Round #1

by Alejandro Gonzalez Voyer, 16 May 2022 19:15

Decision on submitted manuscript: Do closely related species interact with similar partners?

I have read with interest the submitted preprint Do closely related species interact with similar partners? Testing for phylogenetic signal in bipartite interaction networks. I think the manuscript is well written and clearly presented in general. I think it could make for a valuable contribution to the field given the meticulous analyses of the performance of different metrics to test for phylogenetic signal in interaction networks. The two expert reviewers also agree that the work is well written and could be of interest to evolutionary biologists and evolutionary ecologists. The two reviewers have made a number of excellent suggestions on how to improve the work which should be addressed prior to recommendation. I have very little to add to the thorough reviews by both expert reviewers.

I look forward to receiving a revised version of your manuscript.

> Thank you. We have addressed all the comments of the reviewers. In particular, we have performed complementary analyses to evaluate the confounding effect of the phylogenetic signal in the number of partners. As recommended by ref #1, we have tested both (1) ecological distances that partition species identity from the number of partners and (2) permutations that keep constant the number of partners per species when evaluating the significance of the Mantel correlation. We updated our recommendations accordingly (Figure 4). In addition, as recommended by ref #2, we now better explain the simulation scheme used to generate interaction networks using a synthetic figure (see new Figure 2) and how we tested the realism of this framework.

Reviews

Reviewed by Joaquin Calatayud, 20 Apr 2022 14:23

Perez-Lamarque et al. present a throughout study that tackle most (if not all) common problems when assessing phylogenetic signal in species interactions. They did so by nicely comparing the performance of two commonly used methods (Mantel test and PBLM) on simulated benchmarks. A theoretically more advanced method was also evaluated (PGLMM). The authors considered different scenarios including interaction sign and strength, phylogenetic signal in generalism and sampling asymmetry. Moreover, they developed an interesting procedure to test for phylogenetic signal across different clades. Finally, based on obtained insights, they explored an empirical

dataset of orchid-mycorrhizal fungus interactions and aimed at providing general guidelines when measuring phylogenetic signal in ecological interactions. Overall, they found that PBLM (and PGLMM) are more prone to type I errors than Mantel test.

The manuscript is well written and the research is well conducted, timely and provides some interesting findings. I also appreciate the huge effort to conduct the large battery of simulations and analyses while keeping a congruent manuscript.

> Thank you for these positive comments.

I have, nevertheless, some conceptual and methodological considerations that may strengthen the research. It must be noted that I am more familiar with the Mantel test and my suggestions are focused in that direction.

1. Comparing Jaccard vs UniFrac distances

The authors compared the performance of Jaccard and UniFrac distances to detect phylogenetic signal in interaction partner use. They found that UniFrac distances outperformed Jaccard distances and concluded: "we advocate the use of weighted UniFrac distances" (line 689). The point here is that Jaccard and UniFrac distances are measuring dissimilarities in different aspects of interacting species (taxonomic vs phylogenetic compositional dissimilarities, respectively) that may reflect different evolutionary processes. For instance, assuming that interactions are trait-mediated and following the author's nomenclature, if the traits that regulate interactions are conserved in guild A but not in guild B, then we should find that phylogenetically related species of guild A would share interaction partners of guild B that are unrelated. Thus, for guild A, we could expect phylogenetic signal in species interactions when using Jaccard distances but not when using UniFrac distances (perhaps Fig. 1A in Calatayud et al. 2016 might help, and sorry for the self-advertising). This exemplified that Jaccard and UniFrac distances (either weighted or not) can reflect different processes and, therefore, that they cannot be safely compared. I would suggest to remove the direct comparison and subsequent recommendations between these two distance indices.

> Agreed. We have rephrased our conclusions in the context of the BipartiteEvol simulations that assume that species interactions are mediated by phylogenetically-conserved traits on both sides of the network. We also now discuss how the choice of Jaccard *versus* UniFrac distances depend on the question at stake. See lines 762-778.

2. Effects of the number of interacting partners (and other generalism levels)

The authors proposed a sequential Mantel test to overcome confounding effects of phylogenetic signal in the number of interacting partners. They conducted a first Mantel test to explore the correlation between phylogenetic and ecological distances and a second one to explore the correlation between phylogenetic distances and differences in the number of interacting species. If both correlations were significant they treated the former as non-significant. While I agree that this approach may work in some situations, it will certainly produce type II errors when both composition and number of partners show phylogenetic signal, as they recognize in the discussion.

