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High proportion of smaller ranged hummingbird species coincides with ecological specialization across the Americas

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1 **High proportion of smaller-ranged hummingbird species coincides with ecological**

2 **specialization across the Americas**

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Abstract

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

1. Introduction

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

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

Contemporary and historical climate may also affect the geographical distribution of 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 disproportionally 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 $1^o \times$

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-occuring 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 (<d'>) 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 <d'> 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 temerature; 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.

(f) Sensitivity analyses of range-size definition.

To evaluate the robustness to the use of different range-size cut-offs, We fitted ten additional linear

models using different range-size cut-offs to define a smaller-ranged species (i.e. from 20 to 30% of

species having the smallest range sizes; figure S6). In addition, we conducted follow up analyses

using a redefined measure of the proportion of smaller-ranged species based on the 1st quartile

species of the global pool of mainland hummingbird species (n = 318) as in Jets, Rahbek & Colwell

[43] rather than the one in our data set (n = 130). Following this method, a species was assigned to

be smaller-ranged if it had a global range-size less than 10 grid cells, as this represent the threshold

between 1st and 2nd quartile of the global species pool. For the 130 species occurring in the dataset,

this cut-off will include the 13% of species with the smallest range sizes. Du to zero inflation in the

corrected SRS variable, we were unable to conduct the above SEMs, which are based on linear

model assumptions. Instead, we used a logistic regression including all data points (n = 46) to test

the association between specialization on the corrected SRS (figure 3a). We note that a chi-square

test applied on the residual deviance and degrees of freedom to assess model fit indicated that SRS

was acceptably represented by a binominal distribution (P = 0.06). Considering specialization as

response variable, we separated the corrected SRS into two variables: one categorical that simply

determines whether communities hold smaller-ranged species or not (n = 46) and one containing

only communities having smaller-ranged species according to the corrected threshold (n = 10). The

association between the corrected SRS and specialization was fitted using ANOVA and simple

univariate linear models, respectively (figure 3b and c).

In addition to the threshold used to define smaller-ranged species, the latitudinal

variation in continental or biome narrowness may constitute hard boundaries to the range size of

species [28,65]**,** which could also influence the association between SRS and specialization. To

account for this, we used dispersion fields to construct a null model, which generates SRS values

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 $1^{o} \times 1^{o}$

331   latitude-longitude resolution. The concept of the biogeographical sourse 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: $SRSz = (SRS_{observed} - \overline{SRS_{null}})/sd(SRS_{null})$.

341

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 (c*oef.* = -0.01, R^2 = 0.07, P = 0.07, n = 46; c*oef.* = -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 3*a*); (*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 3*b*) 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 3*c*). 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.

4. Discussion

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

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.

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Figures and tables

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

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

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

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

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

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

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

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

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

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

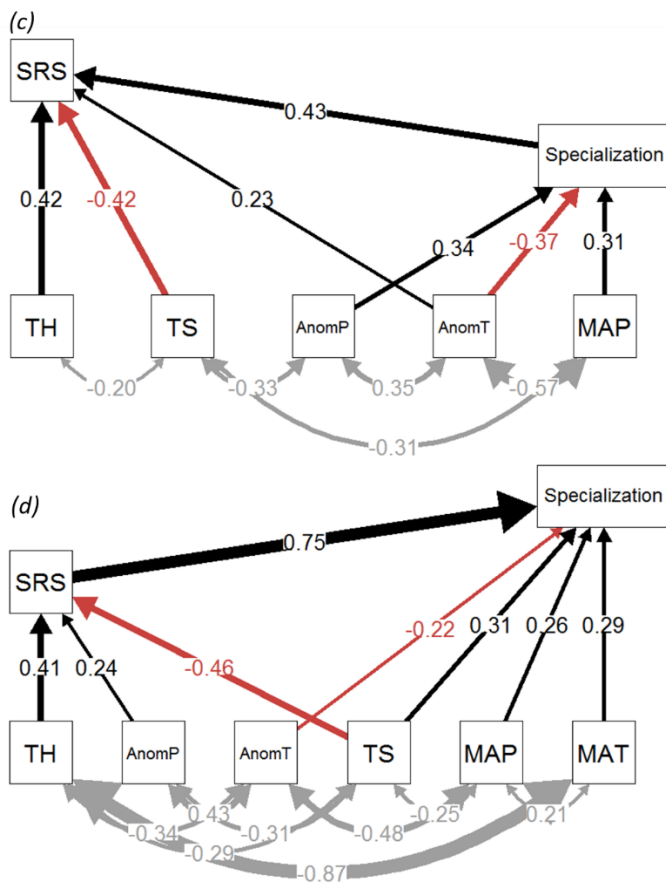*hemileucus*) and Fiery-throated Hummingbird (*Panterpe insignis*). Painting by Jon Fjeldså.

