

Responses to reviewers comments

Editor in chief

Three reviewers and an AE have looked at your manuscript. One reviewer and the AE recommend rejection, because any revision would essentially result in quite a different paper. Two other reviewers are critical, but suspect the manuscript could be revised. On balance, I have decided to keep the door open ajar, and will allow a very significantly revised manuscript to be resubmitted. You may decide the ask is too much, and try publishing elsewhere.

Response: We are grateful for the opportunity to submit a revised manuscript. As you will see from the responses, and the track-changed document attached, we took each and every comment made by the three reviewers to heart, and have made many additions to the text. As a result, the revised document is slightly over the word limit; we do apologize for this, but we feel strongly that it would have been inappropriate to answer the very thorough comments made by the reviewers with only minor changes to the text. If the revised manuscript is too long, we welcome editorial guidance on which parts to cut.

Our interpretation of the comments by the reviewers is that the manuscript was clear to read, and that the underlying scholarship was robust; most of the comments were asking for clarifications, and especially for additional arguments that show the method to be actually robust and usable. To this extent, we have (in addition to the changes in the main text) developed three supplementary material analyses. The first establishes that the threshold used to discriminate between interactions and non-interactions has been correctly estimated (which was a concern expressed by one reviewer), but goes further than that and establishes that the truncated SVD is a well behaved classifier for trophic interactions even on artificially compromised data; the second establishes that the uniform distribution used in trait reconstruction does not lead to over-estimate of interactions (a core concern of reviewer 2), and that in fact it is a very conservative estimate of probabilities; finally, the third supplementary material answers a core concern of reviewer 3, by showing that producing a metaweb does not average out ecological differences between networks.

We are hopeful that the manuscript in its revised form meets the standard of Ecology Letters.

On behalf of the authors,
Timothée Poisot

In particular, it is important that the major criticisms of the AE and reviewer 2 are all addressed. These get to the heart of the issue. The method is elegant, but we just don't know how well it will work in real life situations. We need some validation. The manuscript also requires additional methodological details, and some new model runs. Some of these can be included in Supplementary Information, but they are important.

Response: We are confident that the additional results presented as supplementary material will considerably strengthen both the generality of our approach, and its application to real-life situations.

If we may be allowed a single tongue in cheek comment (and should we be out of line, please know that only the last author is to blame), the non-insignificant proportion of Canadian co-authors would like to emphasize that we are, indeed, “real-life”; although this may not have come across in the original submission (for which we do apologize), we have emphasized the fact that our case study is externally validated on the (very limited) set of data regarding the diet of Canadian mammals we were able to locate.

Associate editor

The manuscript presents an interesting study with promising results directed towards important future research. However, based on the following limitations, it would fit better to a methodological/theoretical journal, and an essentially different paper would only be acceptable for a top journal.

Response: We appreciate the frank assessment by the associate editor; as this manuscript was submitted as a “Methods” contribution, we did put the emphasis on the methodological novelty, which resulted in the text being heavy on the theory. We are especially grateful for the distillation of the reviewers concerns in four core points, which greatly helped in the revision process. We are confident that the thoroughness of our revision, and the results now presented in supplementary material, will establish that an updated version (albeit not a radically different one) is likely to meet the standards of *Ecology Letters*. We list below the main changes we made related to each main point, and have made far more extensive responses to each point in the actual reviews. Throughout this document, the line numbers correspond to the **track changed** document that was uploaded alongside the revised manuscript; please do note that due to the extensive nature of the revision, only the *new* text is present in the tracked changed version (bolded and in blue), and removed text has been hidden.

The presentation could be improved by providing a richer context of the problem,

Response: We assume that this comment is primarily motivated by the desire expressed by one reviewer to have a deeper presentation of the state of the art of network prediction. We do not think this would be appropriate given the number of additions we had to do in sections outside of the introduction; furthermore, we just published (a few months ago) a comprehensive review of network inference, in which we identify challenges that motivated this manuscript (see ll. 15 to 21). We now mention this in the discussion (see *e.g.* ll. 388 to 396), and point readers that want to read a detailed survey of the methods for network prediction (including the difficult question of validation of unstructured data) to the review.