I think there are better alternatives to solve this issue than the sequential Mantel test. The root of the problem here is that both the Jaccard and the UniFrac distances take into account differences in taxonomic (i.e. number of species) and phylogenetic (i.e. sum of phylogenetic branch lengths) generalism, respectively. Hence, species with different levels of taxonomic or phylogenetic generalism will also show differences in interacting partner use when using these indices. This is a common issue in many other situations, and there are well-stablished dissimilarity indices to overcome it (Baselga 2010, Leprieur et al. 2012, see also Calatayud et al. 2016 for their use in a similar context). By only taking into account dissimilarities due to true changes in the partner species/phylogenetic composition, these indices are robust to produce spurious correlations between ecological and phylogenetic distances when generalism levels show phylogenetic signal.

> Thank you for the suggestion. We now test this alternative approach in our manuscript. We have used the betapart R-package to extract the part of the unweighted Jaccard distances that is due to species turnover and not to the number of species, and then correlate these partitioned distances with phylogenetic distances using a regular Mantel test. This approach performs well in terms of statistical power and false positive rates (see Tables S2 and S3, and Fig. S15). Yet, it tends to artefactually detect negative phylogenetic signals, i.e. that closely related species tend to interact with dissimilar partners. Although we discuss that other partitioning distances (that we did not test) might achieve better performances (lines 806-807), we rather tend to recommend the use of Mantel tests with permutations that keep the number of partners per species constant (see below).

Alternatively (or even better complementarily), using appropriate randomization schedules to asses statistical significance in Mantel test can help to get rid of this confounding effect. That is, rather than permuting any of the distance matrices (as I guess the authors did), one can permute the raw interaction matrix by retaining some of its properties. For this case, it would be possible to randomise the interaction matrix keeping constant the number of interaction partners. While this does not affect observed correlation coefficients, it certainly reduces type I errors associated with phylogenetic signal in generalism levels, improving also other issues of Mantel test (Guillot & Rousset 2013).

> Thank you for this additional suggestion. We have incorporated the use of this permutation test for evaluating the significance of the Mantel correlation. For instance, when measuring the phylogenetic signal in guild A, instead of shuffling at random the ecological distance matrix as a regular Mantel test, we evaluate the significance of the correlation by shuffling the interaction network while keeping the number of partners per species of guild A constant. In short, for each species of guild A, we shuffle at random the identity of the species being present. As the number of partners in guild B is not constrained, we replicate the same strategy for measuring the phylogenetic signal in guild B.

This approach performs well in terms of statistical power and false positive rates (see Tables S2 and S3, and Fig. S16), although it tends to have higher false positive rates than regular Mantel tests. In addition, because it requires re-computing the ecological distances for each randomized network obtained using such permutations, this approach is much more computationally intensive (even if we reduce the number of permutations to 1,000; see Fig. S2). Thus, we recommend using this permutation strategy as a second step (Figure 4), to test whether a significant phylogenetic signal revealed by a regular Mantel test (Step 1) can be fully explained or not by a phylogenetic signal in the number of partners.

Note also, that randomizations of raw data can also accommodate other aspects such as unequal sampling effort or spatial patterns (e.g. Vázquez et al. 2009), making Mantel test highly flexible (perhaps this could also be discussed).

> We now shortly discuss this point (the flexibility of the Mantel tests) in the Conclusion of our manuscript (lines 843-845).

In summary, by using appropriate dissimilarity indices and null models it is possible to remove the effects of potential phylogenetic signals in generalism levels. To the best of my knowledge, this is where the state of the art is when using the Mantel test (or any of its updates, see, for example, Ferrier et al. 2007 for generalized regression on distance matrices). Still, the behaviour of these apparently and theoretically more advanced approaches has not been tested using simulated benchmarks. I think the authors have the perfect opportunity to do this, which I believe would certainly improve the research. Though I encourage the author to test this approach, I am totally aware that it might imply a huge (perhaps unfeasible) effort. If this is the case, I would suggest to send the sections "Confounding effect of the phylogenetic signal in the number of partners" to supporting information, especially considering that your simulations should not produce phylogenetic signal in generalism. At the very least, I think the commented alternatives deserve a mention in the discussion, perhaps removing any recommendation to the sequential Mantel test.

