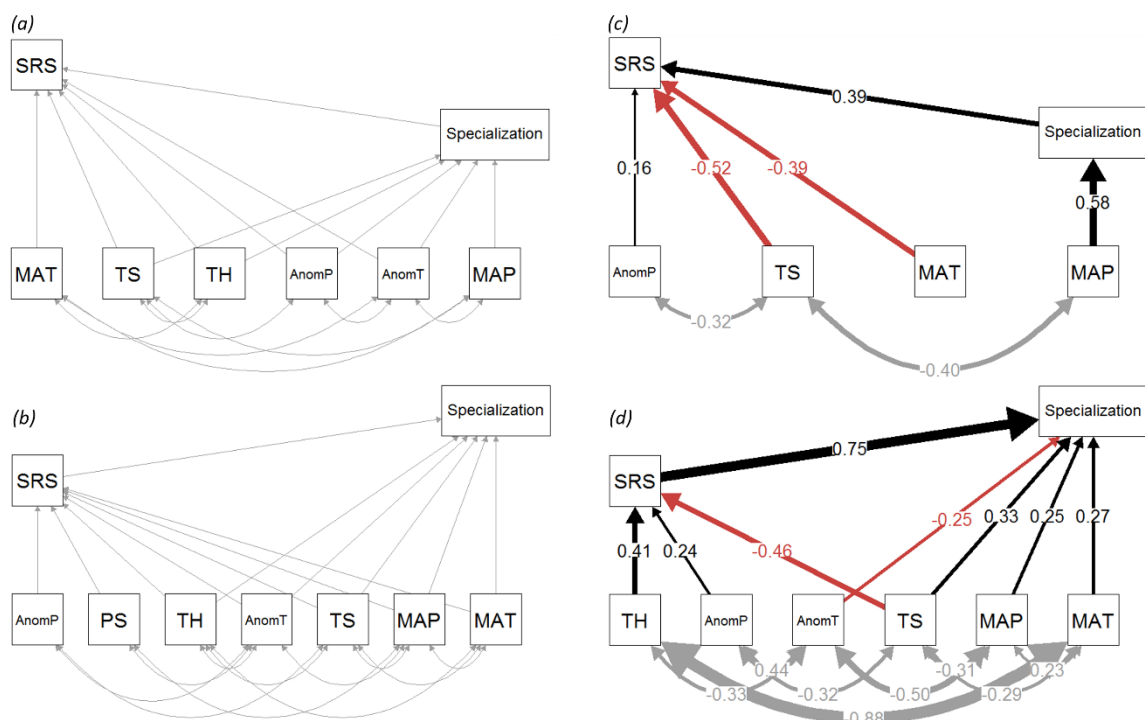
753 **Figure S3.** Results from two structural equation models, SEMs ($n = 46$), correcting specialization
 754 for the correlation with network size (i.e. the summed richness of plants and hummingbirds in the
 755 network). Similar to figure 2 and S2, *a* and *b* show initial SEMs including all predictors present in
 756 the best linear models (i.e. showing $\Delta AIC < 2$ in comparison to the model with lowest AIC). Here,
 757 a SEM predicting SRS through specialization (*a*) and *vice versa* (*b*). Error covariances, shown as
 758 double headed arrows, were added to obtain appropriate fit (see *Materials and Methods*). *c* and *d*
 759 show reduced versions of the same SEMs where non-significant links have been removed. Black
 760 arrows indicate positive relationships, red arrows indicate negative relationships; the thickness of
 761 each arrow illustrates the strength. Other abbreviations are: MAT, mean annual temperature; MAP,
 762 mean annual precipitation; TS, temperature seasonality, PS, precipitation seasonality; AnomT,
 763 temperature anomaly; AnomP, precipitation anomaly; TH, topographic heterogeneity.
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768 **Figure S4.** Results from two structural equation models, SEMs ($n = 46$), correcting specialization
769 for the correlation with network asymmetry (i.e. the ratio between the network richness of
770 hummingbird and plant species). Similar to figure 2 and S2-S3, *a* and *b* show initial SEMs
771 including all predictors present in the best linear models (i.e. showing $\Delta AIC < 2$ in comparison to
772 the model with lowest AIC). Here, a SEM predicting SRS through specialization (*a*) and *vice versa*
773 (*b*). Error covariances, shown as double headed arrows, were added to obtain appropriate fit (see
774 *Materials and Methods*). *c* and *d* show reduced versions of the same SEMs where non-significant
775 links have been removed. Black arrows indicate positive relationships, red arrows indicate negative
776 relationships; the thickness of each arrow illustrates the strength. Other abbreviations are: MAT,
777 mean annual temperature; MAP, mean annual precipitation; TS, temperature seasonality; PS,
778 precipitation seasonality; AnomT, temperature anomaly; AnomP, precipitation anomaly; TH,
779 topographic heterogeneity.