Some major details of the approach need to be re-thought, like trait distribution,

Response: We have provided a justification for the uniform distribution (it is the maximal entropy distribution given only bounds of an interval, see ll. 241 to 250), and made a few manipulations to extract a normal distribution from the same data; as presented in Supp. Mat. 2, the normal distribution model does what reviewer 1 was afraid of, *i.e.* over-predicting interactions. Specifically, the figure in

the margin shows how the normal distribution model assigns strong probabilities to interactions that should be rare according to the uniform model; we discuss in Supp. Mat. 2 why this leads to overestimating some network properties. It notably predicts a lot of trophic interactions between basal species, which are ecologically unrealistic. We have therefore kept the uniform distribution for the manuscript.

One or several case studies should be used for testing/validating the approach,

Response: This was already the case in the original submission, but we did make this clearer at ll. 292 to 294: we externally validate the reconstructed Canadian metaweb on two independent datasets (GLOBI: 366 interactions, 33 missed, 91% success; Newfoundland: 25 interactions, 1 missed, 92% success). These two case studies show that we can identify upwards of 90% of the interactions, which is a very strong predictive ability.

A discussion should clarify the generality of the approach (whether its use is of more tactical or more strategic nature).

Response: We are unsure about what would make an ecological method tactical or strategic. Nevertheless, we have considerably expanded the definition of a metaweb (*i.e.*, how it can be operationalized, see ll. 45 to 71), and get back to this point in the discussion in the context of synthetic data inflation of empirical datasets (see ll. 365 to 372).

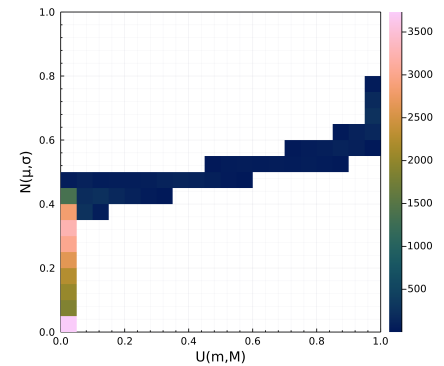
I see a change to transform the manuscript to a very good paper but also in its present form it is useful and appropriate to a minor journal.

Response: We hope that the responses to the reviewers, changes to the texts, and appendices, will establish that we took the revision process with the utmost seriousness, and that the revised manuscript will prove acceptable for Ecology Letters.

Referee 1

The Manuscript ELE-01066-2021 addresses the important question of how to infer species interactions and inherent networks. Authors used machine learning algorithms to this end, using a foodweb of European mammals as training datasets to make predictions on potential foodweb involving Canadian mammals. Results indicate that the algorithm has a good predictive power, although it largely tends to overestimate uncommon interactions. Authors conclude that colonialism and nationalism are detrimental to biodiversity.

Response: We are glad that the reviewer recognizes the good predictive power of our approach. We would like to challenge the claim that we over-estimate uncommon interactions, for at least two reasons. First, the output of our analysis (the metaweb) is probabilistic by design; this implies that we can describe an



interaction as “being here”, but we can moderate this statement by (essentially) saying that it is present with probability p , which strictly speaking represents the chance of success of a Bernoulli trial. We have modified most of the introduction to expand on the original definition of a metaweb (ll. 49 to 55), explain how it has been used in other systems (ll. 60 to 66), and why adopting a probabilistic vision of it is a more cautious approach (ll. 66 to 71). Second, it is expected that uncommon interactions (by which we mean, more difficult to observe in nature) are going to also be less represented in interaction data stemming from observation, despite possibly being over-represented in nature. We have added a paragraph to the discussion, at ll. 353 to 372, to expand on this point.

This is a nice study that sheds some new light into a fascinating problem in ecology, that of inferring species interactions. Although the phenomenological nature of the study and the black box of machine learning do not allow us to understand WHY nor HOW, the algorithm made the correct inference most of the time. I enjoyed reading the paper and I admire its concise way in highlighting the main methodologies and their relevance. This paper will certainly be of interest to ELE readers.