> Following your suggestions, we have removed the recommendations of using sequential Mantel tests, which is indeed a sub-optimal solution. We have tested the alternative approaches you suggested (both the partitioning of the ecological distances and the permutations keeping the number of partners per species constant). We found that they indeed have better statistical performances, and we now recommend using Mantel tests with permutations keeping the number of partners per species constant (lines 796-816). We have therefore updated our recommendations in Figure 4.

3. Minor considerations

I am just not sure whether the mantel test is not also a model-based approach as it implicitly assumes that ecological divergence increase with divergence time (Letten & Cornwell 2015). Indeed, phylogenetic distances used in Mantel test (or analogous) can be modified to accommodate different evolutionary models (e.g. Calatayud et al. 2019). Of course, it is not as explicitly as other models, but I think this classification might be controversial. Just not sure.

> Agreed. We have replaced "model-based approaches" with "process-based approaches". "Process-based approaches" like Pagel's lambda or the PBLM approach assume that trait evolves according to a particular process (e.g. a BM or OU process of trait evolution). In contrast, by default, the Mantel test only measures a correlation and does not, in general, explicitly assume any process.

Figure 2. I think it should be "Guild A" instead of "Clade A".

> Done.

Other potential missing references for the introduction:

Braga, M. P., Janz, N., Nylin, S., Ronquist, F., & Landis, M. J. (2021). Phylogenetic reconstruction of ancestral ecological networks through time for pierid butterflies and their host plants. Ecology Letters, 24(10), 2134-2145.

Futuyma, D. J., & Agrawal, A. A. (2009). Macroevolution and the biological diversity of plants and herbivores. Proceedings of the National Academy of Sciences, 106(43), 18054-18061.

Gómez, J. M., Verdú, M., & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across the entire tree of life. Nature, 465(7300), 918-921.

> We have added these three references in the first paragraph of the introduction.

4. References

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19:134-143

Calatayud, J., Hórreo, J. L., Madrigal-Gonzalez, J., Migeon, A., Rodriguez, M. A., Magalhaes, S., & Hortal, J. (2016). Geography and major host evolutionary transitions shape the resource use of plant parasites. Proceedings of the National Academy of Sciences, 113(35), 9840-9845.

Calatayud, J., Rodríguez, M. Á., Molina-Venegas, R., Leo, M., Horreo, J. L., & Hortal, J. (2019). Pleistocene climate change and the formation of regional species pools. Proceedings of the Royal Society B, 286(1905), 20190291.

S Ferrier, G Manion, J Elith, K Richardson, Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Divers Distrib 13, 252–264 (2007).

Guillot, G., & Rousset, F. (2013). Dismantling the Mantel tests. Methods in Ecology and Evolution, 4(4), 336-344.

Leprieur F, Albouy C, De Bortoli J, Cowman PF, Bellwood DR, et al. (2012) Quantifying Phylogenetic Beta Diversity: Distinguishing between "True" Turnover of Lineages and Phylogenetic Diversity Gradients. PLoS ONE 7(8): e42760.

Letten, A. D., & Cornwell, W. K. (2015). Trees, branches and (square) roots: why evolutionary relatedness is not linearly related to functional distance. Methods in Ecology and Evolution, 6(4), 439-444.

Vázquez, D. P., Chacoff, N. P., & Cagnolo, L. (2009). Evaluating multiple determinants of the structure of plant–animal mutualistic networks. Ecology, 90(8), 2039-2046.

Reviewed by Thomas Guillerme, 25 Apr 2022 13:41

Please find below my comments on the manuscript entitled “Do closely related species interact with similar partners? Testing for phylogenetic signal in bipartite interaction networks”. In this manuscript, the authors investigate the ability of different statistical

methods to recover phylogenetic signal of species interactions on a set of simulated networks and then propose an empirical example with best practices guidelines stemming from their findings.

Overall, this paper proposes a very useful benchmarking of the false positive error for species interactions analysis and would be of great help to ecologists and evolutionary biologists. I especially like the clarity of the results as presented in Figure 2: the Mantel test approach very often outperforms the Phylogenetic Bipartite Linear Model method by having a much lower false positive rate.

> Thank you for these positive comments.

I have however several major comments and some minor ones (often semantic) that I think the authors should address prior to publication but I have little doubts that they will affect the general findings (Mantel test > PBLM for network interactions).

