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Functional diversity mediates macroecological variation in planthummingbird interaction networks

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115

116 **Abstract (up to 300 words)**

117 **Aim:** Species interaction networks are known to vary in structure over large spatial scales.
118 We investigated the hypothesis that environmental factors affect interaction network structure
119 by influencing the functional diversity of ecological communities. Notably, we expect more
120 functionally diverse communities to form interaction networks with a higher degree of niche
121 partitioning.

122 **Location:** Americas.

123 **Time period:** Current.

124 **Major taxa studied:** Hummingbirds and their nectar plants.

125 **Methods:** We used a large dataset comprising 74 quantitative plant-hummingbird interaction
126 networks distributed across the Americas, along with morphological trait data for 158
127 hummingbird species. First, we used a model selection approach to evaluate associations
128 between environment (climate, topography and insularity), species richness, and
129 hummingbird functional diversity as predictors of network structure (niche partitioning, i.e.,
130 complementary specialization and modularity). Second, we used Structural Equation Models
131 (SEMs) to ask whether environmental predictors and species richness affect network structure
132 directly and/or indirectly through their influence on hummingbird functional diversity. For a
133 subset of 28 networks, we additionally evaluated whether plant functional diversity was
134 associated with hummingbird functional diversity and network structure.

135 **Results:** Precipitation, insularity and plant richness, together with hummingbird functional
136 diversity (specifically functional dispersion), were consistently strong predictors of niche
137 partitioning in plant-hummingbird networks. Moreover, SEMs showed that environmental
138 predictors and species richness affected network structure indirectly through their effects on

139 hummingbird functional diversity. Plant functional diversity, however, was unrelated to
140 hummingbird functional diversity and network structure.

141 **Main conclusions:** We reveal the importance of hummingbird functional diversity for niche
142 partitioning in plant-hummingbird interaction networks. The lack of support for similar
143 effects for plant functional diversity potentially indicate that consumer functional diversity
144 may be more important for structuring interaction networks than resource functional diversity.
145 Changes in pollinator functional diversity are therefore likely to alter the structure of
146 interaction networks and associated ecosystem functions.

147

148 **KEYWORDS**

149 functional dispersion, insularity, modularity, network structure, niche partitioning, plant-
150 pollinator interactions, pollination networks, specialization, trait diversity

151 **1 INTRODUCTION**

152 Species' traits influence niche partitioning between pairs of species, and thus should affect the
153 structuring of entire networks of interacting organisms (Fründ, Dormann, Holzschuh &
154 Tscharrntke, 2013; Junker et al., 2013; Maruyama, Vizentin-Bugoni, Oliveira, Oliveira &
155 Dalsgaard, 2014; Maglianesi, Böhning-Gaese & Schleuning, 2015). We may therefore expect
156 a correspondence between community trait composition (i.e., functional diversity) and
157 interaction network structure, such that communities in which species differ strongly in traits
158 related to their ecological interactions should exhibit a high resource partitioning. Despite the
159 potential importance for community stability and ecosystem functioning (Fontaine, Dajoz,
160 Meriguet & Loreau, 2005; Fründ et al., 2013; Mouillot, Graham, Villéger, Mason &
161 Bellwood, 2013; Schleuning, Fründ & Garcia, 2015), the relationship between functional
162 diversity and the structure of species interaction networks remains untested at large
163 geographical scales (Kissling & Schleuning, 2015; Gravel, Albouy & Thuiller, 2016).

164 Several recent studies have used mutualistic networks to examine how large-scale
165 variation in environmental factors, notably climate, relate to network structure (e.g.,
166 Dalsgaard et al., 2011; Schleuning et al., 2012, 2014; Trøjelsgaard & Olesen, 2013; Martín
167 González et al., 2015). Likewise, studies have reported relationships between environment
168 and functional diversity of assemblages, for both plants and pollinators (Swenson et al., 2012;
169 Grass, Berens & Farwig, 2014; Rader, Bartomeus, Tylianakis & Laliberté, 2014; Ordonez &
170 Svenning, 2017). However, apart from a few local and regional studies on a small number of
171 networks (e.g., Junker, Blüthgen & Keller 2015; Maglianesi, Blüthgen, Böhning-Gaese &
172 Schleuning 2015), the way in which functional diversity influences species interaction
173 networks is poorly understood. In addition, despite the reported relationships between
174 environmental factors and network structure, the mechanisms behind such relationships

175 remain speculative (reviewed in Trøjelsgaard & Olesen, 2016 and Tylianakis & Morris,
176 2017).

177 One plausible way environmental factors may affect interaction network structure is
178 through effects on the distribution of species and, hence, community composition (Dalsgaard
179 et al., 2011; Bartomeus et al., 2016; Sonne et al., 2016, Tylianakis & Morris, 2017).
180 Environmental [factors](#) have been shown to affect the distribution of species traits, e.g., body
181 size (Olson et al., 2009), as well as plant [richness](#) (Kreft & Jetz, 2007). Moreover, high
182 species [richness](#) has been linked to an increase in competition, which should promote greater
183 trait differentiation within plant and pollinator [communities](#) (MacArthur & Levins, 1967;
184 Inouye, 1978; [Vamosi et al., 2006](#); [Fründ et al., 2013](#)). [For example, traits linked to](#)
185 [pollinators' body size and shapes have been shown to determine interaction partitioning](#)
186 [within plant-pollinator interactions \(e.g., Inouye, 1978; Vizentin-Bugoni, Maruyama &](#)
187 [Sazima, 2014\)](#). Thus, one hypothesis is that environmental factors influence species and
188 functional diversity in communities (Kreft & Jetz, 2007, Olson et al., 2009, Ordonez &
189 Svenning, 2017), which then mediate effects on network structure (Fründ et al., 2013;
190 Mouillot et al., 2013; Bartomeus et al., 2016, Tylianakis & Morris, 2017). Specifically, a
191 higher functional diversity in communities should lead to networks with a greater partitioning
192 of interactions (Inouye, 1978; Junker et al., 2013, [2015](#); Maruyama et al., 2014; [Maglianesi,](#)
193 [Blüthgen et al., 2015](#)).

