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.

Seed dispersal is a fundamental ecosystem service (Fleming & Kress 2013). This mutualism between angiosperms and, mainly, vertebrates started about 80 Mya (Eriksson, 2016, 2014), and currently between 70-90% of woody species rely on vertebrate species to seed dispersal (Jordano, 2000). Accordingly, many vertebrate groups have fruits as at least part of their diet (56% of bird families, and up to 95% of species for some mammal groups, in addition to squamates, chelonians, fishes, and even frogs – Jordano, 2000, Donatti et al. 2011). The radiations of important groups of seed-dispersers, such as birds and mammals, are hypothesized to be linked to the angiosperm rise and dominance during the Cenozoic (Eriksson, 2016), although the causal links are elusive. In particular, some bird groups are consistently recognized as specialized frugivores (Snow, 1981; Fleming et al. 1987, Kissling et al. 2009).

In the past decades, studies on seed-dispersal networks have: 1- provided important insights of how mutualisms are structured and maintained at the local level (Bascompte & Jordano, 2007); 2- have supported the role of coevolution in shaping traits (Eriksson, 2016); 3- have shown how fast selection imposed by frugivores lead to trait evolution (Galetti et al. 2013). However, most studies have focused on describing and understanding patterns and processes at ecological timescales. The few studies with broader temporal scales are either those investigating community phylogenetics (see Harmon et al. 2019 and references therein), the potential association between diversification rates and diet, including those specialized in fruit (e.g. Burin et al 2016), the patterns of phylogenetic conservatism of specialization/generalization of interactions (Gómez et al. 2010), or more broadly the effect of mutualisms on diversification rates in vertebrates (e.g. Gómez & Verdú, 2012) and plants (e.g. Weber & Agrawal 2014).

On the other hand, we are beginning to understand how diversification dynamics may affect the assembly process, and consequently, the structure of interaction networks (e.g. Nuismer & Harmon, 2015, Roopnarine et al. 2019). Although the whole interaction networks might be plastic both in time and space (Ponisio et al. 2017), some evidence suggests that the core of seed dispersal network is somewhat robust to short-term (yearly) fluctuations of fruit availability and bird species presence (Plein et al. 2013). Moreover, theory suggests that predictable and stable species in a particular place should interact with more partners (Olesen et al. 2008, Yang et al. 2013), supporting the idea that at least

the core of the network might show some temporal stability. Lastly, the identity of interacting partners typically shows phylogenetic signal, meaning that related species tend to share similar interactions (Rezende et al. 2007, Gómez et al. 2010). Although the existence of non-random structures in seed-dispersal networks suggest some long-term mechanisms driving the assembly of networks (Fleming & Kress, 2013), it is still unknown whether or how these non-random structures are maintained and detectable over longer timescales, and what are potential mechanisms behind it.

Using diversification rates estimated from molecular phylogenies, and a dataset composed of 29 frugivory networks we tested the hypothesis that macroevolutionary predictable lineages are more likely to contribute with species to the core of ecological networks, providing an explicit macroevolutionary mechanism for network assemblage (see figure 1 for schematic version of general approach, and data used). To test this idea, we use a hierarchical Bayesian approach to investigate the potential association between the species' ecological roles and their macroevolutionary stability, therefore integrating two areas of knowledge. We define as stable lineages those that either have low extinction fraction (i.e. relative low extinction when compared to speciation), and/or higher net diversification (, i.e. lineages that can accumulate species at a faster pace). We estimated the species' ecological role by using tools derived from network science. We then incorporated phylogenetic and ecological uncertainties, along with environmental factors, in order to properly address how the interplay between biotic and abiotic factors drives the assembly of local networks due to macroevolutionary dynamics. Lastly, we tested whether the sorting of macroevolutionary regimes takes place at the regional or at a global scale.