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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 ($n = 10$).
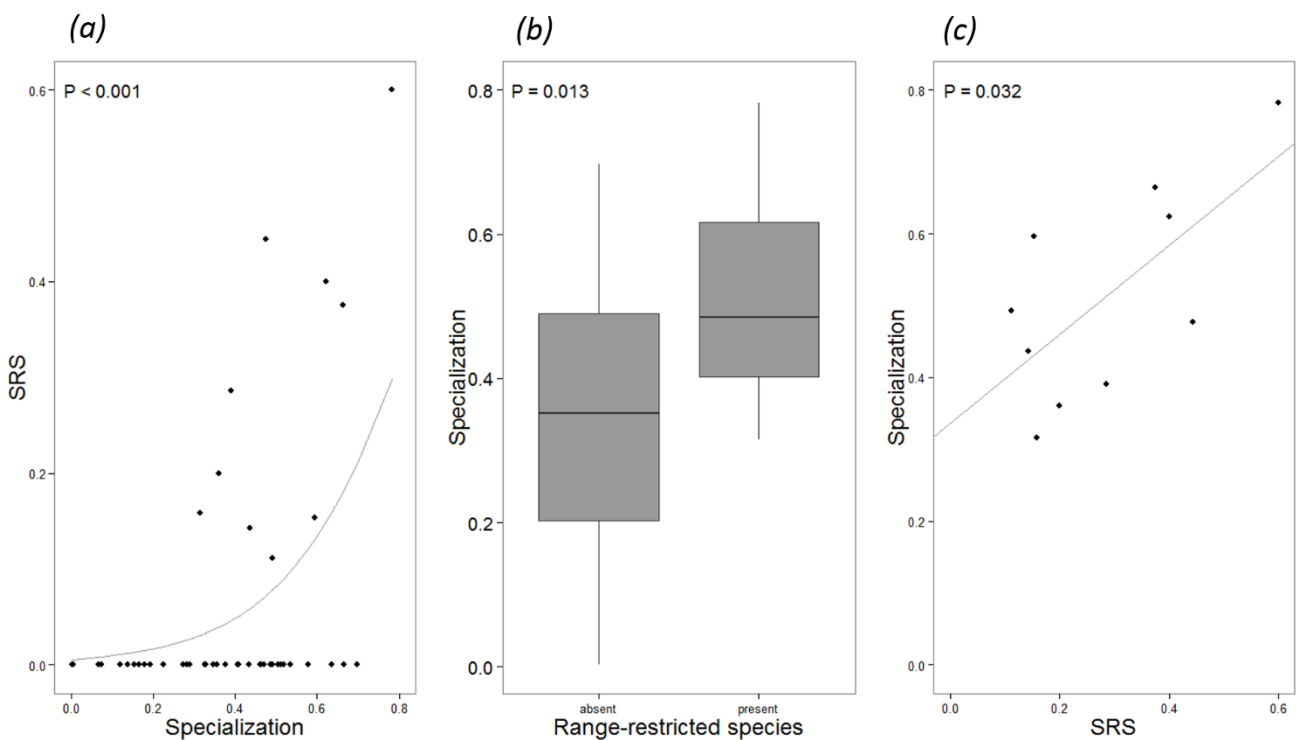
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722 **Figure 4.** Scatterplot showing the correlation between specialization and a geographic null model