194 We investigate this hypothesis using a large dataset of 74 quantitative plant-
195 hummingbird mutualistic interaction networks distributed widely across the Americas.
196 Hummingbirds, a species-rich family of nectar-feeding birds, are important pollinators in the
197 New World, showing specialized interactions with the plants they pollinate (Stiles, 1981;
198 Cronk & Ojeda, 2008; Zanata et al., 2017). Due to their high diversity and strong

199 specialization for nectarivory, hummingbirds have frequently been used as a model system to
200 study the evolutionary, historical and ecological factors structuring the assembly of species
201 into communities (Snow & Snow, 1972; Stiles, 1981; Graham Parra, Tinoco, Stiles &
202 McGuire, 2012; Vizentin-Bugoni et al., 2014; Maglianesi, Böhning-Gaese et al., 2015; Martín
203 González et al., 2015; Sonne et al., 2016). We here evaluate the relationships between
204 environmental **factors**, species richness, functional trait diversity, and network structure. Our
205 aim is to elucidate whether functional trait diversity mediates the effects of environmental
206 **factors** on network structure at a macroecological scale. We focused on hummingbird body
207 mass, bill length and shape, as these traits are known to influence their interactions with their
208 nectar-plants (Feinsinger & Colwell, 1978; Dalsgaard et al., 2009; Maglianesi, Blüthgen,
209 Böhning-Gaese & Schleuning, 2014; Maglianesi, Böhning-Gaese, et al., 2015; López-
210 Segoviano, Bribiesca & Arizmendi, 2018). Because hummingbirds depend on floral nectar for
211 energy intake **and partition floral resources according to their morphology, we expected that**
212 hummingbird communities with higher degree of functional diversity should form specialized
213 interaction networks with higher degree of niche partitioning (MacArthur & Levins, 1967;
214 Feinsinger & Colwell, 1978; Inouye, 1978; **Stiles, 1981**; Maglianesi, Blüthgen, et al., 2015).
215 **We similarly expected a positive relationship between plant functional diversity and the**
216 **degree of interaction niche partitioning as plant traits have been shown to constrain plant-**
217 **hummingbird interactions (Maglianesi et al., 2014; Vizentin-Bugoni et al., 2014). Moreover,**
218 we expected that predictors linked to productivity, such as temperature and precipitation, **are**
219 positively **associated** with both functional diversity (e.g., Ordonez & Svenning, 2017) and
220 network specialization (Dalsgaard et al., 2011; Trøjelsgaard & Olesen, 2013; Martín González
221 et al., 2015), whereas past climate instability **should decrease** specialization (Dalsgaard et al.,
222 2011; Ordonez & Svenning, 2017). Climatic seasonality, on the other hand, may increase both
223 the functional diversity (Swenson et al., 2012) and interaction partitioning (Schleuning et al.,

224 2014) by causing regular species turnover related to predictable environment variability. In
225 addition to climatic effects, we expected that topographical heterogeneity has a positive effect
226 on both functional diversity and network specialization by generating habitat heterogeneity
227 and enabling species to track changing climates more easily (Sonne et al., 2016; Ordonez &
228 Svenning, 2017), while insularity is expected to have a negative effect due to ecological
229 release and increased generalization on islands (Traveset, Olesen, et al., 2015). We tested
230 these hypotheses by examining how environmental predictors affect network structure both
231 directly and indirectly through their influence on functional diversity.

232

233 **2 METHODS**

234 **2.1 Plant-hummingbird networks**

235 We used a dataset of 74 quantitative plant-hummingbird interaction networks distributed
236 across the Americas (Figure 1), from 38°58' North to 31°48' South (updated from Martín
237 González et al., 2015; see Appendix S1 in Supporting Information). Each network describes
238 interactions among plant and hummingbird species for a given community, with interactions
239 summarized as a quantitative bipartite matrix having plants as rows and hummingbirds as
240 columns, and each cell filled with the observed frequency of pairwise interactions. We
241 focused on mutualistic interactions among plants and hummingbirds, and thus excluded
242 instances of nectar robbery or theft, as they characterize other interaction types (Maruyama,
243 Vizentin-Bugoni, Dalsgaard, Sazima & Sazima, 2015). Species names and classification
244 followed The Plant List (www.theplantlist.org) and the International Ornithological
245 Committee World Bird List (IOC, www.worldbirdnames.org), respectively. In total, our

246 dataset comprised 158 species of hummingbirds (~46% of the 345 species in the IOC Bird
247 List, Appendix S2) and 984 species of plants from 85 families (Appendix S3).

248 **2.2. Hummingbird morphological traits and functional diversity**

249 For all hummingbird species, we compiled information on three morphological traits that
250 influence their interactions with flowers as well as interspecific competition for nectar: bill
251 length, bill curvature and body mass (Snow & Snow, 1972; Feinsinger & Colwell, 1978;
252 Stiles, 1981; Dalsgaard et al., 2009; Maruyama et al., 2014; Vizentin-Bugoni et al., 2014;
253 Maglianesi et al., 2014, Maglianesi, Blüthgen, et al. 2015; López-Segoviano et al., 2018). Bill
254 length and curvature were measured by inspecting an average of 10 adult specimens, both
255 males and females, deposited at museums (see details in Appendix S6); body mass data were
256 gathered from the literature (Appendix S2). For all three traits, we used the mean trait values
257 per species, as interspecific trait variation is larger than intra-specific variation and plays a
258 larger role in determining the division of floral resources among coexisting hummingbird
259 species (Graham et al., 2012; Tinoco, Graham, Aguilar & Schleuning, 2017). In our data, the
260 intraspecific coefficient of variation across all hummingbird species averaged 6.2% for bill
261 length and 8.3% for bill curvature, while interspecific variation amounted to 42.4% and
262 246.9%, respectively (see also Appendix S2).

263 To calculate hummingbird FD metrics, we computed the pairwise Euclidean distances
264 between hummingbird species based on their traits. These distances were projected into a
265 functional trait space using a Principal Coordinate Analysis (Villéger, Mason & Mouillot,
266 2008; Figure 2). Traits were standardized to zero mean and unit variance prior to the
267 calculation of Euclidean distances. We used two measures to quantify distinct facets of FD in
268 hummingbird communities. First, we calculated from the multivariate trait space the sum of
269 the branch length of the Minimum Spanning Tree (MST) connecting all hummingbirds co-

270 occurring in a community. This measure estimates the total trait variability within each
271 community and is similar to functional richness (Villéger et al., 2008), but has the advantage
272 that it can be calculated for communities comprising only two co-existing species (as was the
273 case for some communities in North America and the Caribbean islands). Large MST values
274 indicate the occurrence of species with distinct traits, but do not consider species abundance
275 in its calculations. Second, we calculated the Functional Dispersion (FDis) of each
276 community by computing the mean distance of all species in a community to its centroid in
277 functional trait space (Laliberté & Legendre, 2010). FDis accounts for differences in species'
278 frequencies in the community, by weighting the mean distance and the position of the
279 community centroid with species' abundances. In this study, we approximated hummingbird
280 species abundance by using the sum of interactions for each hummingbird species in the
281 interaction matrices (see details in Appendix S7, S8). High values of hummingbird FDis
282 indicate the co-occurrence of hummingbird species with distinct trait combinations (Laliberté
283 & Legendre, 2010). Calculation of FDis was performed with the function *dbFD* in the R
284 package 'FD' (Laliberté & Legendre, 2010). The two functional indices analyzed in this study
285 (MST and FDis) represent complementary aspects of FD and are only moderately correlated
286 (Pearson's $r = 0.57$, $P < 0.05$, $n = 74$ networks). If FDis is calculated without weighting by
287 species abundance, this correlation becomes higher ($r = 0.80$, $P < 0.05$). Moreover, MST
288 showed a stronger correlation with hummingbird species richness (Pearson's $r = 0.76$, $P <$
289 0.05) than did weighted FDis ($r = 0.43$, $P < 0.05$).