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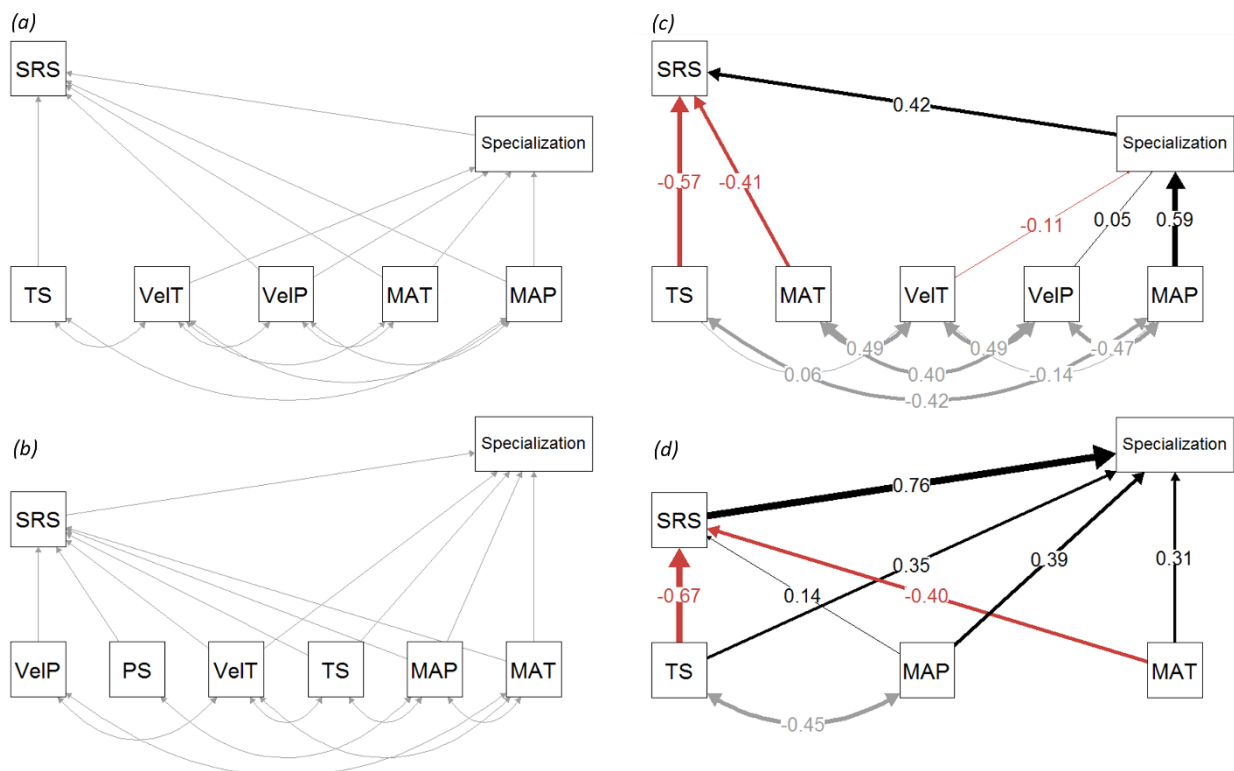