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
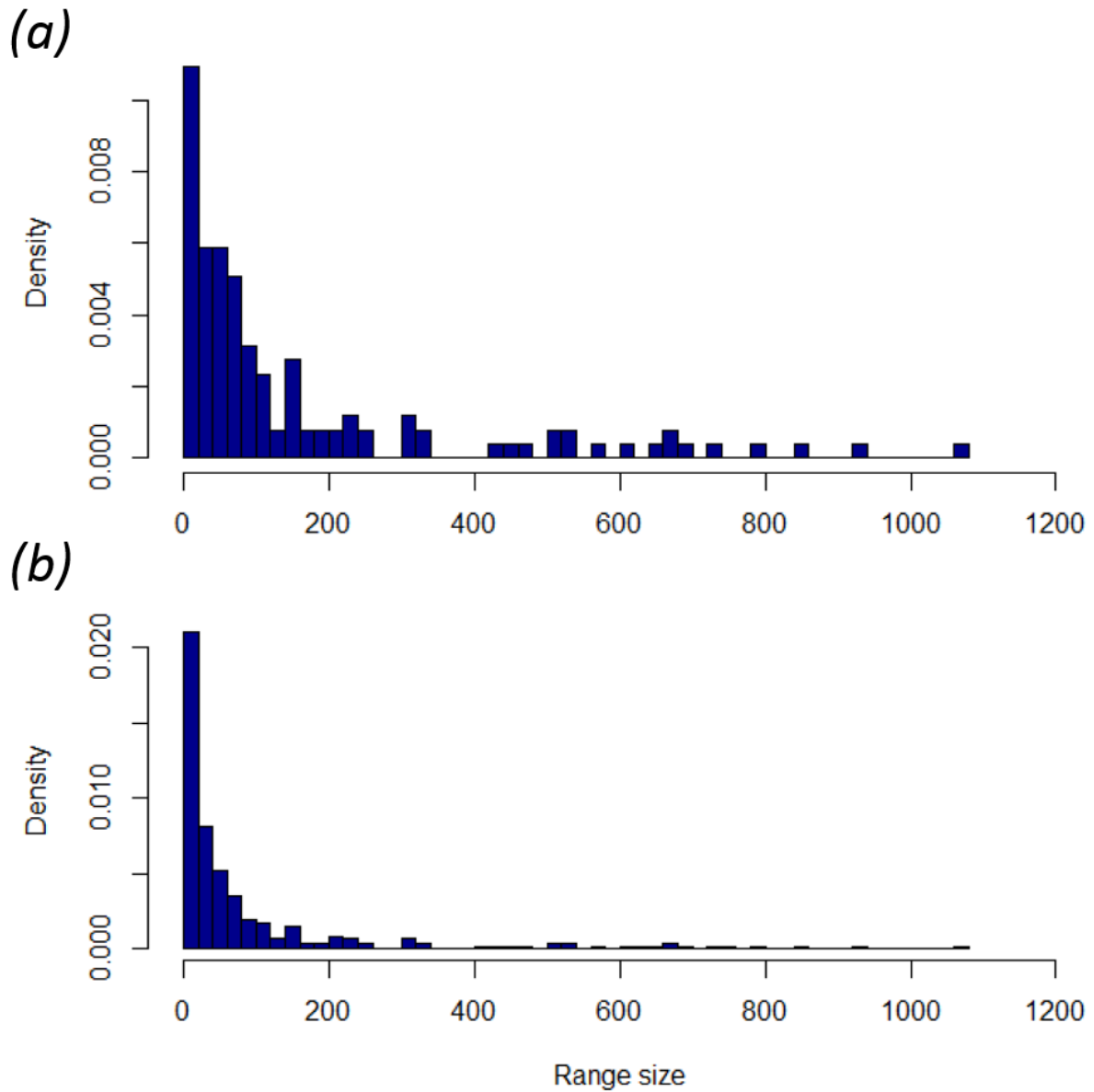
729 spectra of SRSz-scores.