290 **2.3. Plant functional diversity**

291 For a subset of 28 networks, including mainland and island communities and comprising 103
292 hummingbird and 467 plant species (51.2% and 47.5% of the complete dataset, respectively),
293 we also computed plant functional diversity. We considered three traits that have been

294 associated with hummingbird specialization and partitioning of interactions among flowers: 1)
295 floral corolla length (e.g., Maglianesi et al., 2014; Maruyama et al., 2014); 2) color spectrum
296 visible to human eye of the visited flowers, reflecting different degrees of specialization to
297 ornithophily (Wilson, Castellanos, Hogue, Thomson & Armbruster, 2004; Dalsgaard et al.,
298 2009); and 3) plant life form, reflecting resource availability (Feinsinger & Colwell, 1978)
299 and/or vegetation strata (Jordano, Bascompte & Olesen, 2006; see details on plant trait
300 assessment at Appendix S4-S6). We calculated plant FDis for each network, based on the
301 pairwise Gower distances as suggested for the combination of continuous and categorical trait
302 variables (Laliberté & Legendre, 2010). Weights of individual species in the FDis metric were
303 given by independent measures of local floral abundances (Appendix S6). For this same
304 subset of communities, we also re-calculated hummingbird FDis to test whether it relates to
305 plant functional diversity. In addition, we estimated plant and hummingbird FDis based only
306 on corolla and bill length, respectively, as we only had the corolla length as a continuous
307 variable for plants. Results from single-trait analyses were qualitatively identical and are
308 therefore not shown.

309 **2.4 Network indices and sampling intensity**

310 To characterize network structure, we calculated two quantitative indices widely used in the
311 literature to quantify the extent to which species partition their interactions, namely
312 complementary specialization (H_2' and d' , Blüthgen, Menzel & Blüthgen, 2006), and
313 quantitative bipartite modularity (Q , Dormann & Strauss, 2014). Although conceptually
314 distinct, these indices characterize a similar ecological pattern from the hummingbird's
315 perspective, namely the partitioning of interactions along a niche dimension represented by
316 the plant species in the network (Blüthgen, 2010). The complementary specialization indices
317 derive from Shannon's entropy and quantify how realized species' interactions differ from

318 those expected in randomly interacting communities relative to partner availability, i.e. reflect
319 the niche partitioning among species (Blüthgen et al., 2006; Blüthgen, 2010). Two variants,
320 the network-wide specialization H_2' and the species level specialization d' are commonly
321 used; a guild level specialization can be estimated as the weighted mean of d' across all
322 species from the same guild $\langle d' \rangle$ (Blüthgen et al., 2006). In our dataset, hummingbird
323 specialization $\langle d' \rangle$ was strongly correlated with network wide specialization H_2' (Pearson's r
324 = 0.93, $P < 0.05$). We **mostly** focused on $\langle d' \rangle$ as we calculated FD based on morphological
325 data for hummingbird species.

326 A complementary measure of interaction partitioning is modularity Q , which
327 quantifies the prevalence of preferentially interacting subgroups in the networks (Dormann &
328 Strauss, 2014). The formation of such modules of interacting species can be related to a high
329 degree of trait matching between species (Maruyama et al., 2014, Maruyama, Vizentin-
330 Bugoni, Dalsgaard, Sazima & Sazima, 2015). Here, we used the QuanBiMo, a modularity-
331 searching algorithm specifically designed for quantitative bipartite networks (Dormann &
332 Strauss, 2014). Both $\langle d' \rangle$ and Q scale from 0 to 1, with zero indicating low
333 specialization/modularity and 1 high specialization/modularity (Blüthgen et al., 2006;
334 Dormann & Strauss, 2014). Network analyses were conducted using the 'bipartite' package in
335 R (Dormann, Fründ, Blüthgen & Gruber, 2008; R Core Team, 2016).

336 Intrinsic characteristics of the networks, such as size (i.e., number of interacting
337 species) and sampling effort, may affect network indices (Blüthgen et al., 2006; Vizentin-
338 Bugoni et al., 2016). The quantitative network indices used here take species interaction
339 frequencies into account and are less sensitive to sampling insufficiency than metrics based
340 on binary networks that only report the presence or absence of interactions between species
341 pairs (Blüthgen et al., 2006; Vizentin-Bugoni et al., 2016). Nevertheless, to minimize

342 potential biases due to differences in sampling among networks, we Δ -transformed our
343 metrics (Schleuning et al., 2012, [Dalsgaard et al., 2017](#)). In this transformation, the mean
344 value of a metric obtained by multiple randomizations of a null network is subtracted from the
345 observed value (Schleuning et al., 2012, [Dalsgaard et al., 2017](#)). Here, we used the Patefield
346 null model, which fixes the network size and the marginal totals, i.e. species richness and
347 species' total number of interactions, while shuffling interactions randomly (Dormann et al.,
348 2008). The specialization index $\langle d' \rangle$ is already subject to a correction for the marginal totals
349 of the species in the network (Blüthgen et al., 2006), but modularity is not (Dormann &
350 Strauss, 2014); thus, we report the null model corrected ΔQ values in the main results.
351 Nonetheless, results for both untransformed and Δ -transformed specialization and modularity
352 metrics were similar (see [Appendix S9](#)).

353 In addition to null model corrections, we calculated sampling intensity (SI) and
354 network asymmetry, both of which may affect the degree of specialization (Blüthgen et al.,
355 2006; Schleuning et al., 2012). Sampling intensity is defined as the square root of the number
356 of interaction events divided by the geometric mean of the total species number in the given
357 bipartite network (Schleuning et al., 2012) and network asymmetry is defined as the ratio
358 between hummingbird and plant richness. Since network asymmetry was only weakly related
359 to the calculated metrics ($r = -0.21$, $P = 0.07$ for $\langle d' \rangle$ and $r = -0.09$, $P = 0.42$ for ΔQ), we did
360 not consider it further. However, SI was included in the models (see Table 1).