We find that central species tend to belong to macroevolutionary stable lineages. The standardized extinction fraction is negatively correlated with species' ecological role represented by their centrality values (figure 2). Similarly, net diversification rates are positively correlated with species centralities (figure 2). In both cases the posterior distributions are clearly off centered with respect to a slope value of zero. These results hold after accounting for multiple sources of uncertainty. Median standardized effects for extinction fraction and net diversification were -0.14 and 0.19, respectively, indicating the two components of macroevolutionary stability contribute with similar intensity to the

structuring of the networks. Sensitivity analysis based on the medians of the posterior distributions for most parameters for each individual tree (figure 2) suggests that this signal holds irrespective of phylogenetic uncertainty.

Our results provide evidence that this macro-evolutionary sorting mechanism is predominantly a regional-scale phenomenon, since we only observed evidence for the sorting when analyzing the standardized rates (deviations from the mean rate per network), but not for the raw absolute rates (Fig S3). This suggests that the macro-evolutionary sorting mechanism acts at the relative rank of stability for the available lineages, and not on absolute values of extinction fraction or diversification rates. We also found that environmental conditions affect the relationship between ecological role and macroevolutionary stability, with warmer, wetter, non-seasonal environments having a stronger sorting of macroevolutionary stability regimes (figure 2). Interestingly, these environments harbor the highest frugivorous species richness (Kissling et al. 2009), and it is possible that such species rich environments allow for a finer sub-division of ecological roles on which this macroevolutionary sorting mechanism could more efficiently act. In fact, networks found on those tropical-forest-like environments are more centralized (i.e. a higher difference in centrality between the more central and more peripheral species - see figure 2 panel PC1) than networks commonly found on colder, drier, and seasonal environments. An analysis using a different dataset, in this case species dietary composition, suggests a tendency for many networks from warm/wet climates to show broader total amplitude in dietary “types” (figure 3A), corroborating the finding that warm and humid environments possess a broader range of species types (not only more species) on which the macro-evolutionary sorting can more efficiently act. Moreover, warmer, more humid and less seasonal climates allow for a more homogeneous occupation of the dietary space without increasing the dietary overlap between species, as indicated by the positive association between temperature/humidity and the average pairwise dietary distance (figure 3A), and by the absence of association between climatic conditions and the shortest dietary distances between species (figure 3B)

Although some clades are known to be important seed-dispersers across multiple continents (some families of Passeriformes, Galliformes, Piciformes, etc. - Snow 1981,

Fleming et al. 1987, Kissling et al. 2009), a spatial analysis of those networks reinforces the idea that such macroevolutionary sorting mechanism acts regionally on the available pool of species, and that the role of available species is, as expected, geographically structured. To evaluate if species within the same lineage play a similar role in different networks, we calculated the average centrality value for each different lineage (either family or genus) for all networks. The association between the mean centrality value of each lineage in different networks decays as a function of the geographical distances between those networks (figure 4). These results suggest that geographically close networks tend to have similar lineages playing similar ecological roles, but those roles are taken by different lineages in different parts of the planet.

In summary, our results provide evidence for a macroevolutionary sorting mechanism (species selection in a broad sense - Jablonski 2008) on network assembly where central species tend to belong to evolutionary lineages that are more stable over deep time. Moreover, we found that those central species not only interact with a higher number of species, but also that those partner species belong to a wider range of plant families (figure 3C). Hence our results suggest potential bi-directional selective regimes between ecological roles and diversification regimes, which might shape the fate of groups of very distantly related lineages (birds and plants) linked through ecological interactions.