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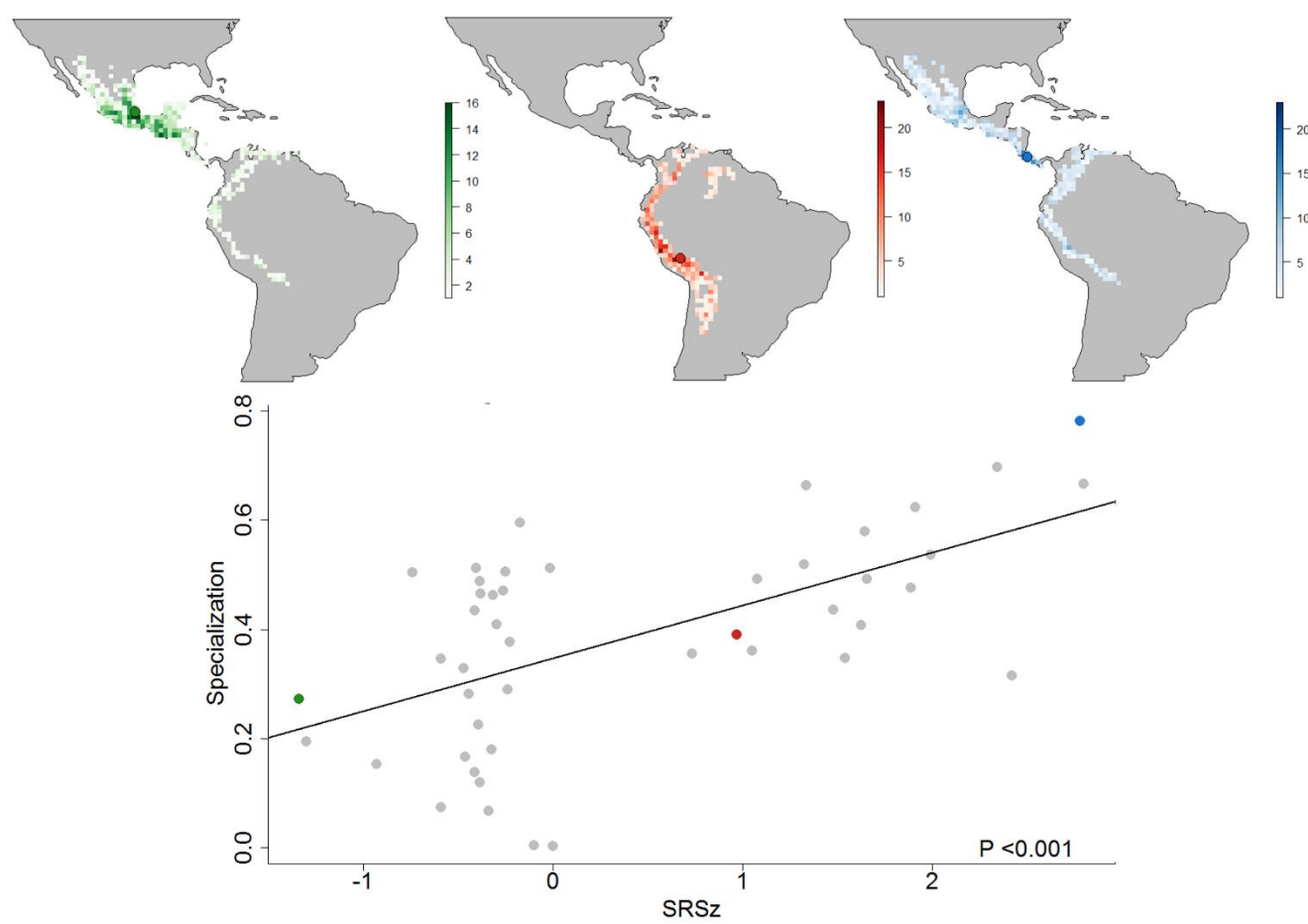
Supplementary Material