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784 **Fig. S5.** Results from two structural equation models, SEMs ($n = 46$), considering the interactive
785 effect of topography and historical climate change through estimates of temperature and
786 precipitation velocity (VelT and VelP). Similar to figure 2 and S2-S4, *a* and *b* show initial SEMs
787 including all predictors present in the best linear models (i.e. showing $\Delta AIC < 2$ in comparison to
788 the model with lowest AIC). Here, a SEM predicting SRS through specialization (*a*) and *vice versa*
789 (*b*). Error covariances, shown as double headed arrows, were added to obtain appropriate fit (*see*
790 *Materials and Methods*). *c* and *d* show reduced versions of the same SEMs where non-significant
791 links have been removed. Black arrows indicate positive relationships, red arrows indicate
792 negative relationships; the thickness of each arrow illustrates the strength. Other abbreviations are:
793 MAT, mean annual temperature; MAP, mean annual precipitation; TS, temperature seasonality, PS
794 and precipitation seasonality.

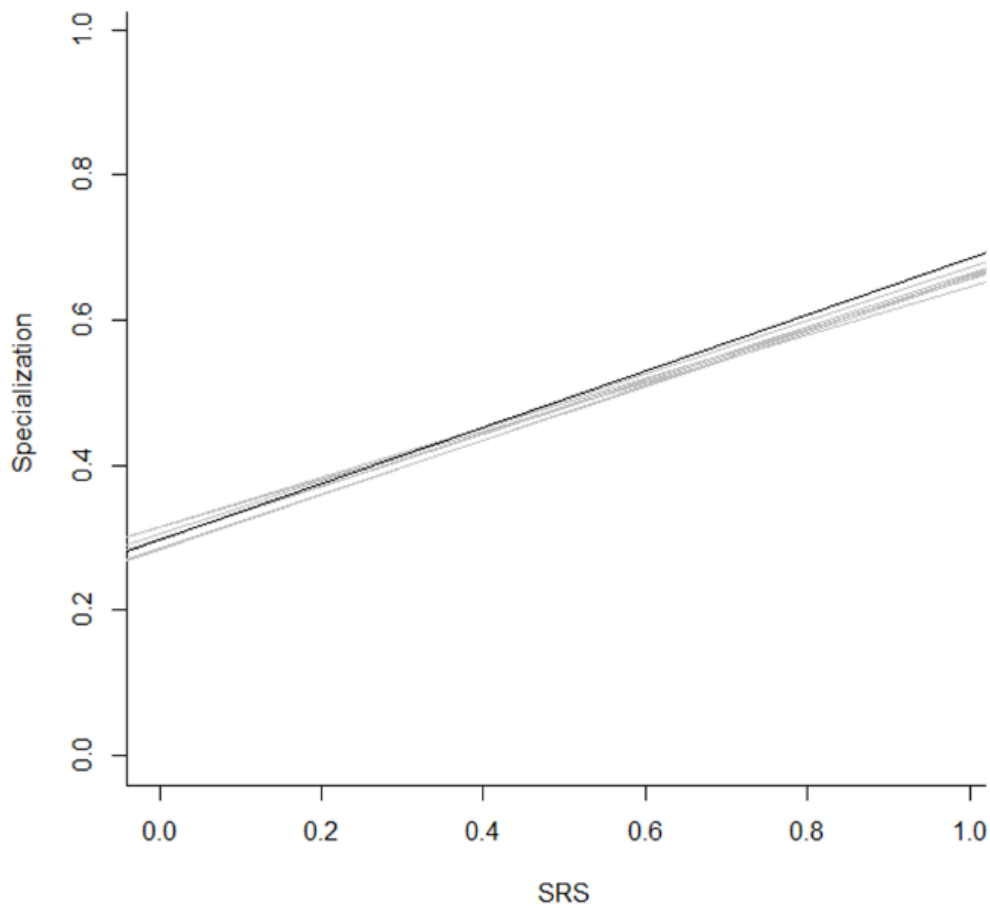


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799 **Fig. S6.** Results from 10 linear models predicting the degree of specialization by the proportion of
800 smaller-ranged species (SRS) calculated by considering cut-offs from 20-30% of the species data
801 with the smallest range sizes. The black line indicate the 25% cut-off, which has been used to
802 calculate SRS for the structural equation models (figure 2, S2-S5). Among the 10 regression
803 models, the slope ranged from 0.33-0.39 (standard deviation = 0.02). all models were significant at