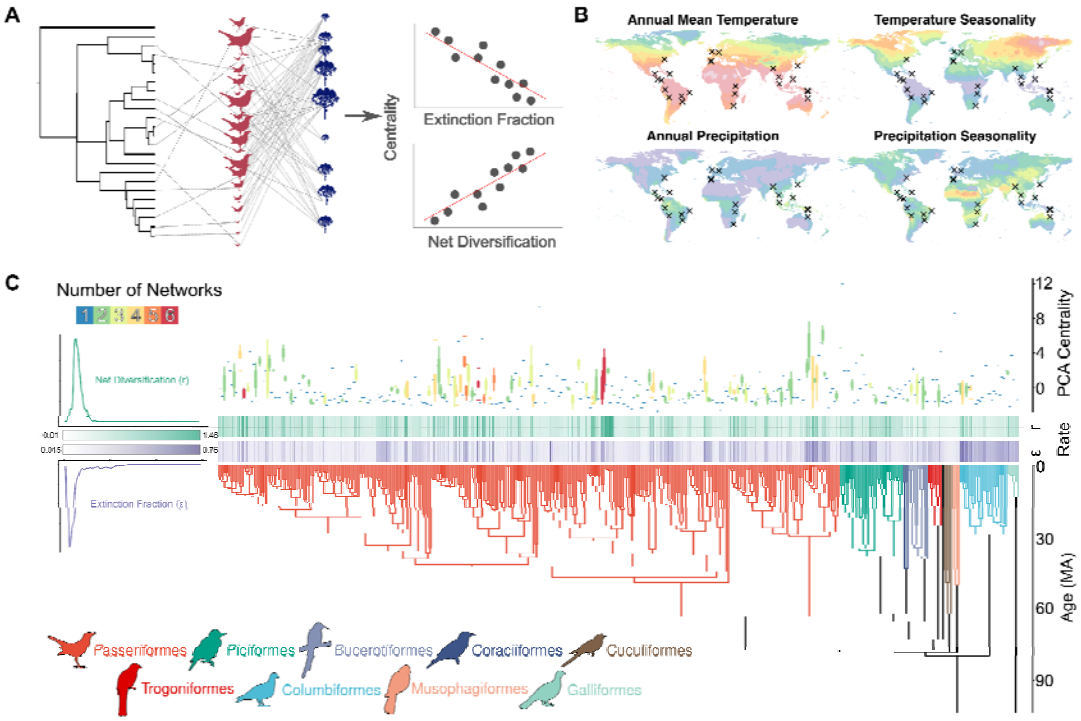

Figure 1: Conceptual framework and data used - Panel A (top left): Conceptual representation of the study; Panel B (top right): Geographical and climatic distribution of the 29 networks used in the study. Panel C (bottom): Exemplar pruned phylogeny with branch colors indicating the bird orders, along 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.