Figure S1. Range size frequency distributions (RSFD) of all continental hummingbird species (*n* = 318; *a*) in comparison to the RSFS for continental hummingbird species occurring in the sampled 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 ΔAIC < 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.
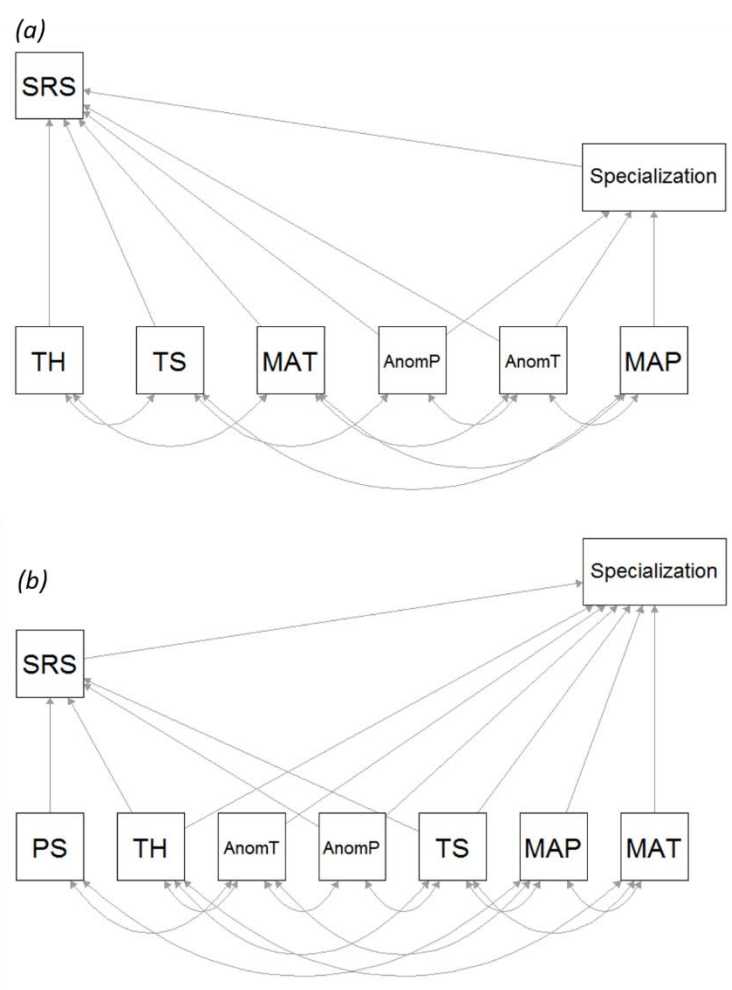

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753   **Figure S3.** Results from two structural equation models, SEMs ($n = 46$), correcting specialization