Major suggestions Simulation protocol

The findings of the authors essentially relies on the simulation protocol and mainly on the RPANDA::build_network.BipartiteE function. I suggest the authors spend more time explaining how this function works (even though it is already described in Maliet et al 2020). Furthermore, I found the methods section on simulations quite complicated to read. There is a lot of information and at the time of the reading, the reader doesn't know which one is essential and which ones are just parameters details. I suggest making a figure or a table summarising the simulations: 1) what are the specific simulated scenarios for (i.e. what aspect are the authors trying to simulate), what are the important parameters used to approximate that and, 3) what are the expected results from that scenario (e.g. no phylogenetic signal, etc).

> We have now included a new Figure (Figure 2) in the main text that recapitulates the framework we used here for generating interaction networks with or without phylogenetic signals in species interactions. The Figure clarifies the assumptions of the BipartiteEvol simulations, the influence of the main parameters we use (in particular the α parameters that determine the effect of the partner's traits on the fitness of the individuals), and the patterns that we expect to see depending on the simulated scenarios. We have also updated the descriptions in the Methods section to make them easier to read.

Also, I believe the authors could strengthen their results by demonstrating the robustness or realism of their simulation pipeline. For example, part of their work is

looking at the effect of tree uncertainty on measuring signal in interaction networks (l. 316-328). Here the authors propose to simulate a network (using RPANDA::build_network.BipartiteEvol), then simulate DNA sequences (using HOME::simulate_alignment), inferring a tree from the simulate sequences (using ape::nj), and then measuring the phylogenetic signal from the resulting networks to compare them with the results without tree uncertainty. Although this is a perfectly good approach for measuring it, it relies on the effect of each intermediary algorithm which, from experience, although they are the best algorithms available can perform poorly at simulating realistic data in some conditions. This makes the authors' results slightly less convincing since the reader has to put faith in the different intermediary simulations.

> This comment made us realize that our comparison of the structures of the networks simulated with BipartiteEvol with the structures of empirical networks were too hidden in the supplementary data, and we have now clarified this point in the methods lines 211-216 and in the first paragraph of the Results section (lines 438-443). We did compare the structures of our simulated networks to those of empirical networks obtained from the Web of Life database (web-of-life.es (Fortuna *et al.*, 2014)) and the database of Michalska-Smith & Allesina (2019) in terms of connectance, nestedness, and modularity (see Supplementary Methods 2). We found that these simulated networks have structural properties comparable to that of the empirical networks (Figure S4), suggesting that our simulations are realistic (lines 438-443).

About the test of phylogenetic reconstruction, we agree that simulations are not always realistic, but they are required to test the performance of statistical approaches under known processes (we don't know the processes that have shaped empirical data). The best we can do is check the realism of our simulations (as we have done for the networks), or check that our simulations behave as expected. In order to check that our simulations of phylogenetic uncertainty behave as expected, we checked that phylogenetic uncertainty increases when the length of the simulated DNA sequence used to perform phylogenetic reconstruction decreases (lines 606-608). We now report the correlation between the original tree and the tree reconstructed from simulated DNA sequences (with variable length), see in the new Supplementary Figure 24, and find that the strength of this correlation indeed decreases with decreasing sequence length.

Maybe one way to solve this problem would be to benchmark the author's results with some already published empirical data for which the answer is known? The authors could replicate the results of Martos et al 2012 not only for the application/guideline section but also for benchmarking of the simulations. For example, in the tree uncertainty scenario, they could compare the range of their simulated results to the one they would obtain from measuring the phylogenetic signal on the tree distribution from Martos et al 2012.

> We are sorry but we don't understand the suggestion to benchmark the results with already published empirical data for which the answer (i.e whether species interactions are evolutionary conserved?) would be known. Answers to this question from published empirical data rely on specific statistical tests (such as Mantel tests or PBLM) that we test here using simulations. For example, we suggest that many of the empirical systems for which a phylogenetic signal has been detected using PBLM are false positives, given the >70% of false positives we discover when using PBLM on simulated data (for which the answer is known, because simulated).

Our 2,400 simulations under different simulated scenarios/parameters enable us to generalize our conclusions, which would not be possible if we were to benchmark them using a single study case (e.g. the mycorrhizal network from La Réunion). Unfortunately, we do not have a measure of phylogenetic uncertainty in the orchid phylogeny, as we obtain only one species tree (see below for the corresponding answer), and so we cannot perform the analyses suggested by the reviewer. We therefore prefer to keep the empirical data for the guideline only.

We now emphasize that our simulated networks are comparable to empirical ones (lines 438-443) and that our simulation of phylogenetic uncertainty behave as expected (e.g. lines 606-608).

