Macroevolutionary imprints on the assembly of frugivory networks

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Biological interactions are a key aspect of ecological communities (Delmas et al., 2018). Current interaction network structures are snapshots of dynamic processes of community assembly (Thompson, 2005), and represent the product of the evolutionary history of interacting species over millions of years. Thus, assessing the deep time mechanisms affecting the assembly of ecological networks are key to better understand biodiversity changes in broader time scales (Jablonski, 2008). Here we integrate tools from macroevolutionary studies with network science to show that more central species in frugivory networks belong to lineages with higher macroevolutionary stability. This association is more pronounced in warmer, wetter, less seasonal environments, which highlights the role of environmental factors in shaping ecological networks. Furthermore, our results suggest that these environments possess a more diverse (either in species number or ecology) assemblage of species that can be sorted during network assembly. Lastly, we found evidence that the macro-evolutionary contribution to network stability changes in geographical space. This reinforces the idea that the macroevolutionary sorting mechanism acts at the regional pool of species, rather than selecting absolute paces of diversification. Hence our results suggest an interplay between ecological roles and diversification regimes in shaping the fate of lineages of plants and seed dispersing birds.

27   Seed dispersal is a fundamental ecosystem service (Fleming & Kress 2013). This

28   mutualism between angiosperms and, mainly, vertebrates started about 80 Mya

29   (Eriksson, 2016, 2014), and currently between 70-90% of woody species rely on

30   vertebrate species to seed dispersal (Jordano, 2000). Accordingly, many vertebrate

31   groups have fruits as at least part of their diet (56% of bird families, and up to 95% of

32   species for some mammal groups, in addition to squamates, chelonians, fishes, and even

33   frogs – Jordano, 2000, Donatti et al. 2011). The radiations of important groups of seed-

34   dispersers, such as birds and mammals, are hypothesized to be linked to the angiosperm

35   rise and dominance during the Cenozoic (Eriksson, 2016), although the causal links are

36   elusive. In particular, some bird groups are consistently recognized as specialized

37   frugivores (Snow, 1981; Fleming et al. 1987, Kissling et al. 2009).

38   In the past decades, studies on seed-dispersal networks have: 1- provided

39   important insights of how mutualisms are structured and maintained at the local level

40   (Bascompte & Jordano, 2007); 2- have supported the role of coevolution in shaping traits

41   (Eriksson, 2016); 3- have shown how fast selection imposed by frugivores lead to trait

42   evolution (Galetti et al. 2013). However, most studies have focused on describing and

43   understanding patterns and processes at ecological timescales. The few studies with

44   broader temporal scales are either those investigating community phylogenetics (see

45   Harmon et al. 2019 and references therein), the potential association between

46   diversification rates and diet, including those specialized in fruit (e.g. Burin et al 2016),

47   the patterns of phylogenetic conservatism of specialization/generalization of interactions

48   (Gómez et al. 2010), or more broadly the effect of mutualisms on diversification rates in

49   vertebrates (e.g. Gómez & Verdú, 2012) and plants (e.g. Weber & Agrawal 2014).

50   On the other hand, we are beginning to understand how diversification dynamics

51   may affect the assembly process, and consequently, the structure of interaction networks

52   (e.g. Nuismer & Harmon, 2015, Roopnarine et al. 2019). Although the whole interaction

53   networks might be plastic both in time and space (Ponisio et al. 2017), some evidence

54   suggests that the core of seed dispersal network is somewhat robust to short-term (yearly)

55   fluctuations of fruit availability and bird species presence (Plein et al. 2013). Moreover,

56   theory suggests that predictable and stable species in a particular place should interact

57   with more partners (Olesen et al. 2008, Yang et al. 2013), supporting the idea that at least

58   the core of the network might show some temporal stability. Lastly, the identity of

59   interacting partners typically shows phylogenetic signal, meaning that related species

60   tend to share similar interactions (Rezende et al. 2007, Gómez et al. 2010). Although the

61   existence of non-random structures in seed-dispersal networks suggest some long-term

62   mechanisms driving the assembly of networks (Fleming & Kress, 2013), it is still

63   unknown whether or how these non-random structures are maintained and detectable

64   over longer timescales, and what are potential mechanisms behind it.