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 ΔAIC < 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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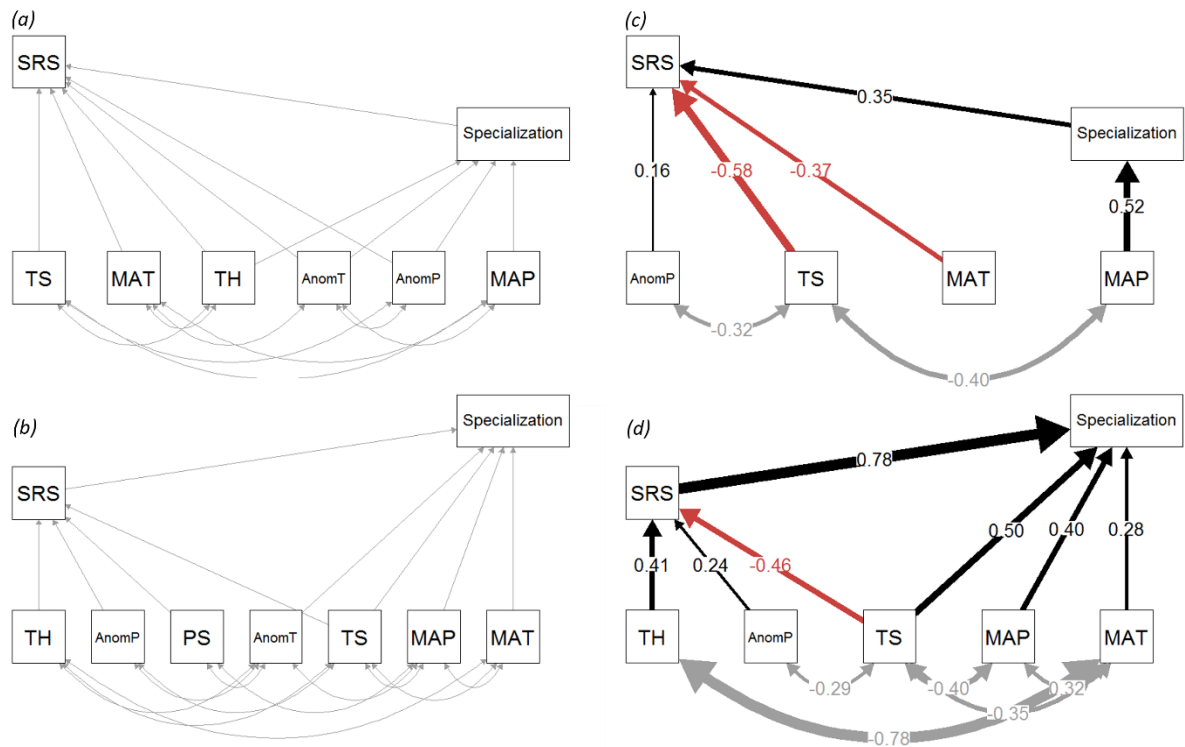
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768 **Figure S4.** Results from two structural equation models, SEMs (*n* = 46), correcting specialization

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 ΔAIC < 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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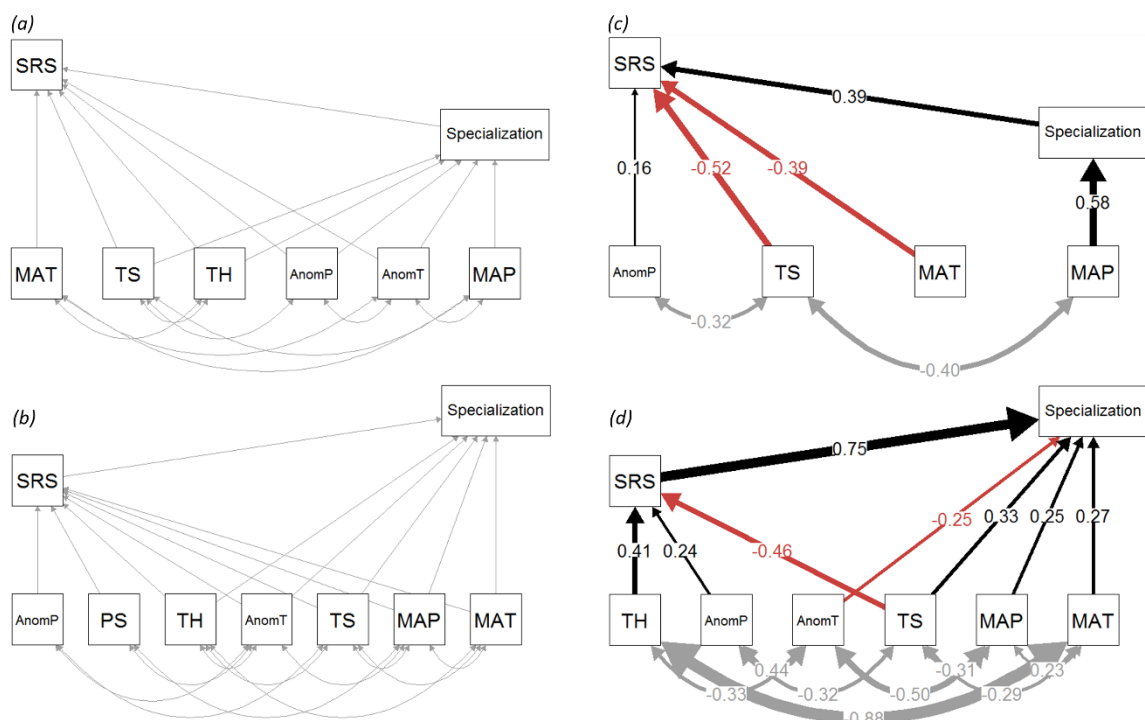
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784   **Fig. S5.** Results from two structural equation models, SEMs ($n = 46$), considering the interactive