Data availability and reproducibility

The authors seem to provide all their code and data for reproducibility (I haven't checked all scripts though) which is a great! I have two minor suggestions on that point though:

- Although the authors provide their code for the simulations in the GitHub repository (and the link to the original publication containing the data), I think the repo would benefit of having an additional entry in the README to explain which script does what (and not just for script_phylogenetic_signal_network.R).

> We have updated the GitHub README pages to better explain the different scripts. In the main README, we now include other functions to measure phylogenetic signals (https://github.com/BPerezLamarque/Phylosignal_network). In the README about simulations (https://github.com/BPerezLamarque/Phylosignal_network/tree/master/simulations), we now detail the different scripts that are needed to replicate our analyses.

- I suggest adding a link to the (mpfr help page)[https://www.mpfr.org/mpfr-current/mpfr.html] in the README since mpfr (and dependent Rmpfr) might not be straightforward to install.

> We have now added the link to the README file.

Minor suggestions

- l.34: Although "Type I error" is a perfectly valid term here, I would suggest changing it to "false positive" throughout the manuscript to make it easier for the reader (I personally always need to google which type error is which one even after years working with it).

> Done.

- l.154: Is the opposition of the terms "modular" and "nested" common in the interactions field? They seem slightly confusing to me as opposed terms in the context of this sentence (can modular interactions not be neatly nested as well?).

> We are referring here to the results obtained by Maliet et al. (2020) on their simulations, where simulated antagonistic networks are modular and simulated mutualistic networks are nested. But we agree that this is not a generality. We have therefore rephrased the sentence to avoid any confusion.

- l.163: I am not sure about the coining of the term "anti-phylogenetic signal" throughout the manuscript. This particularly led to confusion in the conclusions (l.672-678). Although I do understand the naming of it as the inverse of a phylogenetic signal, in the broader sense of phylogenetic comparative methods it could introduce some confusion where phylogenetic signal is broadly understood as being a link between a trait and the tree structure and no phylogenetic signal being the absence of it. Then an anti-phylogenetic signal would be the non-link between a trait and a tree? Which doesn't make much sense to me and I believe is not what the authors mean here. Maybe they could change it to something like "phylogenetic signal for dissimilarity" or something like that.

> Agreed. Following Elias *et al.* (2013) we now use the term "negative phylogenetic signal" instead of "anti-phylogenetic signal". We also clarify its definition every time we refer to it.

- l.168-169: It is unclear to me how the traits are generated here and why six traits are generated. Under what distribution(s) (and which parameters) are these traits generated?

> Trait mutation occurred at birth with probability μ=0.01. When mutating, new traits are drawn independently in a normal distribution centered on the parent traits and with a variance of 1. We have clarified this lines 202-205.

- Why did the authors chose to use six traits?

> We have chosen to use six-dimensional traits as biological interactions are likely influenced by many traits in nature, so we thought that using more traits would be more realistic. Maliet et al. (2020) found that changing the number of traits does not significantly change the behavior of BipartiteEvol simulations.

- And what is the correlation between these generated traits?

> Traits are drawn independently from a normal distribution, so we don't expect a correlation between traits (besides a residual correlation originating from the shared evolutionary history of species). We have clarified this in the Methods section.

- l.167-197: I think the reader could benefit of a table recapitulating the different simulation scenarios and parameters (number of interacting pairs, α values, expected phylogenetic signal, etc. . .).

> We have summarized these different parameters in Figure 2. We could also add a table in supplementary if the reviewer thinks this is not enough.

- l.202: I suggest adding a comparison of computational time and resources between both methods in the supplementary materials to convince the reader to which degree a PGLMM is more "computationally intensive" than a Mantel test.

> We have now reported the computation time of the different methods in Supplementary Figure 2 for 10 small networks. We can see that PGLMM is two orders of magnitude slower than classical Mantel tests. Computation times of PGLMM and PBLM increases also exponentially with network sizes, as illustrated by their wider boxplots. It also requires much more memory.

- l.221: Why did the author chose to use so many permutations? I think 1000 would be plenty (or even 100 since they consider that enough for the Kendall correlations). I am not entirely sure if the amount of permutations have an effect

on the calculations of the statistics in this specific case but from experience, I know that it can induce some false negative error due to the pseudo-replication (so in doubt I would suggest reducing the number of permutations).