361 **2.5 Environmental variables**

362 We extracted information on current climate, topography, and long-term climate stability
363 within a 10 km radius around each study site from WorldClim 30 arc-second rasters
364 (Hijmans, Cameron, Parra, Jones & Jarvis, 2005). Current climate was represented by mean
365 annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality

366 (estimated as the standard deviation across monthly temperatures; TS), and precipitation
367 seasonality (estimated as the coefficient of variation for monthly precipitation means; PS). To
368 determine the topographical variation (Topography) at each study site, we also used the
369 WorldClim digital elevation model (DEM). This combines the SRTM gap-filled 30 arc
370 second DEM (CGIAR - <http://srtm.csi.cgiar.org/>), covering from 60N to 60S with the
371 GTOPO30 DEM (<https://lta.cr.usgs.gov/GTOPO30>) for other parts of the world. Topography
372 was represented by the standard deviation of elevation within a 10 km radius around each
373 study site. We described paleoclimate stability using the change in temperature and
374 precipitation from the Last Glacial Maximum (LGM) to the present, as estimated using two
375 different models, CCSM3 (Collins et al., 2006; Otto-Bleisner et al., 2006) and MIROC 3.2
376 (K-1 model developers, 2004). For each site, we calculated the change in temperature and
377 precipitation from the LGM to the present (Anomaly), and its spatial rate of displacement
378 (Velocity) as complementary measures of past to present climate variability (Loarie et al.,
379 2009). As our data cover a large geographical extent, we assumed that the regionally
380 downscaled climate estimates are good indicators of the variation of local climate among
381 communities. In addition to data on past and current climate and topography, we included
382 insularity as a dummy variable (1 - island, 0 - mainland). To meet statistical assumptions of
383 normality, MAP was square root transformed and TS was log-transformed prior to further
384 analyses. All variables were scaled to zero mean and unit variance. As velocity and anomaly
385 both describe historical climate change, and are derived from the same model projection, we
386 built one model for each of the two measures of historical climate change. As velocity
387 includes topographical heterogeneity in the calculations (Loarie et al., 2009), we did not
388 include velocity and topography in the same models. In the main text, we report the results
389 regarding anomaly and topography; results regarding velocity as an integrated measure of

390 historical climate variability were qualitatively similar and are reported in the Supplement
391 (Appendix S10).

392 **2.6 Macroecological analysis**

393 We divided the macroecological analysis into two steps in order to simplify and reduce the
394 number of predictors in the Structural Equation Models (SEMs). First, we fitted multi-
395 predictor linear models for both specialization $\langle d' \rangle$ and modularity ΔQ , considering the two
396 indices for hummingbird FD (MST and FDis), separately, plus hummingbird richness
397 (Hummingbirds). Besides these predictors, we included the following environmental
398 predictors: temperature (MAT), precipitation (MAP), temperature seasonality (TS),
399 precipitation seasonality (PS), topography (Topo), temperature anomaly (AnomT),
400 precipitation anomaly (AnomP) and insularity (Insu). Finally, we included plant species
401 richness (Plants) that has been shown to influence resource partitioning in flower-bird
402 networks (Zanata et al., 2017), potentially independent of floral functional diversity (Souza et
403 al., 2018). For the subset of 28 networks with plant FDis measures, we used linear models to
404 test whether plant FDis predicted network level specialization H_2' and ΔQ . The same
405 procedure was repeated with hummingbird FDis within this subset.

406 We fitted four principal models incorporating the combinations of two measures of FD
407 (MST and FDis) and the two network indices ($\langle d' \rangle$ and ΔQ). The two FD measures were
408 always fitted separately as these were correlated; for comparison, we also fitted a model with
409 unweighted FDis (i.e., without incorporating abundance; Appendix S11). We checked for
410 multicollinearity in the full model by evaluating the condition number ($CN \leq 5$) and the
411 variance inflation factor ($VIF \leq 5$). This led to the exclusion of MAT and Hummingbird
412 richness as predictors (see additional results in Supporting Information). Models considering
413 hummingbird richness instead of FD measures had less statistical support (Appendix S12).

414 Model performance of all combinations of predictor variables was assessed based on the
415 Akaike Information Criterion with correction for small samples (AIC_C). Model selections
416 were performed with the function *dredge* in the R package ‘MuMIn’ (Barton, 2014),
417 according to their AIC_C . In all cases, multiple models presented ΔAIC_C values ≤ 2.0 in
418 relation to the best model, i.e., no single best model was identified (Burnham & Anderson,
419 2002). Hence, model averaging was performed across all possible models using the function
420 *model.avg* in ‘MuMIn’ (Barton, 2014). We report the averaged coefficient values and the
421 relative importance of each predictor variable by summing the Akaike weights across the
422 models including the respective variable across all possible models (i.e., Σw_i ; Burnham &
423 Anderson, 2002). We did not include interaction terms between predictors in our models due
424 to the lack of a clear hypothesis justifying their inclusion. Spatial autocorrelation in models’
425 residuals was assessed by computing Moran’s *I* correlograms [using the ‘ncf’ package in R](#)
426 [\(Bjornstad, 2016\)](#), with distance classes of 500 km and a truncation distance of 5000 km. The
427 linear model with specialization $\langle d' \rangle$ showed significant positive spatial autocorrelation.
428 Therefore, we re-ran this model using a simultaneous autoregressive (SAR) model that
429 specifies the autoregressive processes within the error term (Kissling & Carl, 2008). The SAR
430 modeling was conducted using the “spdep” package in R (Bivand & Piras, 2015). The spatial
431 connections between networks were determined as the three nearest neighbors. For the SAR
432 model, no significant spatial auto correlation remained in the residuals (see also Appendix
433 [S6](#)).

434 The second step of our analysis used SEMs to quantify the extent to which predictors
435 influence network structure directly or indirectly via FD. The advantage of SEMs is that both
436 direct and indirect associations among variables are considered simultaneously, hence
437 allowing a hierarchical model structure (Shipley, 2002). We constructed two sets of SEMs for

438 each of the network metrics: (i) one based on the hypothesis that environmental and species
439 richness predictors affect FD and network metrics in parallel, resulting in covariation between
440 FD and network metrics, and (ii) another based on the hypothesis that FD directly affects
441 network metrics (no covariation between FD and network metrics). *A priori* SEMs were
442 constructed based on results from the previous model selection, which consistently
443 demonstrated that insularity, MAP and plant richness had the greatest importance in
444 determining network structure. All other predictors, **except hummingbird FDis**, had
445 consistently low importance values, usually with a Σw_i below 0.3, and thus were not included
446 in the SEMs (see Table 1, **S9–S12**). As MST was found not to influence $\langle d' \rangle$ or ΔQ , only
447 SEMs for FDis were constructed. By including the same set of predictors in each SEM,
448 models were directly comparable, enabling a direct interpretation of whether environmental
449 **factors** and plant richness are likely to affect network structure directly or indirectly through
450 the functional composition of morphological traits (Shipley, 2002). Appropriate fits for SEMs
451 were obtained by including error covariance links based on high modification indices and
452 large residual correlations. Model fit was evaluated with a chi-square test, a comparative fit
453 index (CFI), and a Root Mean Square Error of Approximation (RMSA). The chi-square test
454 measures the coincidence between the empirical and the fitted variance-covariance structure
455 in the data. Here, models were accepted if $P > 0.05$. The CFI relates the chi-square of the
456 model, with the chi-square value of an independent model assuming zero correlation among
457 variables while also accounting for sample size (Shipley, 2002). CFI ranges between 0 and 1,
458 and models with $CFI > 0.09$ were considered to have an appropriate fit (Shipley, 2002).
459 Finally, the RMSA index was included due to its sensitivity to the number of fitted
460 parameters. A $RMSA < 0.07$ indicated an appropriate model fit (Shipley, 2002). All SEM
461 analyses were conducted using the ‘lavaan’ package (Rosseel, 2012) in R (R Core Team,
462 2016).