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 removedved. 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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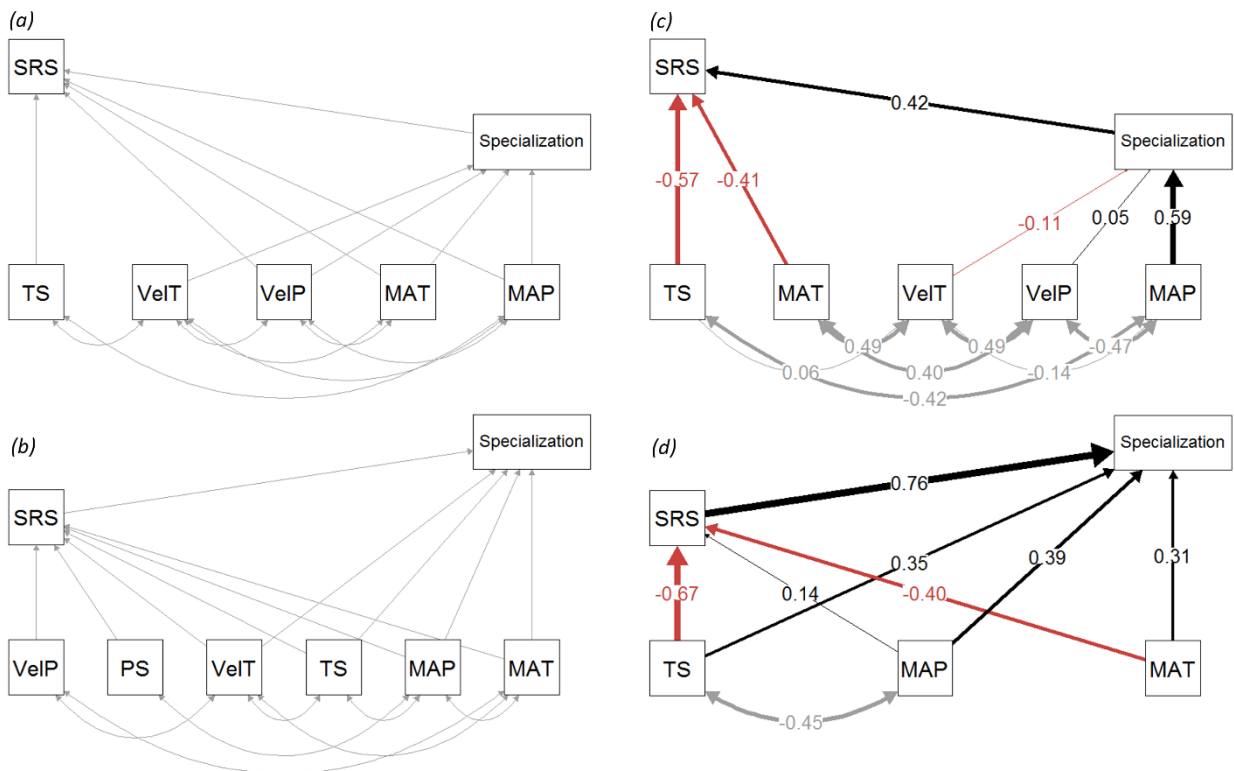
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799 **Fig. S6.** Results from 10 linear models predicting the degree of specialization by the proportion of