Response: We are glad that the reviewer found the article concise and enjoyable to read; we certainly worked hard at making the text accessible. We do recognize that the algorithm is, in a sense, a black box. Not so much in that it relies on mathematical concepts that are obscure, but in that the mechanisms used for inference are not necessarily ecological. This being said, there have been a number of interesting results in the ecological modeling forecasting that show mechanisms-free models outperforming models based on ecological knowledge: this has notably been shown for forecasting of spatio-temporal data; we have updated the text at ll. 140 to 148 to reflect this. Taking a broader perspective, a common saying in machine learning is that data are “unreasonably effective”; we discuss this statement at the place cited above, as it has an important implication: accurate algorithms are very often able to “learn” the mechanisms, even if they do not do so in a way that is epistemologically transparent. Finally, we discuss the role of AI/ML algorithms as data generators in the discussion, specifically ll. 365 to 369. As an aside, our method is no more of a black box than a PCA; indeed, as we now mention in the text at ll. 131 to 133, PCA is a special case of SVD, and so ecologists should be familiar with the concepts.

I have some suggestions that shall improve the clarity of the manuscript and the strength of its claims.

Response: We have addressed all of these suggestions, and thank the reviewer for them.

It sounds like authors are reinventing the wheel. Please provide a more thorough introduction to current methods and knowledge on predicting ecological networks.

Response: The field of ecological networks prediction is relatively novel (at least when it comes to producing interaction-level predictions). It has been very recently reviewed by Strydom et al. (2021), now cited in the introduction at ll. 15 to 21; this review identified a number of challenges for the field to solve in order to move forward, which we discuss in the first paragraph, thereby outlining

how our approach can be useful. We are confident that this will provide readers with a stronger justification for why our approach is solving problems that are not currently solvable.

Especially, the submitted manuscript looks scarily similar to that of Runghen, R. et al. (incomplete reference in the list). Such similarity poses some doubts regarding its novelty and originality. Also, the literature cited is quite self-referential.

Response: We have clarified the Runghen 2020 et al. citation at ll. 171 to 175 — their aim was to predict human movement from external metadata. We hope that this clarifies how different our method is. We agree that the literature is in part self-referential; this is because this manuscript is part of a larger research program, and originated from two synthesis workshops; we are pleased to note that the reviewer has not identified citations that were not justifiable, or citations that were missing, suggesting that we are crediting ideas appropriately.

Some fundamental information is missing. This current paper must be self-contained. Please provide more information about the European network: which community, species interaction type, ecosystem, biome, climate, spatial extent, time scale. Authors cannot force readers to go get such information somewhere else.

Response: In addition to keeping the original citation to both the data and the manuscript describing them, we have expanded the description of the European metaweb further, by outlining how the metaweb was assembled, which species were considered, as well as the geographic extent; these changes have been made in the manuscript at ll. 88 to 94.

Trait distribution. Please run the model using a normal distribution instead of a uniform one. Why did you chose a UD?

Response: We picked a uniform distribution because it is the maximal entropy distribution available when the two parameters known are upper and lower bounds for a series of random deviates, which is the case for the ancestral character estimation model we used; we now mention this information in the text at ll. 239 to 244.

“Traits” are NOT uniformly distributed at all. How does this affect the estimates? Please provide new results.

Response: As per the previous suggestion, we added a series of simulations using a node-level normal distribution. The inference of the normal distribution parameters was done by converting the lower and upper bounds of the random uniform estimates at a 95% confidence interval, and turning this into a standard deviation (the mean is simply half the sum of the bounds, and invariant w.r.t. the confidence interval width). As we explain in Supp. Mat. 2, the normal distribution model makes wildly unrealistic predictions. First, it over-estimates the number of interactions, but it also assigns higher probabilities to all possible interactions. As can be seen in the figure in the margin, this leads to the network inferred under the Normal model to have extremely high connectance. We share the concern

expressed by the reviewer of not over-estimating uncommon interactions, and using a normal distribution model would do just that. We have mentioned the existence of the Supp. Mat. in the text at ll. 244 to 247, but have not discussed the normal model further. We also show in Supp. Mat. 1 that RDPG is extremely good at eliminating spurious interactions, making us extremely confident that we are not over-predicting interactions.

Furthermore, please do not create false expectation in the reader by continuing referring to traits when, in fact, those are just node topological properties. Please mind the difference between a node degree and a species trait; here, there are no actual functional nor phenotypic traits, being node degree rank a purely topological property.