65   Using diversification rates estimated from molecular phylogenies, and a dataset

66   composed of 29 frugivory networks we tested the hypothesis that macroevolutionary

67   predictable lineages are more likely to contribute with species to the core of ecological

68   networks, providing an explicit macroevolutionary mechanism for network assemblage

69   (see figure 1 for schematic version of general approach, and data used). To test this idea,

70   we use a hierarchical Bayesian approach to investigate the potential association between

71   the species' ecological roles and their macroevolutionary stability, therefore integrating

72   two areas of knowledge. We define as stable lineages those that either have low

73   extinction fraction (i.e. relative low extinction when compared to speciation), and/or

74   higher net diversification (, i.e. lineages that can accumulate species at a faster pace). We

75   estimated the species' ecological role by using tools derived from network science. We

76   then incorporated phylogenetic and ecological uncertainties, along with environmental

77   factors, in order to properly address how the interplay between biotic and abiotic factors

78   drives the assembly of local networks due to macroevolutionary dynamics. Lastly, we

79   tested whether the sorting of macroevolutionary regimes takes place at the regional or at a

80   global scale.

81   We find that central species tend to belong to macroevolutionary stable lineages.

82   The standardized extinction fraction is negatively correlated with species' ecological role

83   represented by their centrality values (figure 2). Similarly, net diversification rates are

84   positively correlated with species centralities (figure 2). In both cases the posterior

85   distributions are clearly off centered with respect to a slope value of zero. These results

86   hold after accounting for multiple sources of uncertainty. Median standardized effects for

87   extinction fraction and net diversification were -0.14 and 0.19, respectively, indicating

88   the two components of macroevolutionary stability contribute with similar intensity to the

89   structuring of the networks. Sensitivity analysis based on the medians of the posterior

90   distributions for most parameters for each individual tree (figure 2) suggests that this

91   signal holds irrespective of phylogenetic uncertainty.

92   Our results provide evidence that this macro-evolutionary sorting mechanism is

93   predominantly a regional-scale phenomenon, since we only observed evidence for the

94   sorting when analyzing the standardized rates (deviations from the mean rate per

95   network), but not for the raw absolute rates (Fig S3). This suggests that the macro-

96   evolutionary sorting mechanism acts at the relative rank of stability for the available

97   lineages, and not on absolute values of extinction fraction or diversification rates. We

98   also found that environmental conditions affect the relationship between ecological role

99   and macroevolutionary stability, with warmer, wetter, non-seasonal environments having

100 a stronger sorting of macroevolutionary stability regimes (figure 2). Interestingly, these

101 environments harbor the highest frugivorous species richness (Kissling et al. 2009), and it

102 is possible that such species rich environments allow for a finer sub-division of

103 ecological roles on which this macroevolutionary sorting mechanism could more

104 efficiently act. In fact, networks found on those tropical-forest-like environments are

105 more centralized (i.e. a higher difference in centrality between the more central and more

106 peripheral species - see figure 2 panel PC1) than networks commonly found on colder,

107 drier, and seasonal environments. An analysis using a different dataset, in this case

108 species dietary composition, suggests a tendency for many networks from warm/wet

109 climates to show broader total amplitude in dietary "types" (figure 3A), corroborating the

110 finding that warm and humid environments possess a broader range of species types (not

111 only more species) on which the macro-evolutionary sorting can more efficiently act.

112 Moreover, warmer, more humid and less seasonal climates allow for a more

113 homogeneous occupation of the dietary space without increasing the dietary overlap

114 between species, as indicated by the positive association between temperature/humidity

115 and the average pairwise dietary distance (figure 3A), and by the absence of association

116 between climatic conditions and the shortest dietary distances between species (figure

117 3B)

118   Although some clades are known to be important seed-dispersers across multiple

119 continents (some families of Passeriformes, Galliformes, Piciformes, etc. - Snow 1981,

120 Fleming et al. 1987, Kissling et al. 2009), a spatial analysis of those networks reinforces

121 the idea that such macroevolutionary sorting mechanism acts regionally on the available

122 pool of species, and that the role of available species is, as expected, geographically

123 structured. To evaluate if species within the same lineage play a similar role in different

124 networks, we calculated the average centrality value for each different lineage (either

125 family or genus) for all networks. The association between the mean centrality value of

126 each lineage in different networks decays as a function of the geographical distances

127 between those networks (figure 4). These results suggest that geographically close

128 networks tend to have similar lineages playing similar ecological roles, but those roles are

129 taken by different lineages in different parts of the planet.