804 0.001 level.



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809 **Table S1.** Location, network size (total species richness), specialization ($\langle d' \rangle$), SRS (the
810 proportion of smaller-ranged species) of the plant-hummingbird networks and null model corrected
811 SRS (SRSz; see material and method section for algorithmic details).

Network ID	Site	Latitude	Longitude	Network Size	Specialization	SRS
1	Atlantic forest, SE Brazil	-20.75	-42.92	22	0.43	0.00
2	Montane meadow, SW USA	34.22	-116.95	6	0.00	0.00
3	Sub-alpine meadow, Central USA	38.98	-106.97	4	0.01	0.00
4	Atlantic forest, SE Brazil	-23.35	-44.83	54	0.49	0.08
5	Tropical dry deciduous forest, W Mexico	19.5	-105.05	20	0.35	0.00
6	Pampa, S Brazil	-31.8	-52.42	35	0.23	0.00
7	Highland Atlantic forest, SE Brazil	-22.5	-44.83	37	0.46	0.00
8	Caatinga, NE Brazil	-7.87	-36.4	36	0.07	0.00
9	Altitudinal caatinga, NE Brazil	-11.48	-41.32	35	0.35	0.13
10	Amazonas riverine, SE Colombia	-3.82	-70.27	46	0.50	0.00
11	High andean forest, Colombia	1.25	-77.43	40	0.49	0.44
12	Atlantic Forest, low elevation	-27.27	-49.01	24	0.67	0.17
13	Atlantic Forest, mid elevation	-27.26	-49.02	14	0.29	0.00
14	Atlantic Forest, high elevation	-27.26	-49.02	11	0.38	0.00
15	Highland temperate mosaic forest, Central Mexico	19.23	-98.97	21	0.15	0.00
16	Suburban forest, Central Mexico	19.28	-98.23	10	0.07	0.00
17	Protected cloud forest, Central Mexico	19.5	-96.95	15	0.19	0.00
18	Rainforest, Colombia	0.07	-72.45	52	0.52	0.13
19	Caatinga forest, NE Brazil	-8.6	-38.57	11	0.18	0.00
20	Highland caatinga, NE Brazil	-13.12	-41.58	35	0.41	0.14
21	Open cerrado, NE Brazil	-13.12	-41.57	19	0.58	0.13
22	Campos rupestres, NE Brazil	-12.98	-41.33	42	0.44	0.14