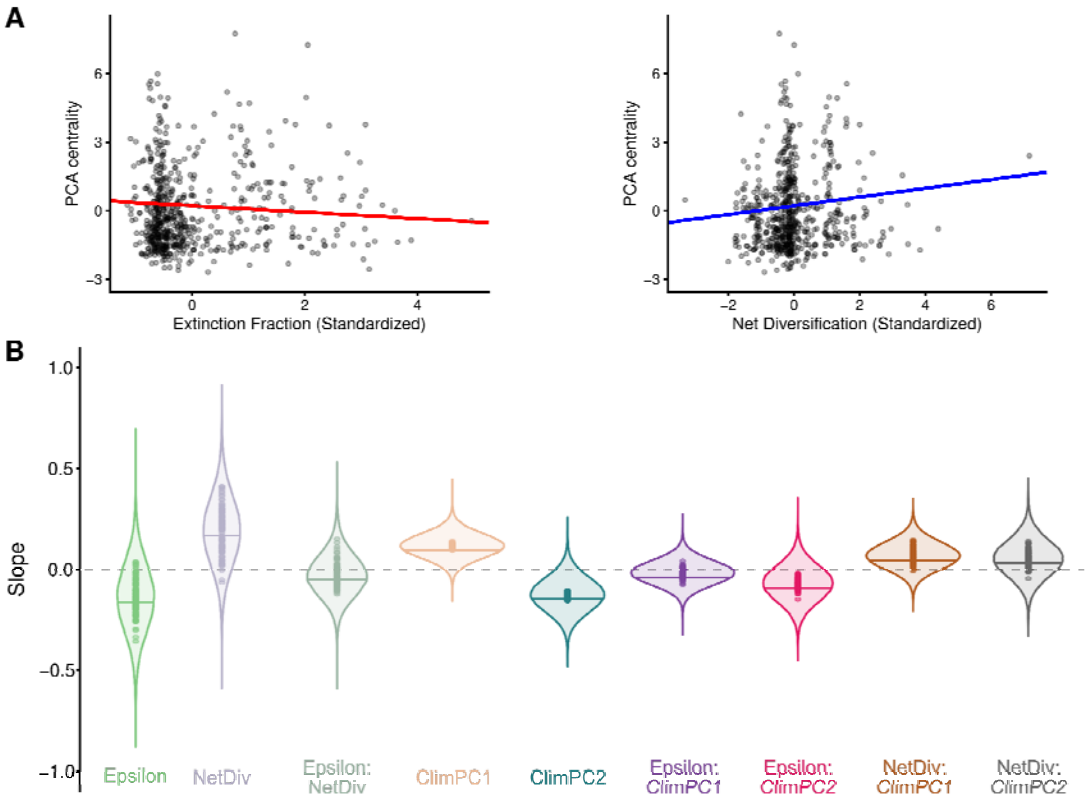

Figure 2: Association between network centrality and macroevolutionary stability - A - exemplar association between PCA centrality values and extinction fraction and net diversification rates estimated from one phylogenetic tree. B - Posterior distributions of all parameters (except the intercept for 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.

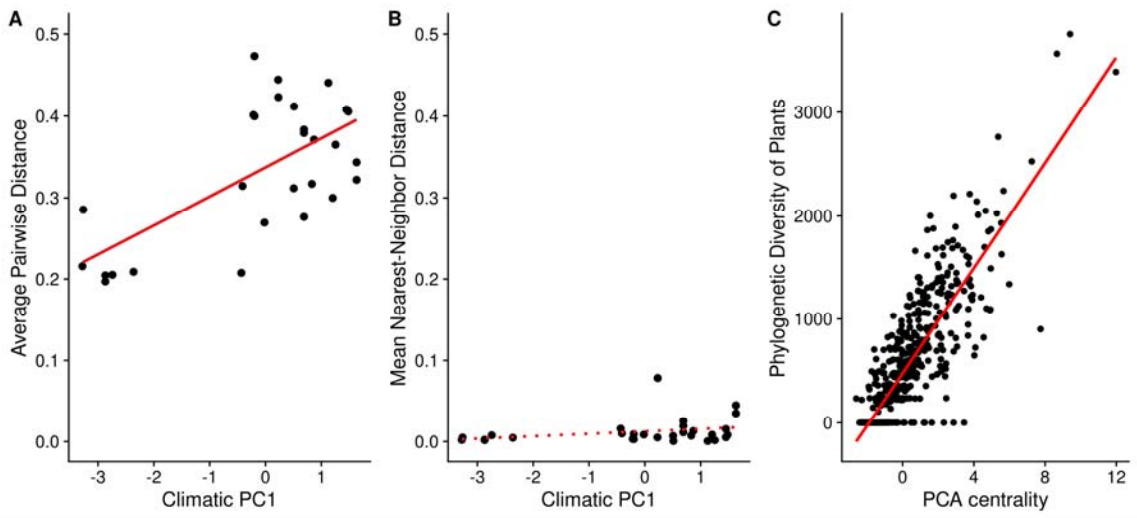

Figure 3: Different axes of specialization of bird species analyzed in the study - A) Plot showing that the average pairwise distance of species along dietary PC1 increases towards warmer, wetter, less seasonal environments (climatic PC1, p-value = 0.001, $R^2 = 0.4316$). . B) Scatterplot between mean 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.