130   In summary, our results provide evidence for a macroevolutionary sorting

131 mechanism (species selection in a broad sense - Jablonski 2008) on network assembly

132 where central species tend to belong to evolutionary lineages that are more stable over

133 deep time. Moreover, we found that those central species not only interact with a higher

134 number of species, but also that those partner species belong to a wider range of plant

135 families (figure 3C). Hence our results suggest potential bi-directional selective regimes

136 between ecological roles and diversification regimes, which might shape the fate of

137 groups of very distantly related lineages (birds and plants) linked through ecological

138 interactions.

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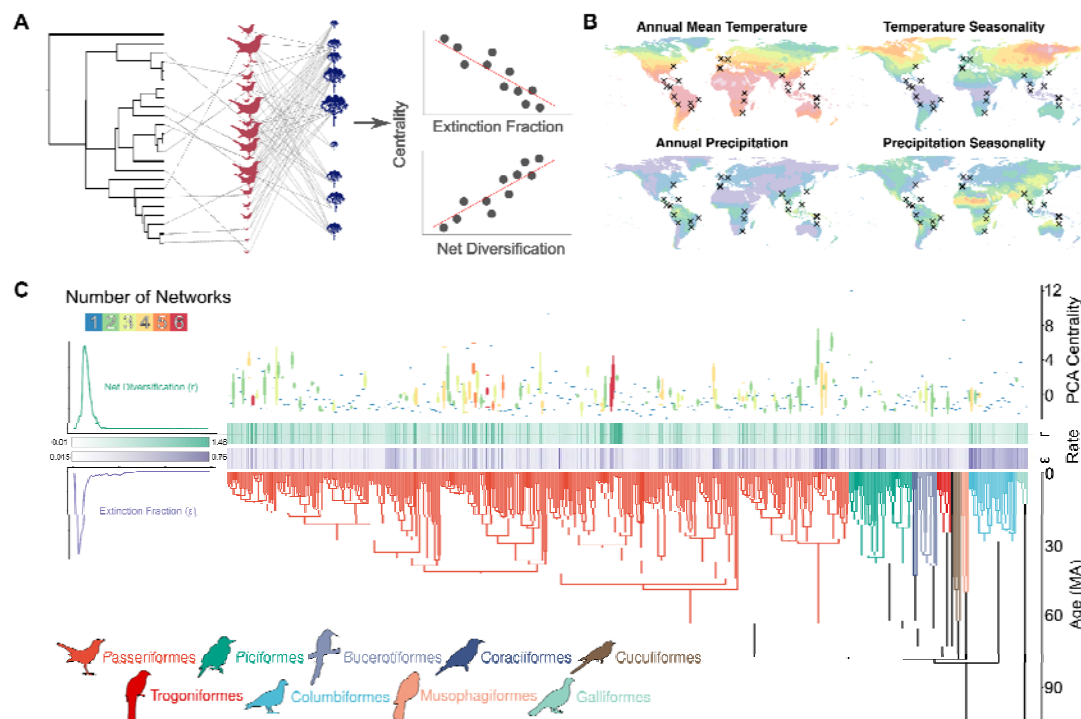
Figure 1: Conceptual framework and data used - Panel A (top left): Conceptual representation of the study; Panel B (top right): Geographical and climatic distribution of the 29 networks used in the study. Panel C (bottom): Exemplar pruned phylogeny with branch colors indicating the bird orders, along with the extinction fraction (purple dashes and density), net diversification rates (green dashes and density) in the center, and the PCA centrality values (top row of panel C) for each of the species of all species used in the analyses. Some species were present in more than one ecological network, and this is information is displayed by points or bars of different colors in the PCA centrality graph.