463 3 RESULTS

464 Communities varied considerably in measures of hummingbird functional diversity
465 (coefficient of variation - CV; MST = 55.3%; FDis = 43.4%) and network structure (CV;
466 $\langle d' \rangle = 53.1\%$; $Q = 48.5\%$, Figure 1). No strong latitudinal trend was observed for these
467 variables (linear models with absolute latitude as a predictor; hummingbird FDis: $R^2 = 0.08$, P
468 $= 0.02$; $\langle d' \rangle$: $R^2 = 0.05$, $P = 0.05$; Q : $R^2 = 0.09$, $P < 0.01$), although MST was higher at low
469 latitudes ($R^2 = 0.37$, $P < 0.01$).

470 All best-fitting models included hummingbird FDis as a predictor, showing a positive
471 association with both hummingbird complementary specialization $\langle d' \rangle$ and network
472 modularity ΔQ (Table 1; Figures 1–2). Moreover, FDis was the only variable that consistently
473 had high importance values across different models, with a positive effect on both
474 untransformed and Δ -transformed network indices (Table 1, Appendix S9). On the other
475 hand, MST had a negligible importance in predicting network structure (Table 1), as did
476 unweighted FDis (Appendix S11) and hummingbird richness (Appendix S12). MAP was
477 positively related to hummingbird specialization $\langle d' \rangle$ (Table 1), whereas plant richness was
478 positively and insularity negatively related to modularity ΔQ (Table 1). Other environmental
479 variables were not important in any of our models.

480 For the subset of 28 networks with plant abundance and trait data, plant FDis showed
481 less variation than hummingbird FDis (Coefficient of Variation = 24.2% vs. CV = 43.2%,
482 Appendix S5). Plant FDis was unrelated to plant richness ($R^2 = 0.01$, $P = 0.51$) and
483 hummingbird FDis ($r = 0.07$, $P = 0.70$), and also to network structure (H_2' : $R^2 = 0.01$, $P =$
484 0.54 ; ΔQ : $R^2 = 0.04$, $P = 0.34$). Within this subset, hummingbird FDis was positively
485 associated with the degree of interaction partitioning (H_2' : $R^2 = 0.36$, $P < 0.01$; ΔQ : $R^2 = 0.55$,
486 $P < 0.01$), consistent with the analysis across all networks.

487 SEMs indicated that the combined influence of precipitation, insularity and plant
488 richness explained a larger amount of the variation in specialization and modularity than in
489 FDis (Figure 3a, c). Notably, including [hummingbird](#) FDis as predictor of network structure
490 (Figure 3b, d) increased the overall explanatory power of the models (adjusted R^2 , Figure 3).
491 Environmental predictors affected network structure more strongly through direct links, but
492 also had indirect effects through their influence on functional diversity. Precipitation (MAP)
493 affected specialization both directly ($\beta = 0.32$; Figure 3b) and indirectly through FDis
494 (indirect coefficients are obtained by multiplication of coefficients, i.e., $0.41 \times 0.31 = 0.13$;
495 Figure 3b). In the case of modularity, the indirect association with precipitation ($0.41 \times 0.39 =$
496 0.16 ; Figure 3d) was similar to the direct one ($\beta = 0.14$; Figure 3d). Plant species richness
497 (specialization: direct = 0.19, indirect = 0.07; modularity: direct = 0.27, indirect 0.09; Figure
498 3b, d) and insularity (specialization: direct = -0.21, indirect = -0.06; modularity: direct = -0.28,
499 indirect -0.07; Figure 3b, d) showed stronger direct and weaker indirect associations with
500 network metrics.

501

502 **4 DISCUSSION**

503 Functional diversity [of hummingbirds](#) was correlated with network structure in plant-
504 hummingbird communities across the Americas, with hummingbird communities composed
505 of functionally distinct species (i.e., those with a high functional dispersion) forming
506 specialized and modular interaction networks with their nectar plants. [In contrast, plant](#)
507 [functional diversity was unrelated to network structure](#). Our result that precipitation was both
508 directly and indirectly related to network structure through its association with [hummingbird](#)
509 functional [diversity](#) illustrates how the environment, through its effects on community trait

510 composition, may influence the realization of species interactions within local communities
511 (McGill, Enquist, Weiher & Westoby, 2006).

512 In addition to precipitation, we show that plant richness was positively related to the
513 extent to which hummingbirds partition floral resources, with both direct and indirect effects
514 through hummingbird functional diversity. This association may be driven by the resource
515 diversity for hummingbirds, and partly be related to precipitation since the annual number of
516 days with rainfall – a variable closely related to annual precipitation – is one of the major
517 drivers of global vascular plant richness (Kreft & Jetz, 2007). This notion is reinforced by the
518 importance of plant species richness in our models, and its covariation with precipitation
519 (Table 1, Figure 3). A global analysis of nectarivorous birds, including hummingbirds,
520 honeyeaters and sunbirds (Zanata et al., 2017), had previously reported a positive relationship
521 between plant richness and network specialization. Interestingly, the association between
522 plant richness and network structure was not mirrored by co-variation between network
523 structure and plant functional diversity (see also Souza et al., 2018). One possible reason for
524 this is that, in contrast to birds, interaction frequencies of plants usually do not reflect their
525 abundances (Vizentin-Bugoni et al., 2014; Weinstein & Graham et al., 2017). For instance,
526 plant species with long corollas often have low abundances (see Vizentin-Bugoni et al.,
527 2016), thus contributing little to abundance-weighted estimates of plant FDis. However, long
528 corolla flowers are frequently visited by abundant long-billed hummingbirds, thus generating
529 interaction partitioning (Maruyama et al., 2014; Maglianesi, Böhning-Gaese et al., 2015;
530 Weinstein & Graham et al., 2017). This potentially results in a mismatch between the
531 functionally most distinct plant species and those that provide most floral resources, i.e.,
532 higher floral abundance. A closer association between consumer FD and network
533 specialization may also result from phenological differences between plants and animals.

534 While most hummingbirds stay in the community for most of the year, plant species
535 flowering turnover is usually high, meaning that morphologically specialized plant species are
536 temporarily replaced by other functionally similar ones (Bergamo et al., 2017). This means
537 that from the plant side, there is higher redundancy between species and the processes driving
538 niche partitioning may differ between plants and animals. For instance, hummingbirds often
539 compete for floral resources, as exemplified by their frequent aggressive defense of floral
540 resources (Feinsinger & Colwell, 1978), which likely enforces niche partitioning among birds
541 more than among co-flowering plant species. Overall, our results indicate that total
542 resource/niche space, as expressed by plant richness, allows for a finer division of resources
543 (Dalsgaard et al. 2011)

544 In addition to the positive effect of precipitation and plant richness, insularity had a
545 negative association with functional diversity and network metrics (Figure 3). Although the
546 direct links between insularity, specialization and modularity were stronger than the indirect
547 effects, we could also detect indirect relationships between network structure and insularity
548 through **bird** functional diversity. Island communities, especially from oceanic islands, tend to
549 show a high degree of generalization, consistent with an interaction release and niche
550 expansion in improvised communities (Traveset, Olesen, et al., 2015). Consequently, plant-
551 pollinator interaction networks on these islands can be less specialized than those on
552 continents, for instance by showing higher pollinator overlap among plants (Traveset, Tur, et
553 al., 2015). In accordance with this, higher generalization has been previously shown for
554 insular plant-hummingbird networks (Martín González et al., 2015), and our results here
555 indicate that part of this higher generalization is associated **with the** lower functional diversity
556 of hummingbirds on islands.