Network ID	Site	Latitude	Longitude	Network Size	Specialization	SRS
23	Cloud forest, mid elevation, Costa Rica	10.27	-84.08	33	0.66	0.38
24	Cloud forest, high elevation, Costa Rica	10.18	-84.11	28	0.48	0.44
25	Cloud forest, low elevation, Costa Rica	10.44	-84.01	29	0.51	0.13
26	Cerrado, Central Brazil	-18.99	-48.3	25	0.28	0.00
27	Cerrado, Central Brazil	-19.16	-48.39	43	0.46	0.00
28	Cerrado, Central Brazil	-17.78	-48.68	21	0.33	0.00
29	Protected cloud forest, Central Mexico	19.5	-96.95	21	0.27	0.00
30	Pantanal wetland, SW Brazil	-19.52	-56.98	17	0.47	0.00
31	Campos rupestres, SE Brazil	-19.25	-43.52	56	0.70	0.17
32	Cerrado, W Brazil	-20.44	-54.65	20	0.14	0.00
33	Montane Forest, SE Brazil	-22.73	-45.58	31	0.49	0.00
34	Andean forest, Colombia	4.53	-73.85	22	0.36	0.33
35	Andean forest, Colombia	5.9	-73.42	34	0.60	0.17
36	Andean forest, Colombia	5.92	-73.53	19	0.36	0.17
37	Coastal cloud forest, SE Brazil	-23.63	-45.85	31	0.41	0.00
38	Primary forest, Bolivia	-17.51	-63.64	9	0.54	0.17
39	Primary forest, Bolivia	-16.96	-65.41	9	0.51	0.00
40	Campo rupestre, W Brazil	-19.95	-43.9	16	0.12	0.00
41	Atlantic forest, SE Brazil	-23.28	-45.05	56	0.51	0.00
42	Subtropical humid montane forest, Perú	-13.22	-72.12	12	0.39	0.33
43	Lowland primary forest, Perú	-12.85	-69.37	15	0.17	0.00
44	Andean rainforest, mid-elevation, Ecuador.	-0.02	-78.77	84	0.32	0.37
45	Elfin forest, Costa Rica	9.57	-83.73	22	0.62	0.50
46	Undisturbed highland páramo, Costa Rica	9.48	-83.48	30	0.78	0.60

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- 1 Abreu, CRM & Vieira, MF. 2004. Os beija-flores e seus recursos florais em um fragmento florestal de Viçosa, sudeste brasileiro. *Lundiana* 5: 129-134.
 - 2 Alarcón, R., N. M. Waser and J. Ollerton. 2008. Year-to-year variation in the topology of a plant-pollinator interaction network. *Oikos* 117:1796-1807.
 - 3 Ollerton, J., R. Alarcón, N. M. Waser, M. V. Price, S. Watts, L. Cranmer, A. Hingston, C. Peter, and J. Rotenberry. 2009. A global test of the pollination syndrome hypothesis. *Annals of Botany*: 103: 1471-1480.
 - 4 Araujo, AC 1996. Beija-flores e seus recursos florais numa área de planície costeira do litoral norte de São Paulo, sudeste do Brasil. Dissertação de mestrado. UNICAMP. 69p.
 - 5 Arizmendi, MC & Ornelas, JF. 1990. Hummingbirds and their floral resources in a tropical dry forest in Mexico. *Biotropica* 22: 172-180.
 - 6 Vizontin-Bugoni, J & Rui, AM. Unpublished data.
 - 7 Canela, M.B.F. 2006. Interações entre plantas e beija-flores numa comunidade de floresta atlântica montana em itatiaia, RJ. Ph.D thesis, Universidade Estadual de Campinas.
 - 8 Las Casas, FMG, Azevedo Júnior, SM & Dias Filho, MM. 2012. The community of hummingbirds (Aves: Trochilidae) and the
-

- assemblage of flowers in a Caatinga vegetation. *Brazilian Journal of Biology*, 72: 51-58.
- 9 Moura, AC & Machado, CG. Hummingbirds and their flowers at altitudinal dryland vegetation in Chapada Diamantina, northeast Brazil. *In preparation*.
- 10 Cotton, P.A. 1998 The hummingbird community of a lowland Amazonian rainforest. *Ibis*, 140: 512-521.
- 11 Gutierrez Zamora, EA & Rojas Nossa, SV. 2001. Dinámica anual de la interacción colibrí-flor en ecosistemas altoandinos del volcán Galeras, Sur de Colombia. Tesis de Grado Universidad Nacional de Colombia.
- 12 Kohler, G. 2011. Redes de interação planta-beija-flor em um gradiente altitudinal de Floresta Atlântica no Sul do Brasil. MSc Dissertation, Universidade Federal do Paraná, Curitiba, Brazil.
- 13 Kohler, G. 2011. Redes de interação planta-beija-flor em um gradiente altitudinal de Floresta Atlântica no Sul do Brasil. MSc Dissertation, Universidade Federal do Paraná, Curitiba, Brazil.
- 14 Kohler, G. 2011. Redes de interação planta-beija-flor em um gradiente altitudinal de Floresta Atlântica no Sul do Brasil. MSc Dissertation, Universidade Federal do Paraná, Curitiba, Brazil.
- 15 Lara, C. 2006. Temporal dynamics of flower use by hummingbirds in a highland temperate forest in México. *Ecoscience*, 13: 23-29.