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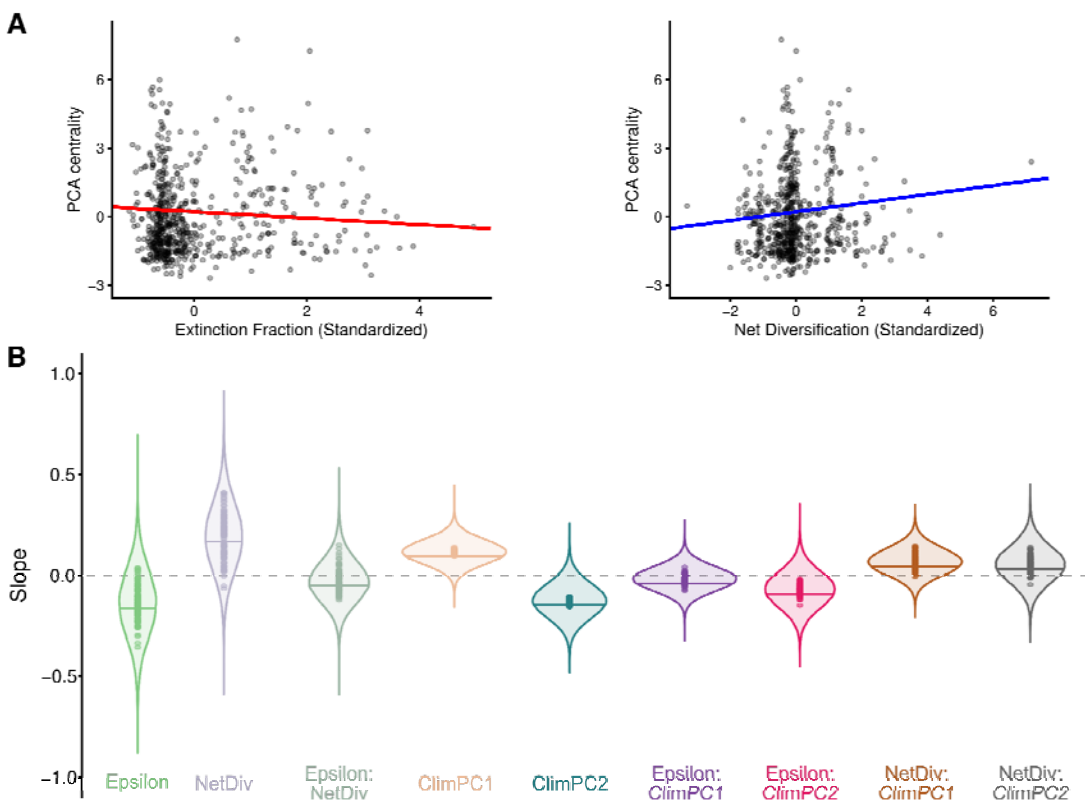
Figure 2: Association between network centrality and macroevolutionary stability - A - exemplar association between PCA centrality values and extinction fraction and net diversification rates estimated from one phylogenetic tree. B - Posterior distributions of all parameters (except the intercept for a matter of scale) for the Bayesian generalized linear mixed model analysis. The points within the violin plot represent the median values taken from the analysis done for each different phylogenetic tree (that are highly correlated with the mean and the mode, since the distributions are highly symmetrical). Posterior distribution of slopes for Extinction fraction (green violin plot) and Net diversification rates (purple violin plot) are clearly off-centered from the slope value of zero in the expected direction (negative for extinction fraction; positive for net diversification), indicating that species belonging to macroevolutionary more stable lineages (low Epsilon and/or high Net Diversification) are more central in the networks.

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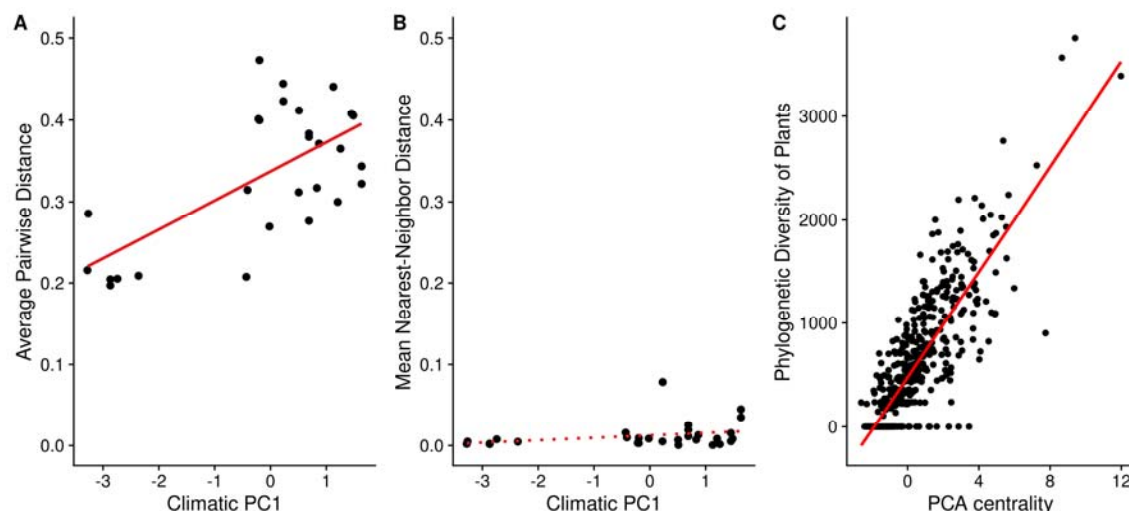
Figure 3: Different axes of specialization of bird species analyzed in the study - A) Plot showing that the average pairwise distance of species along dietary PC1 increases towards warmer, wetter, less seasonal environments (climatic PC1, p-value = 0.001, R^2 = 0.4316). . B) Scatterplot between mean nearest-neighbor distance and the climatic PC1, highlighting the much smaller variation in comparison to panel A. We used the same scale from panel A on the y-axis to highlight the much lower, non-significant association (p-value = 0.1196, R^2 = 0.0535). C) Association between PCA centrality and the phylogenetic diversity of plant families with which each bird species interacts, indicating that more central species interact with more diverse plant families (p-value $< 2.2*10^{-16}$, R^2 = 0.7033). On all panels continuous lines indicate statistically significant associations while dotted lines a lack of significant association.