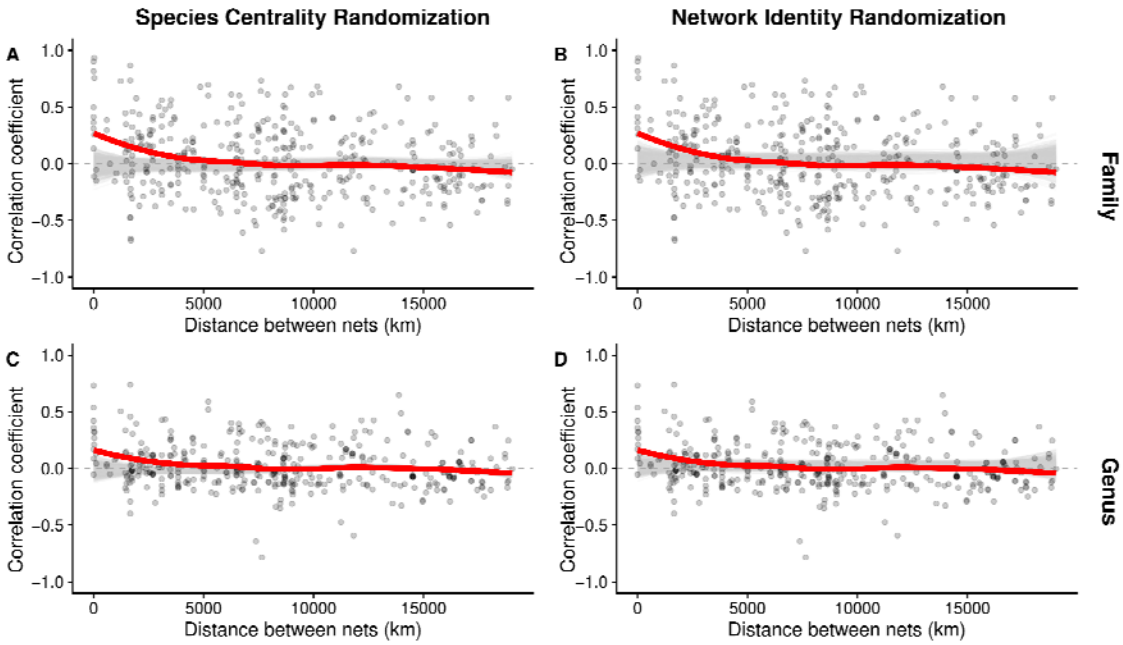

Figure 4: Association between mean centrality per family (panels A and B) or genus (panels C and D) and geographical distance - Each point represents a pairwise correlation between ecological roles in two different networks, and the red lines represent a loess smoothing to show the general trend of the 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.

Data and Code Availability

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

Author Contributions

GB, PRG and TBQ designed the study; GB gathered and analyzed the data; GB and TBQ wrote the first draft of the manuscript; GB, PRG and TBQ significantly contributed to the last version of the manuscript.

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Supplementary information is available for this paper

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Material and Methods

To investigate the potential effect of diversification rates on the assembly of current ecological networks we first characterized each frugivore species with respect to its potential ecological role in the network, and then estimated speciation and extinction rates related to each bird lineage using a comprehensive molecular phylogeny containing approximately 67% of all bird species (see below). We then tested for an association between the network metric and the macroevolutionary rate (see figure 1 main text for a cartoon version of the general approach) using phylogenetic generalized linear mixed models (MCMCglmm - Hadfield 2010). Phylogenetic correction was used because the network metrics showed significant phylogenetic signal (mean value for Pagel's lambda = 0.537, although for each tree the corresponding lambda value was used).

Diversification Rates

To estimate speciation and extinction rates we used the most recent bird phylogeny, which comprises the 99.3% of the extant species (9993 species in the phylogeny from an estimated total of 10,064 species – (Jetz et al. 2012). To avoid any potential bias introduced by adding species without DNA sequences (using a pure-birth algorithm) on our estimates of speciation and extinction rates (Rabosky 2015), we used the trees that contain only species for which molecular data were available from the original phylogenetic paper (Jetz et al 2012). This tree had 6670 species, but species not sampled were taken into account by the model. We analyzed the bird molecular phylogeny using a Bayesian framework (BAMM v. 2.5; Rabosky 2014) to estimate the rates of speciation and extinction while explicitly taking into account the sampling