- 16 Lara, C. Unpublished data.
- 17 Lara, C. Unpublished data.
- 18 Rosero, L. 2003. Interações planta/beija-flor em três comunidades vegetais da parte sul do Parque Nacional Natural Chiribiquete, Amazonas (Colombia).
- Rosero-Lasprilla, L & Sazima, M. 2004. Interacciones planta-colibrí en tres comunidades Vegetales de la parte suroriental del Parque Nacional Natural Chiribiquete, Colombia. *Ornitologia Neotropical* 15, 183–190.
- 19 Leal, FC, Lopes, AV & Machado, IC. 2006. Polinização por beija-flores em uma área de caatinga no Município de Floresta, Pernambuco, Nordeste do Brasil. *Revista Brasil. Bot.* 29: 379-389.
- 20 Machado, C.G. 2009. Hummingbirds (Aves: Trochilidae) and their floral resources in an area of caatinga vegetation in the Chapada Diamantina, Bahia State, Northeast Brazil. *Zoologia*, 26: 55-65.
- 21 Machado, C. G. 2014. The hummingbird community and the plants which they visit at a savannah in the Chapada Diamantina, Bahia, Brazil, *Bioscience Journal*, 2014, 30: 1578-1587
- 22 Machado, C.G., Coelho, A.G., Santana, C.S., Rodrigues, M. 2007. Hummingbirds and their flowers in the ‘campos rupestres’ of Chapada Diamantina, Bahia, northeastern Brazil. *Revista Brasileira de Ornitologia*, 15: 215-227
-

- 23 Maglianesi, MA, Blüthgen, N, Böhning–Gaese, K & Schleuning, M. (accepted) Morphological traits determine specialization and resource use in plant–hummingbird networks in the Neotropics. 95: 3325-3324.
- 24 Maglianesi, MA, Blüthgen, N, Böhning–Gaese, K & Schleuning, M. (accepted) Morphological traits determine specialization and resource use in plant–hummingbird networks in the Neotropics. Ecology 95: 3325-3324.
- 25 Maglianesi, MA, Blüthgen, N, Böhning–Gaese, K & Schleuning, M. (accepted) Morphological traits determine specialization and resource use in plant–hummingbird networks in the Neotropics. Ecology 95: 3325-3324.
- 26 Araújo, FP, Sazima, M & Oliveira, PE. 2013. The assembly of plants used as nectar sources by hummingbirds in a Cerrado area of Central Brazil. *Plant Systematics and Evolution*, 299: 1119-1133.
- Machado, AO. 2012. Diversidade de recursos florais para beija-flores nos cerrados do Triângulo mineiro e região. Ph.D Thesis. Universidade Federal de Uberlândia.
- Maruyama, PK, Oliveira, GM, Ferreira, C, Dalsgaard, B & Oliveira, PE. 2013. Pollination syndromes ignored: importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. *Naturwissenschaften*, 100: 1061-1068.
- 27 Araújo, FP, Sazima, M & Oliveira, PE. 2013. The assembly of plants
-

used as nectar sources by hummingbirds in a Cerrado area of Central Brazil. *Plant Systematics and Evolution*, 299: 1119-1133.