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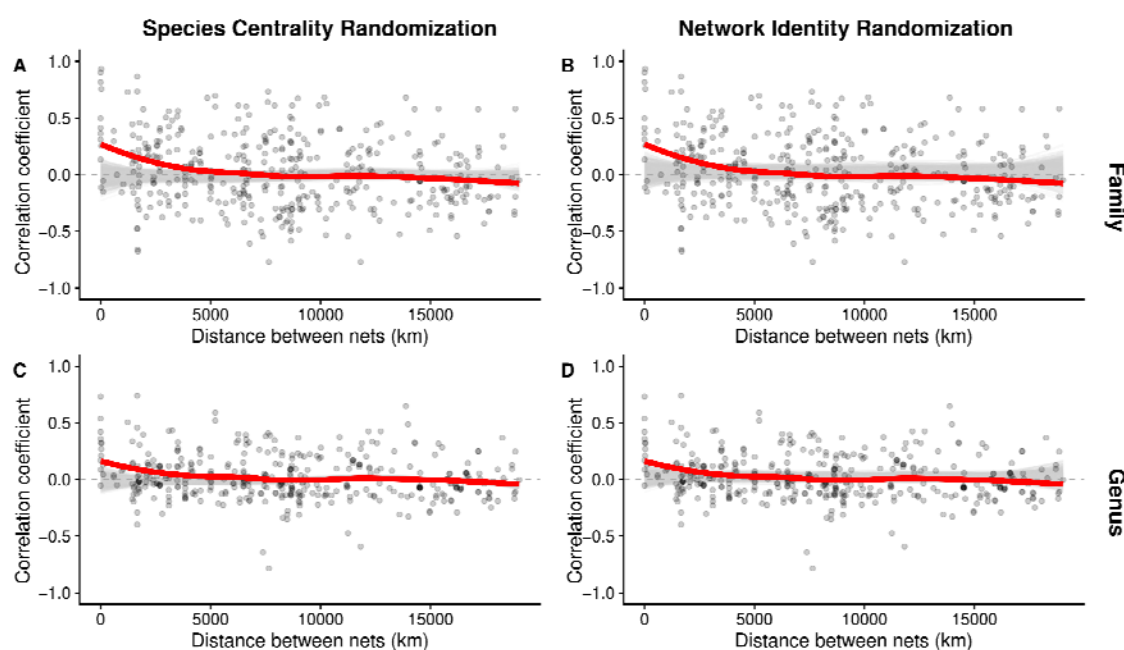
Figure 4: Association between mean centrality per family (panels A and B) or genus (panels C and D) and geographical distance - Each point represents a pairwise correlation between ecological roles in two different networks, and the red lines represent a loess smoothing to show the general trend of the data. The grey areas represent the null models that were built by randomizing centrality values per species within networks (panels A and C), or by randomizing the identity of networks for each geographical distance (panels B and D). Regardless of the null model selected, the associations between mean centrality of families/genera is higher than expected by the null model for geographically close networks, and this similarity dissipates with distance, suggesting that there is no single group driving the association between macroevolutionary stability and ecological role.