557 The incorporation of functional diversity constitutes an important step towards
558 identifying determinants of network structure at large spatial scales and is particularly
559 promising for scaling up our understanding of natural systems from local to global scales
560 (Kissling & Schleuning, 2015; Gravel et al., 2016). Furthermore, it may allow a better
561 assessment of the association between community structure, ecosystem functioning and
562 responses to disturbance (Fontaine et al., 2005; Fründ et al., 2013; Mouillot et al., 2013;
563 Schleuning et al., 2015; Tylianakis & Morris, 2017). For instance, niche partitioning among
564 morphologically distinct hummingbirds may promote optimal foraging, as trait-matching
565 leads to an increased efficiency in floral resource use (Maglianesi et al., 2014). In addition, an
566 increase in floral niche partitioning among pollinators is likely to increase the quality of
567 pollination services among plants through an increase in conspecific pollen transfer (Inouye,
568 1978; Brosi & Briggs, 2013). Hence, if [pollinator](#) functional diversity is reduced in response
569 to climate change or direct human-induced disturbances (e.g., Grass et al., 2014; Rader et al.,
570 2014), [this is likely to result in a reduced resource partitioning among pollinators and lower](#)
571 [pollination effectiveness](#) (Fontaine et al., 2005; Fründ et al., 2013; Schleuning et al., 2015). In
572 this regard, we note that not only species traits, but also species' abundances seem to be
573 relevant, as unweighted functional diversity metrics (MST and unweighted FDis) were only
574 weakly associated with network structure. Other studies have similarly found that unweighted
575 functional diversity indices were only weakly associated with ecosystem functions delivered
576 by animal communities (e.g., Gagic et al., 2015). Therefore, functionally distinct species in a
577 community must be sufficiently abundant to fulfill their functional roles in interactions
578 networks and contribute to ecosystem functioning. [The apparent asymmetry between plant](#)
579 [and bird functional diversity could stem from generally low floral abundances of](#)
580 [morphologically specialized plant species, each playing a minor role at the community level,](#)

581 compared to functionally specialized hummingbirds with high abundances, which fulfill
582 critical ecological roles in many communities.

583 Taken together, our results show an association between environmental factors,
584 pollinator functional diversity, and network structure at a continental scale, in which
585 environmental and species richness predictors determined network structure both directly and
586 indirectly through functional trait diversity. Moving forward, studies should investigate how
587 interaction networks affect the evolution of the traits of the species embedded in networks
588 (Guimarães, Jordano & Thompson, 2011) and the assembly of interacting species within
589 communities (Bartomeus et al., 2016). For instance, simulation studies may be able to
590 evaluate how present network structure will affect the diversity of species and their functional
591 traits in potential future communities, which in turn should feedback on the structure of
592 interaction networks (Guimarães et al., 2011, Bartomeus et al., 2016). In conclusion, we
593 believe that our results showing that environmental factors exert indirect effects on interaction
594 niche partitioning mediated by consumer trait diversity yield a first step towards a
595 mechanistic understanding of how the environment influences the structure of species
596 interaction networks. Hence, potential future changes in pollinator functional diversity are
597 expected to alter the structure of interaction networks and associated ecosystem functions
598 such as pollination.

599

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801

802 **Data Accessibility statement**

803 All the predictors and network indices used for the macroecological analysis, as well as
804 hummingbird trait data are supplied as supporting information and will be uploaded to
805 Figshare upon acceptance of the manuscript in the journal (Here we will provide the link).

806 **Biosketch**

807 Pietro K. Maruyama is an ecologist, with a broad interest ranging from natural history to
808 macroecology of plant–animal mutualistic interactions. This study is part of the HumLab
809 research team (www.humlab.weebly.com), an ongoing research collaboration on plant–
810 hummingbird networks across the Americas involving numerous researchers from a wide
811 range of institutions and countries.