> A large number of permutations enables a better estimation of the p-value (Hommola *et al.*, 2009), therefore increasing the number of permutations generally improves the statistical performance of a model. In the context of a classical Mantel test, which shuffles the rows/columns of one of the distance matrix, pseudo-replication is very unlikely. For instance, if there are n=10 species, there are n!=3,628,800 possible permutations, therefore, by performing 10,000 permutations, we are very unlikely to obtain many pseudo-replications. We thus kept 10,000 simulations when computationally feasible.

Same on line 353.

> We have increased the number of permutations to 100,000 for analyses of clade-specific phylogenetic signals because we simultaneously performed a Bonferroni correction for multiple testing. The "corrected p-value" using a Bonferroni correction is the original p-value (e.g. p=0.001 with 1,000 permutations) multiplied by the number of multiple testing (e.g. 50), so the corrected p-value is 0.05, and it would be p=0.5 if using only 100 permutations. In that case, it is mandatory to perform a large number of permutations to avoid a drop in the statistical power of the Mantel test due to the Bonferroni correction.

- l.254: Although the unit is interpreted as exactly the same, I suggest changing "Go" to "Gb" which I believe is more popularly used.

> Done.

- l.265-266: I don't understand what "the absolute differences in degrees" are.

> For clarity, we have replaced "degree" with "numbers of partners" everywhere. We refer here to the absolute difference in the number of partners between a pair of species.

- l.354: I suggest using "False positive" instead of "alpha-risk" to avoid introducing yet another technical term.

> We have replaced it with the "risk of false positives".

- l.355: Similarly here, I suggest changing "we generated a synthetic network" to "we simulated a network" to keep in line with the vocabulary used in the rest of the methods.

> Done.

- l.374-378: I suggest adding more information to this section: how did the authors chose the calibration(s) for the tree? (I suggest following Parham et al 2012 Syst. Biol. 61(2):346–359 recommendations). How did the authors obtained species-level trees (do they mean a fully resolved tree?) with polytomies at 10 Mya? (and why choosing this arbitrary time?)? Or do the authors mean they resolved polytomies by adding arbitrary 10 Mya branches to make the nodes binary? To which side of the node where these branches added (i.e. did that made the unresolved node more ancient - 10 Mya extra per multifurcation) or did make the species splits arbitrarily 10 Mya younger? Regardless, this process seems to generate a stochastic distribution of trees. Did the authors used a tree distribution for the subsequent analyses or did they just generated a single tree?

> We have calibrated the orchid phylogeny by setting the divergence between Orchidoideae and Epidendroideae at 65 million years following Givnish *et al.* (2015). To obtain a species-level orchid phylogeny, missing species were grafted into the phylogeny by arbitrarily adding 10 million-year-old polytomies in the corresponding unresolved genera, namely *Habenaria, Benthamia, Cynorkis, Phaius, Liparis, Bulbophyllum,* and *Polystachya*. We therefore obtained a single species-level orchid tree using these methods that do not contain any stochasticity. We have clarified these methods lines 429-433.

We tested the robustness of our results to these methodological choices: using other ages for the polytomies (e.g. 5 Myr or 12 Myr) did not qualitatively affect or results (not shown).

- l.448: Did the authors meant "guilds A and B" or "clades A and B"?

> We refer here to "guilds A and B". We have replaced "clade" with "guild" in Figure 3 for clarity.

- Figure 3: I suggest adding the function's package name in the examples of the guideline (i.e. RPANDA::phylosignal_network) and maybe changing the font to courier to make it clear this is an example code snippet.

> Done.

References:

Elias, M., Fontaine, C., and Frank Van Veen, F.J. (2013) Evolutionary history and ecological processes shape a local multilevel antagonistic network. *Curr Biol* **23**: 1355–1359.

Fortuna, M.A., Ortega, R., and Bascompte, J. (2014) The Web of Life. *arXiv Popul Evol*.

Givnish, T.J., Spalink, D., Ames, M., Lyon, S.P., Hunter, S.J., Zuluaga, A., et al. (2015) Orchid phylogenomics and multiple drivers of their extraordinary diversification. *Proc R Soc B Biol Sci* **282**: 20151553.

Hommola, K., Smith, J.E., Qiu, Y., and Gilks, W.R. (2009) A permutation test of host-parasite cospeciation. *Mol Biol Evol* **26**: 1457–1468.

Michalska-Smith, M.J. and Allesina, S. (2019) Telling ecological networks apart by their structure: A computational challenge. *PLoS Comput Biol* **15**: 1–13.