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148 **Data and Code Availability**
149 Bird phylogenies were obtained from birdtree.org (Jetz et al. 2012), and ecological
150 networks were obtained from http://dx.doi.org/10.5061/dryad.2br2b (Pigot et al. 2016).
151 All data and code used in this study is also available for download at
152 https://doi.org/10.5281/zenodo.3560680. Codes are also available at
153 https://www.github.com/gburin/macroevoNet.
154

155 **Author Contributions**
156 GB, PRG and TBQ designed the study; GB gathered and analyzed the data; GB and TBQ
157 wrote the first draft of the manuscript; GB, PRG and TBQ significantly contributed to the
158 last version of the manuscript.
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167 **Supplementary information** is available for this paper
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240

241   ## Material and Methods

242   To investigate the potential effect of diversification rates on the assembly of

243   current ecological networks we first characterized each frugivore species with respect to

244   its potential ecological role in the network, and then estimated speciation and extinction

245   rates related to each bird lineage using a comprehensive molecular phylogeny containing

246   approximately 67% of all bird species (see below). We then tested for an association

247   between the network metric and the macroevolutionary rate (see figure 1 main text for a

248   cartoon version of the general approach) using phylogenetic generalized linear mixed

249   models (MCMCglmm - Hadfield 2010). Phylogenetic correction was used because the

250   network metrics showed significant phylogenetic signal (mean value for Pagel's lambda

251   = 0.537, although for each tree the corresponding lambda value was used).

252   **Diversification Rates**

253   To estimate speciation and extinction rates we used the most recent bird

254   phylogeny, which comprises the 99.3% of the extant species (9993 species in the

255   phylogeny from an estimated total of 10,064 species – (Jetz et al. 2012). To avoid any

256   potential bias introduced by adding species without DNA sequences (using a pure-birth

257   algorithm) on our estimates of speciation and extinction rates (Rabosky 2015), we used

258   the trees that contain only species for which molecular data were available from the

259   original phylogenetic paper (Jetz et al 2012). This tree had 6670 species, but species not

260   sampled were taken into account by the model. We analyzed the bird molecular

261   phylogeny using a Bayesian framework (BAMM v. 2.5; Rabosky 2014) to estimate the

262   rates of speciation and extinction while explicitly taking into account the sampling

263   fraction of species. The incompleteness (about 1/3 of species without DNA data) was

264   considered within BAMM by using the percentage of missing species within each clade

265   of the maximum clade credibility tree obtained by Jetz et al. (2012). Rabosky (2014) has

266   developed an algorithm that finds sub-trees within a phylogeny, which share speciation

267   and extinction rates through a Bayesian framework using reversible-jump Markov Chain

268   Monte Carlo sampling. Each diversification shift configuration has an associated

269   posterior probability, and each configuration can assign different diversification rates to a

270   particular species or clade. Since it is impossible to not know which is the true

271   configuration, we used the mean rates averaged by the marginal posterior probabilities of

272   each distinct shift configuration. Lastly, we calculated our rates of interest: the extinction

273   fraction ($\varepsilon = \mu/\lambda$) and net diversification rate ($r = \lambda - \mu$) for all species of interest. These

274   two rates represent two different metrics used to quantify the stability/predictability of a

275   given lineage. A higher value of extinction fraction suggests a more volatile dynamics

276   within a given lineage and hence a higher chance of the entire lineage going extinct. A

277   lower net diversification rate suggests that a lineage accumulates species as a smaller

278   pace, and therefore has a higher chance of going extinct than lineages with higher net

279   diversification rate. To our purposes, we assume that those two rates (each of them plus

280   their interaction) affects the likelihood that a given lineage might be evolutionary reliable

281   at long temporal scales.

282   **Ecological Networks**

283   To evaluate the ecological role of different species we used data from 34 different

284   frugivory networks compiled by previous authors (Pigot et al 2016). Those networks

285   comprise both temperate and tropical areas and a total of 546 unique bird species (838

286   total unique interactions). From the original dataset, we discarded 5 networks due to

287   biases in species composition (networks that focused on specific bird or plant groups, and

288   therefore do not represent the whole interacting assemblage), resulting in a final dataset

289   of 468 species (700 unique interactions). Although some networks (23) had information

290   on the strength of interactions, we decided to binarize all networks for two reasons. First,

291   it allows us to work with a larger dataset. Second, it is known that interaction strengths

292   vary across time (e.g. Ponisio et al. 2017), rendering quantitative estimates not

293   necessarily meaningful as a long-term description. We also removed pairs of species that

294 only interacted with each other, and were, by definition, disconnected from the rest of the

295 network. Those represent only 14 species from only 6 different networks from a total of

296 468 species from 29 networks. This was done because some of the network metrics are

297 not defined for networks that are not fully connected.