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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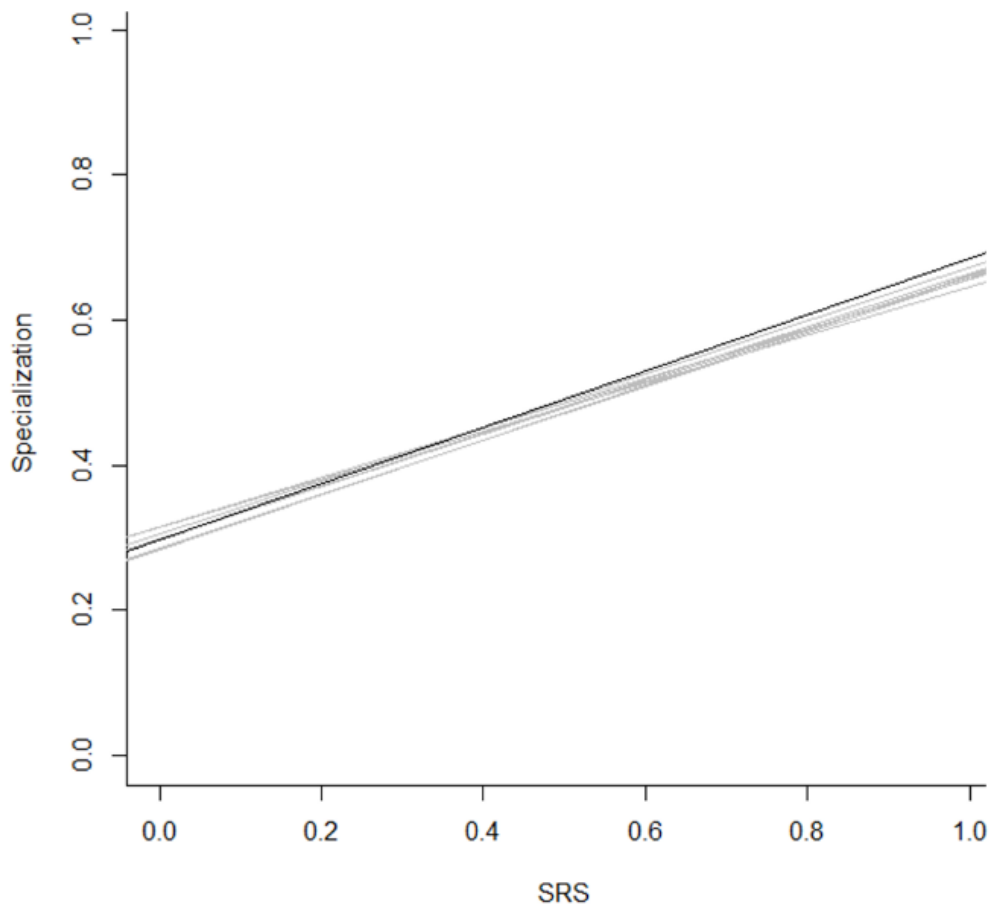
Table S1. Location, network size (total species richness), specialization (<d'>), SRS (the proportion of smaller-ranged species) of the plant-hummingbird networks and null model corrected SRS (SRSz; see material and method section for algorithmic details).

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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