812

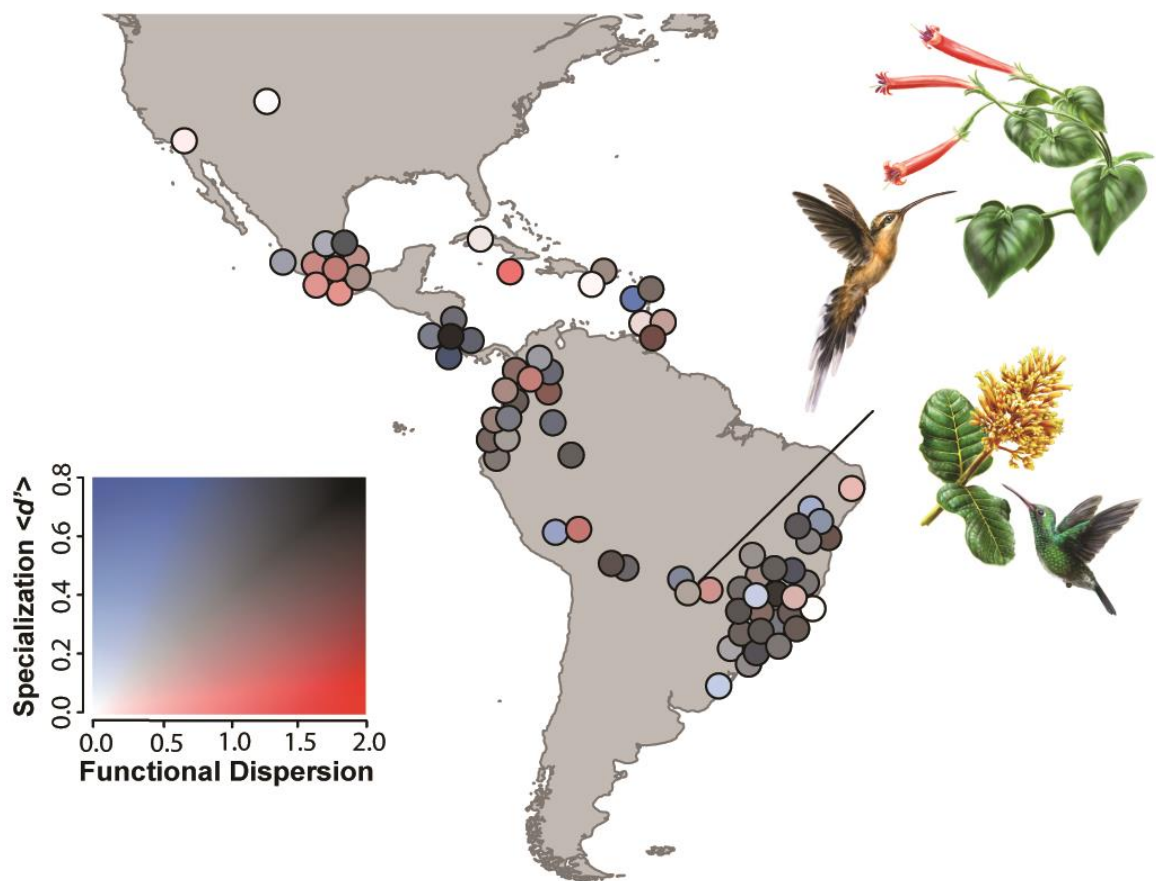
813

814 **TABLE 1** Model selection and averaging results of the multi-predictor linear models explaining the variation of hummingbird specialization
815 $\langle d' \rangle$ and network modularity ΔQ , corrected by the Patefield null model. We used two functional diversity measures, functional dispersion
816 (FDis) and minimum spanning tree (MST) reflecting different aspects of trait diversity in hummingbird communities. Important predictors in
817 explaining network indices variation ($\Sigma w_i > 0.8$) are highlighted in bold. We also show the AICc: corrected Akaike's information criterion;
818 AVM: standardized coefficients of the averaged model across all models; MAM: standardized coefficients of the minimum adequate model with
819 the lowest AICc value; R^2 adj: variation explained by the minimum adequate model with the lowest AICc. Acronyms of the predictors - FDis:
820 functional dispersion; MST: minimum spanning tree; Plants: plant richness; MAP: mean annual precipitation; TS: temperature seasonality; PS:
821 precipitation seasonality; AnomT: temperature anomaly; AnomP: precipitation anomaly; Topography: topographical variation; SI: sampling
822 intensity. See Methods for details.

823

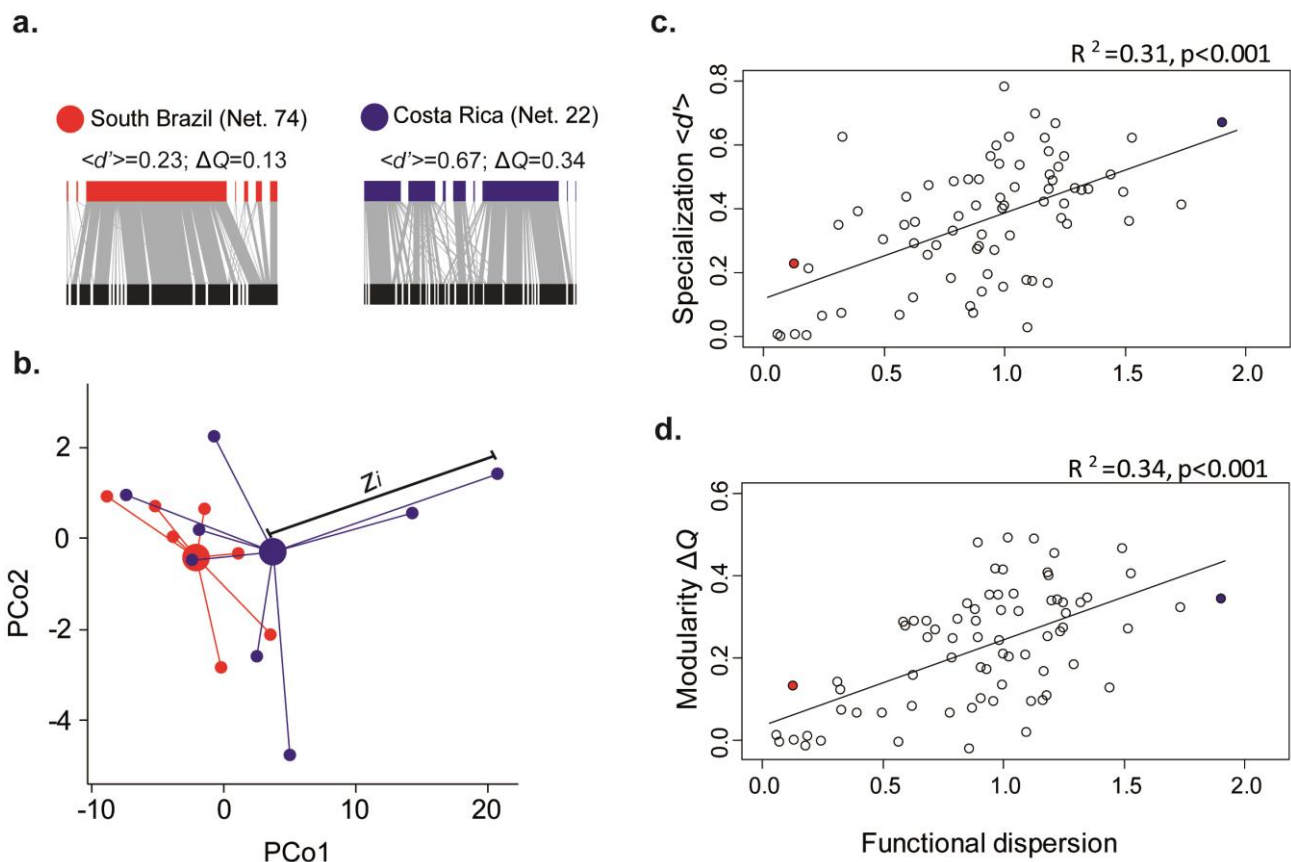
	Complementary specialization $\langle d' \rangle$						Modularity ΔQ					
	FDis			MST			FDis			MST		
	Σw_i	AVM	MAM	Σw_i	AVM	MAM	Σw_i	AVM	MAM	Σw_i	AVM	MAM
FD index	0.97	0.33	0.31	0.28	0.02	-	1.00	0.43	0.43	0.55	0.12	-
Plants	0.75	0.16	0.19	0.89	0.23	0.26	0.98	0.28	0.28	0.98	0.34	0.35
MAP	0.92	0.30	0.33	0.99	0.44	0.45	0.32	0.03	-	0.70	0.17	0.30
TS	0.32	0.03	-	0.30	0.03	-	0.23	-0.01	-	0.25	0.01	-
PS	0.23	-0.01	-	0.23	0.01	-	0.54	-0.08	-0.16	0.36	-0.04	-
AnomT	0.27	-0.02	-	0.26	-0.02	-	0.26	0.01	-	0.27	0.02	-
AnomP	0.29	-0.02	-	0.25	-0.01	-	0.44	-0.06	-	0.38	-0.05	-
Topography	0.32	0.03	-	0.33	0.03	-	0.27	-0.02	-	0.26	-0.02	-
Insularity	0.77	-0.17	-0.21	0.86	-0.22	-0.27	0.99	-0.31	-0.28	0.97	-0.32	-0.35
SI	0.29	-0.02	-	0.38	-0.05	-	0.52	0.08	-	0.31	0.03	-
R^2 adj			0.42			0.36			0.48			0.37
AICc			177.3			183.8			168.9			182.7

824 **FIGURE 1** The location of the 74 plant-hummingbird networks used in the study, showing the
 825 relationship between hummingbird specialization $\langle d' \rangle$ and functional dispersion. For clarity,
 826 circles for some study sites were moved slightly to minimize overlap. The illustration on the
 827 right depicts how hummingbirds with distinct morphologies partition their interactions by
 828 associating with flowers of corresponding morphology (from network ID 52; Top: Planalto
 829 Hermit, *Phaethornis pretrei* and *Manettia cordifolia* with long curved corolla; Bottom:
 830 Glittering-throated Emerald, *Amazilia fimbriata* and *Palicourea rigida* with a short corolla).
 831 Points along the white-grey-black gradient indicate communities with better correspondence
 832 between functional dispersion and specialization.