298   To characterize each species' ecological role within the compiled dataset we

299 investigated different node (species) properties of the networks by calculating, using the

300 original bipartite networks, three different centrality metrics: degree (number of

301 interactions), closeness (the reciprocal of the sum of shortest distances, in links,

302 connecting the focal node to all other nodes in the network) and Katz (a measure of the

303 distance, in terms of all possible pathways, between the focal node and all other nodes of

304 the network, using $\alpha = 0.05$). Such metrics provide us with information about the

305 importance of each species network structure when considering only the direct

306 interactions (degree), the shortest pathways (closeness) or all pathways (Katz). To be able

307 to combine the ecological roles estimated for different networks (that have different

308 properties, such as number of species and connectance) into a single analysis, we first

309 standardized the three metrics by calculating their z-scores for each network separately.

310 After compiling each of the three standardized centrality metrics for all species in all

311 networks in a single dataset, we performed a Principal Component Analysis (PCA) in

312 order to obtain a single score that comprised different aspects of the network position (as

313 a proxy for the ecological role). We used only the first Principal Component since it

314 explained 93.3% of the variance in centrality values.

315   **Sources of uncertainties**

316   We incorporated in our analyses two distinct sources of uncertainty. The first one

317 is related to the true evolutionary history of birds. To incorporate the phylogenetic

318 uncertainty, we used 112 different topologies from the bird phylogeny from Jetz et al.

319 2012 (56 of each backbone) to both estimate the rates of diversification and to take into

320 account the phylogenetic structure of the residuals in the linear model. The other source

321 of uncertainty came from the networks. From all the species in the final dataset (N = 468

322 species), 139 are part of more than one network (up to 6), making it impossible to

323 attribute a single centrality value to those species. We thus incorporated this variation as a

324 source of uncertainty in the regression analysis by using species identity as a random

325 factor as described in the modeling section below.

Co-Factors

327 Because the nature and relevance of ecological interactions might be different at 328 different parts of the planet (Mittelbach & Schemske 2015) we ran a global analysis (with 329 all networks combined) using climatic variables as co-factors. Those were: 1- annual 330 mean temperature; 2- temperature seasonality; 3- annual precipitation; 4- precipitation 331 seasonality. To summarize environmental conditions and avoid over-parameterization of 332 the models, we ran a PCA with the four climatic variables, and used the first and second 333 PCs that in combination explain 81.92% of total variance. We note that those two PCs 334 aligned well with the raw temperature and precipitation variables (Annual Mean 335 Temperature, Temperature Seasonality, and Annual Precipitation have scores of 0.619, - 336 0.592, and 0.492 on PC 1, respectively. Annual Precipitation and Precipitation 337 Seasonality have scores of 0.331 and -0.942 on PC 2, respectively - figure S5). The 338 climatic data were obtained from the WorldClim database version 2.0 (Fick & Hijmans, 339 2017).

340 To test if the macroevolutionary effect on network is a phenomenon that depends 341 on the absolute or the relative diversification rates (i.e. if rates of a given species are 342 higher or lower than other species within the same network), we ran each of the three 343 classes of models previously described using raw and standardized (z-scores computed to 344 within each network) macroevolutionary rates.

Modelling

346 We tested the association between ecological roles and macroevolutionary 347 dynamics using a Bayesian generalized linear mixed model (MCMCglmm), implemented 348 in the R package MCMCglmm (Hadfield, 2010). This framework allows us to naturally 349 incorporate both sources of uncertainty. By using species identity and the phylogenetic 350 structure as random factors, we can account for intraspecific variation in the ecological 351 roles on the estimation of the regression parameters while simultaneously controlling for 352 the phylogenetic structure. Moreover, by combining the posterior distributions of 353 parameter values using rates from different trees (topologies), we also can account for 354 phylogenetic uncertainty. We assessed the effect size of each variable used in the model 355 by analyzing the asymmetries in both the combined posterior distributions in relation to

356 zero (no association), and in the medians of individual posterior distributions for each

357 tree (Holland, 2019; Wasserstein et al. 2019). By doing this we embrace sources of

358 uncertainty incorporated in our analysis (ecological and phylogenetic) while looking at

359 the magnitude of the effect (Holland, 2019). All MCMC chains were run for 5000000

360 iterations, with half of the total length discarded as burn-in, and sampling every 2500

361 iterations. We used inversed Wishart distributions as priors for both the fixed and the

362 random effects.