fraction of species. The incompleteness (about 1/3 of species without DNA data) was considered within BAMM by using the percentage of missing species within each clade of the maximum clade credibility tree obtained by Jetz et al. (2012). Rabosky (2014) has developed an algorithm that finds sub-trees within a phylogeny, which share speciation and extinction rates through a Bayesian framework using reversible-jump Markov Chain Monte Carlo sampling. Each diversification shift configuration has an associated posterior probability, and each configuration can assign different diversification rates to a particular species or clade. Since it is impossible to not know which is the true configuration, we used the mean rates averaged by the marginal posterior probabilities of each distinct shift configuration. Lastly, we calculated our rates of interest: the extinction fraction ($\varepsilon = \mu/\lambda$) and net diversification rate ($r = \lambda - \mu$) for all species of interest. These two rates represent two different metrics used to quantify the stability/predictability of a given lineage. A higher value of extinction fraction suggests a more volatile dynamics within a given lineage and hence a higher chance of the entire lineage going extinct. A lower net diversification rate suggests that a lineage accumulates species as a smaller pace, and therefore has a higher chance of going extinct than lineages with higher net diversification rate. To our purposes, we assume that those two rates (each of them plus their interaction) affects the likelihood that a given lineage might be evolutionary reliable at long temporal scales.

Ecological Networks

To evaluate the ecological role of different species we used data from 34 different frugivory networks compiled by previous authors (Pigot et al 2016). Those networks comprise both temperate and tropical areas and a total of 546 unique bird species (838 total unique interactions). From the original dataset, we discarded 5 networks due to biases in species composition (networks that focused on specific bird or plant groups, and therefore do not represent the whole interacting assemblage), resulting in a final dataset of 468 species (700 unique interactions). Although some networks (23) had information on the strength of interactions, we decided to binarize all networks for two reasons. First, it allows us to work with a larger dataset. Second, it is known that interaction strengths vary across time (e.g. Ponisio et al. 2017), rendering quantitative estimates not necessarily meaningful as a long-term description. We also removed pairs of species that

only interacted with each other, and were, by definition, disconnected from the rest of the network. Those represent only 14 species from only 6 different networks from a total of 468 species from 29 networks. This was done because some of the network metrics are not defined for networks that are not fully connected.

To characterize each species' ecological role within the compiled dataset we investigated different node (species) properties of the networks by calculating, using the original bipartite networks, three different centrality metrics: degree (number of interactions), closeness (the reciprocal of the sum of shortest distances, in links, connecting the focal node to all other nodes in the network) and Katz (a measure of the distance, in terms of all possible pathways, between the focal node and all other nodes of the network, using $\alpha = 0.05$). Such metrics provide us with information about the importance of each species network structure when considering only the direct interactions (degree), the shortest pathways (closeness) or all pathways (Katz). To be able to combine the ecological roles estimated for different networks (that have different properties, such as number of species and connectance) into a single analysis, we first standardized the three metrics by calculating their z-scores for each network separately. After compiling each of the three standardized centrality metrics for all species in all networks in a single dataset, we performed a Principal Component Analysis (PCA) in order to obtain a single score that comprised different aspects of the network position (as a proxy for the ecological role). We used only the first Principal Component since it explained 93.3% of the variance in centrality values.

Sources of uncertainties

We incorporated in our analyses two distinct sources of uncertainty. The first one is related to the true evolutionary history of birds. To incorporate the phylogenetic uncertainty, we used 112 different topologies from the bird phylogeny from Jetz et al. 2012 (56 of each backbone) to both estimate the rates of diversification and to take into account the phylogenetic structure of the residuals in the linear model. The other source of uncertainty came from the networks. From all the species in the final dataset (N = 468 species), 139 are part of more than one network (up to 6), making it impossible to attribute a single centrality value to those species. We thus incorporated this variation as a source of uncertainty in the regression analysis by using species identity as a random

factor as described in the modeling section below.

Co-Factors

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

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

Modelling

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

zero (no association), and in the medians of individual posterior distributions for each tree (Holland, 2019; Wasserstein et al. 2019). By doing this we embrace sources of uncertainty incorporated in our analysis (ecological and phylogenetic) while looking at the magnitude of the effect (Holland, 2019). All MCMC chains were run for 5000000 iterations, with half of the total length discarded as burn-in, and sampling every 2500 iterations. We used inversed Wishart distributions as priors for both the fixed and the random effects.