Machado, AO. 2012. Diversidade de recursos florais para beija-flores nos cerrados do Triângulo mineiro e região. Ph.D Thesis. Universidade Federal de Uberlândia.

Maruyama, PK, Oliveira, GM, Ferreira, C, Dalsgaard, B & Oliveira, PE. 2013. Pollination syndromes ignored: importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. *Naturwissenschaften*, 100: 1061-1068.

28 Machado, AO. 2012. Diversidade de recursos florais para beija-flores nos cerrados do Triângulo mineiro e região. Ph.D Thesis. Universidade Federal de Uberlândia.

29 Ornelas, JF. Unpublished data.

30 Araujo, AC & Sazima, M 2003. The assemblage of flowers visited by hummingbirds in the “capões” of Southern Pantanal, Mato Grosso do Sul, Brazil. *Flora* 198: 427-435.

31 Rodrigues, LC & Rodrigues, M. 2014 (in press). Flowers visited by hummingbirds in the open habitats of the southeastern Brazilian moutaintops: species composition and seasonality. *Brazilian Journal of Biology*, 74.

32 Rodrigues, LC. & Araujo AC. 2011. The hummingbird community and their floral resources in an urban forest remnant in Brazil. *Brazilian Journal of Biology*, 71: 611-622.

- 33 Sazima, I, Buzato, S & Sazima, M. 1996. An assemblage of hummingbird-pollinated flowers in a montane forest in southern Brazil. *Botanica Acta* 109: 149-160.
- 34 Snow DW, & Snow BK. 1980. Relationships between hummingbirds and flowers in the Andes of Colombia. *Bulletin of the British Museum of Natural History (Zoology)* 38: 105-139.
- 35 Snow DW, & Snow BK. 1980. Relationships between hummingbirds and flowers in the Andes of Colombia. *Bulletin of the British Museum of Natural History (Zoology)* 38: 105-139.
- 36 Snow DW, & Snow BK. 1980. Relationships between hummingbirds and flowers in the Andes of Colombia. *Bulletin of the British Museum of Natural History (Zoology)* 38: 105-139.
- 37 Snow DW, & Snow BK. 1986. Feeding ecology of hummingbirds in the Serra do Mar, southeastern Brazil. *Hornero* 012: 286-296.
- 38 Abrahamczyk S, Kessler M 2010. Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. *Journal of Ornithology*, 151:615 – 625.
- 39 Abrahamczyk S, Kessler M 2010. Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. *Journal of Ornithology*, 151:615 – 625.
-

- 40 De Vasconcelos, MF & Lombardi, JA. 1999. Padrão sazonal na ocorrência de deis espécie de beija-flores (Apodiformes: Trochilidae) em uma localidade de campo rupestre na Serra do Curral, Minas Gerais. *Ararajuba* 7: 71-79.
- 41 Vizentin–Bugoni, J., P. K. Maruyama and M. Sazima. 2014. Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird–plant network. *Proceedings of the Royal Society of London B* 281:1–8.
- 42 S. Watts. 2008. Plant-flower visitor interaction in the Sacred Valley of Perú. PhD. thesis, University of Northampton, UK.
- 43 S. Watts. 2008. Plant-flower visitor interaction in the Sacred Valley of Perú. PhD. thesis, University of Northampton, UK.
- 44 Walther, BA & Brieschke, H. 2001. Hummingbird-flower relationships in a mid-elevation rainforest near Mindo, northwestern Ecuador. *International Journal of Ornithology* 4: 115-135.
- 45 Wolf, LL, Stiles, FG, & Hainsworth, FR. 1976. Ecological organization of a tropical, highland hummingbird community. *The Journal of Animal Ecology*, 45: 349-379.
- 46 Wolf, LL, Stiles, FG, & Hainsworth, FR. 1976. Ecological organization of a tropical, highland hummingbird community. *The Journal of Animal Ecology*, 45: 349-379.