363   **Geographical patterns of centrality per family/genus**

364   Lastly, to check if the species that play central/peripheral roles in different

365 networks show a spatial structure with respect to their taxonomic identity (e.g. belong to

366 the same family/genus), we calculated the association between the average centrality per

367 lineages (either family or genus) for each pair of networks using Spearman's correlations,

368 ρ. and then plotted ρ as a function of the distance between each pair of networks. We used

369 family or genus as our data points for two reasons. First, it is unlikely that the same

370 species would be present in geographically distant networks. Second, the

371 macroevolutionary effect we are measuring is a lineage effect (e.g. different species

372 represent the macroevolutionary regimes of different lineages). To build a null model, we

373 used two different randomization approaches and two different ways to deal with missing

374 data. Hence, we ended up with four different null models for each analysis, one set for the

375 family and another for the genus level.

376   In the first randomization approach (figure 4 panels A and C), we randomized the

377 species centrality values within each network prior to calculating the average centrality

378 for each lineage (either per family or per genus). The association was then estimated for

379 all pair of networks and plotted as a function of the geographical distance of each

380 network pair. In the second randomization approach (figure 4 panels B and D), instead of

381 randomizing the species centrality values within each network, we randomly draw two

382 networks irrespective of their geographical distance, repeating this procedure for all a set

383 of geographical distances equal to the one seen in the empirical comparison. Hence in our

384 first randomization approach the species identity is randomized but the geographical

385 distances between pairs of networks is kept as in the empirical dataset. In the second

386 randomization approach it is the geographical distance that is randomized while keeping

387   the original species identity.

388   In both randomization approaches, there were instances where a given lineage

389   was only present in one of the two comparing networks. Hence to calculate the

390   association between networks when using lineage (e.g. family or genus) average

391   centralities, we had to deal with the limitation that "valid" average centrality value for a

392   given lineage might not be estimated for some of the networks. To overcome this

393   limitation, we filled the missing values in two different ways. In the first, we simply

394   replaced the missing values in a given network by 0 (hereafter called "single 0 scenario").

395   By doing this we are strongly "breaking" any possible association, which means that only

396   very strong association would still remain significant after adding those zero values

397   (figure 4). The second approach consisted in replacing the average centrality of a lineage

398   (family or genus depending on the analysis) by 0 not only for the network where that

399   lineage was missing but in both networks ("full 0 scenario"). This was done in order to

400   "completely remove" the effect of that lineage from the analysis, while still allowing for

401   the association between the families/genera that are present in both networks to be

402   estimated (supp. figure 4).

403   The prediction of the null model is constructed by doing a LOESS smoothing to

404   each randomized dataset (1000 datasets in total). The empirical LOESS smoothing line is

405   then compared to the group of LOESS smoothing lines defining the null model and the

406   relationship is considered significant if the empirical line does not overlap with the null

407   model lines.

408   **Ecospace Occupation**

409   To analyze how ecospace is occupied in different climates, we used an

410   independent dataset of dietary information (EltonTraits v1.0, Wilman et al., 2014), and a

411   phylogenetic Principal Component Analysis (phyPCA, Garland et al., 1993, Revell 2012)

412   to obtain the axes of greater variation in the diet of all species present in our dataset. The

413   phyPCA was done using only the 468 species present in our network dataset. Using the

414   first Principal Component (PC1 - greatest loading of fruits), we calculated three different

415   disparity metrics for each network: amplitude (that indicates how broad the dietary niche

416   is for the whole network), average pairwise distance and mean nearest-neighbor distance

417   (that indicates, on average, how far each species is from the closest species in their

418 respective network). We tested the relationship between each of the three metrics with

419 climatic PC 1 (which explains about 56% of the variation) to assess any trends of

420 ecospace occupation along climatic gradients.

421   **The degree of interaction generalization**

422   For each bird species in each network, we calculated both the number of unique

423 families with which they interact, and also the plant phylogenetic diversity by summing

424 all branch lengths in the pruned phylogeny containing only the plant families with which

425 the species interact. In order to test if more central species are more generalist (either

426 defined as interacting with a higher number of plant families or by a higher value of plant

427 phylogenetic diversity of their plant partners) we fitted linear models to test for the

428 association between ecological role (PCA centrality) and both the number of families and

429 phylogenetic diversity.

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