Geographical patterns of centrality per family/genus

Lastly, to check if the species that play central/peripheral roles in different networks show a spatial structure with respect to their taxonomic identity (e.g. belong to the same family/genus), we calculated the association between the average centrality per lineages (either family or genus) for each pair of networks using Spearman's correlations, ρ. and then plotted ρ as a function of the distance between each pair of networks. We used family or genus as our data points for two reasons. First, it is unlikely that the same species would be present in geographically distant networks. Second, the macroevolutionary effect we are measuring is a lineage effect (e.g. different species represent the macroevolutionary regimes of different lineages). To build a null model, we used two different randomization approaches and two different ways to deal with missing data. Hence, we ended up with four different null models for each analysis, one set for the family and another for the genus level.

In the first randomization approach (figure 4 panels A and C), we randomized the species centrality values within each network prior to calculating the average centrality for each lineage (either per family or per genus). The association was then estimated for all pair of networks and plotted as a function of the geographical distance of each network pair. In the second randomization approach (figure 4 panels B and D), instead of randomizing the species centrality values within each network, we randomly draw two networks irrespective of their geographical distance, repeating this procedure for all a set of geographical distances equal to the one seen in the empirical comparison. Hence in our first randomization approach the species identity is randomized but the geographical distances between pairs of networks is kept as in the empirical dataset. In the second randomization approach it is the geographical distance that is randomized while keeping

the original species identity.

In both randomization approaches, there were instances where a given lineage was only present in one of the two comparing networks. Hence to calculate the association between networks when using lineage (e.g. family or genus) average centralities, we had to deal with the limitation that “valid” average centrality value for a given lineage might not be estimated for some of the networks. To overcome this limitation, we filled the missing values in two different ways. In the first, we simply replaced the missing values in a given network by 0 (hereafter called “single 0 scenario”). By doing this we are strongly “breaking” any possible association, which means that only very strong association would still remain significant after adding those zero values (figure 4). The second approach consisted in replacing the average centrality of a lineage (family or genus depending on the analysis) by 0 not only for the network where that lineage was missing but in both networks (“full 0 scenario”). This was done in order to “completely remove” the effect of that lineage from the analysis, while still allowing for the association between the families/genera that are present in both networks to be estimated (supp. figure 4).

The prediction of the null model is constructed by doing a LOESS smoothing to each randomized dataset (1000 datasets in total). The empirical LOESS smoothing line is then compared to the group of LOESS smoothing lines defining the null model and the relationship is considered significant if the empirical line does not overlap with the null model lines.

Ecospace Occupation

To analyze how ecospace is occupied in different climates, we used an independent dataset of dietary information (EltonTraits v1.0, Wilman et al., 2014), and a phylogenetic Principal Component Analysis (phyPCA, Garland et al., 1993, Revell 2012) to obtain the axes of greater variation in the diet of all species present in our dataset. The phyPCA was done using only the 468 species present in our network dataset. Using the first Principal Component (PC1 - greatest loading of fruits), we calculated three different disparity metrics for each network: amplitude (that indicates how broad the dietary niche is for the whole network), average pairwise distance and mean nearest-neighbor distance (that indicates, on average, how far each species is from the closest species in their

respective network). We tested the relationship between each of the three metrics with climatic PC 1 (which explains about 56% of the variation) to assess any trends of ecospace occupation along climatic gradients.

The degree of interaction generalization

For each bird species in each network, we calculated both the number of unique families with which they interact, and also the plant phylogenetic diversity by summing all branch lengths in the pruned phylogeny containing only the plant families with which the species interact. In order to test if more central species are more generalist (either defined as interacting with a higher number of plant families or by a higher value of plant phylogenetic diversity of their plant partners) we fitted linear models to test for the association between ecological role (PCA centrality) and both the number of families and phylogenetic diversity.

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