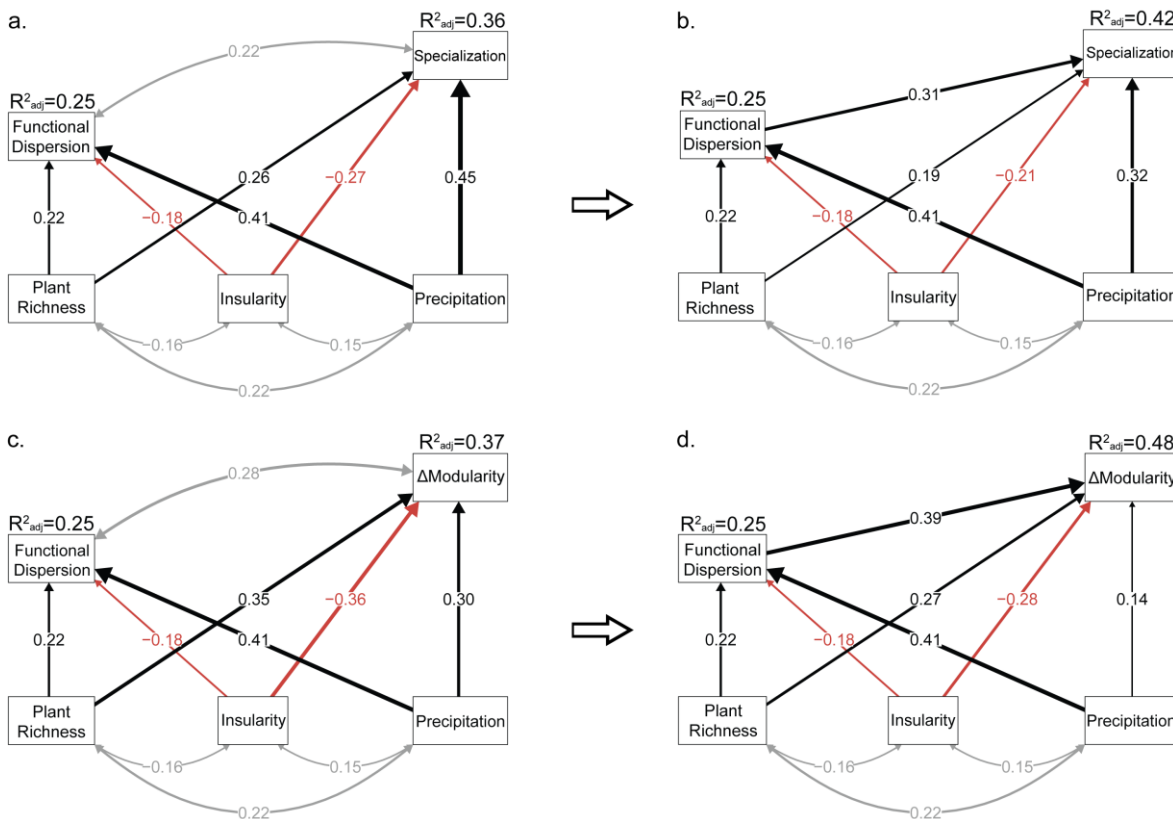
833

834 **FIGURE 2** The relationship between hummingbird functional dispersion (FDis) and network
 835 structure. (a) An example illustrating two networks with similar number of hummingbird
 836 species (Net 74 = 7, Net 22 = 8), but with contrasting FDis. Networks on top depict the
 837 interaction networks with hummingbird species indicated by red and blue boxes at the top and
 838 plant species indicated by black boxes at the bottom (with the interactions indicated by grey
 839 lines). (b) FDis is measured as the mean of the distance (Z_i) of a species (small circles) to its
 840 community centroid (large circles) in multivariate trait space generated by a Principal
 841 Coordinate Analysis. Notice that the community from Costa Rica (blue/right) includes several
 842 species located distantly from the community centroid, in contrast to the community from
 843 Southern Brazil (red/left). Linear regressions showing the relationship between hummingbird
 844 (c) specialization $\langle d' \rangle$ and (d) modularity ΔQ with FDis. Note that the two networks from (a)
 845 are indicated with their respective colors.



846

847 **FIGURE 3** Structural equation models (SEMs) showing the direct and indirect associations
 848 among environmental and richness predictors, functional dispersion (FDIs) with
 849 complementary specialization ($\langle d' \rangle$; 3a, b) and modularity (ΔQ ; 3c, d). Models in (a) and (c)
 850 assume a covariation between FDis and networks structure, while (b) and (d) consider a
 851 directional relationship between FDis and network structure. In both cases, the value of R^2 is
 852 substantially higher in the models that include the direct link between FDis and network
 853 metrics. Black arrows indicate positive relationships while red arrows indicate negative
 854 relationships, with the thickness of each arrow reflecting their standardized path coefficients.
 855 Double-headed grey arrows indicate covariance links.



856

857

858 **APPENDIX 1: Data sources and supporting references**

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946 **Additional Supporting Information:**

947 Appendix S1. Location, details and sources of the plant-hummingbird networks

948 Appendix S2. List of hummingbirds occurring in the studied networks

949 Appendix S3. List of plant species occurring in the studied networks

950 [Appendix S4: List of plant species occurring in the subset of 28 networks with data on plant](#)
951 [traits and abundances. The same nomenclature as in Appendix 3 is used.](#)

952 [Appendix S5: Details and sources of the subset plant-hummingbird networks.](#)

953 Appendix [S6](#). Additional details on Methods

954 Appendix [S7](#). Hummingbird abundance correlations

955 Appendix [S8](#). A plot showing the relationship between the values of FDis calculated using two
956 measures of hummingbird abundance

957 Appendix [S9](#). Model selection results for null model corrected specialization and un-corrected
958 modularity

959 Appendix [S10](#). Model selection results using Velocity, instead of Anomalies as measure of
960 historical climate

961 Appendix [S11](#). Model selection results using unweighted Functional Dispersion index

962 Appendix [S12](#). Model selection results using hummingbird richness

963