Response: There is some semantic confusion for which we apologize; we use “traits” to refer to latent variables. For an epistemic standpoint, latent variables have no meaningful differences from empirical measurements, but in order to minimise the chances of mis-understanding, we have replaced “traits” in this context by “latent variables” throughout. We nevertheless would like to gently push back on the idea that we are *creating* false expectations: we would like to assure the reviewer that no word in this manuscript has been written in bad faith.

Manuscript structure. Intro and discussion are quite sterile, they miss the point. The state-of-the-art is not presented thoroughly as it does not build on what we do and know so far.

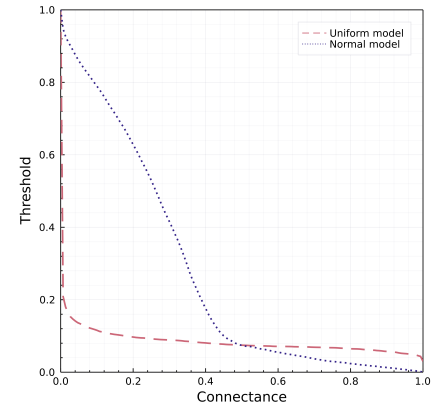
Response: The changes to the introduction, linking it to the recent review on prediction (in the very first paragraph), as well as suggested by other reviewers, will hopefully prove sufficient to alleviate this concern. We would like to note that we are operating under strict word count guidelines, and have preferred to add details to the results and methods when required.

Furthermore, the discussion is a complete separate piece, a random digression detached from the rest of the manuscript. Linked to that, the conclusion, although I truly love it, is quite out of context. Please seriously improve those parts.

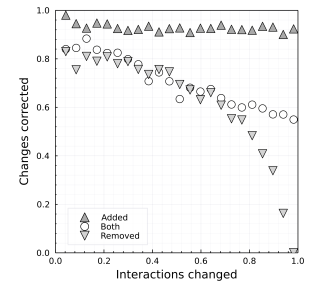
Response: We have modified the flow of the discussion according to the very helpful comments the reviewer made in the annotated PDF of the article, notably by adding a paragraph on why we expect most interactions to be rare and why AI/ML can help (ll. 353 to 372), clarifying the limits to the use of inferential techniques (ll. 399 to 410), and developed the argument for which arbitrary boundaries to species pool are sub-optimal (ll. 416 to 436), the later being done both from a methodological and socio-cultural standpoint. We are confident that the flow is now much better.

Please discuss your results in light of your large overestimations.

Response: As we answered previously, and as Supp. Mat. 2 (and to a lesser extent, 1) shows, we do not think that we are over-estimating by a large amount.



In fact, the marginal figure (from Supp. Mat. 1) shows that RDPG can almost always remove false positive interactions that were artificially introduced in the data. This being said, we have clarified that the metaweb implies that all interactions, even the very rare ones, should be considered, and that this is especially true in a probabilistic metaweb (introduction; ll. 67 to 71). We revisit this question in the discussion (ll. 353 onwards).



Figures 3 and Fig. 6c are of bad quality. Please improve them.

Response: We have re-drawn a number of figures in the process of this revision; lacking substantive advice as to what made the figures bad, we can only hope that these changes will satisfy reviewer 1.

Referee 2

This is a novel paper which uses phylogenetic signal as a way of constructing food webs from community composition data. The approach is illustrated constructing a Canadian mammal food web by drawing on European data. The paper is well written and of an appropriate length. The approach is well described in a clear way.

Response: We are glad that referee 2 recognizes the novelty of our approach, and found the manuscript easy to follow.

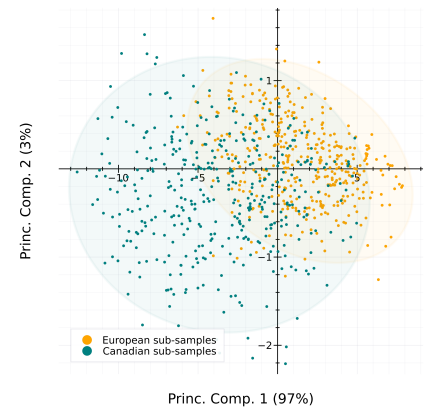
My concern with these modelling approaches (and the broader use of metawebs) is that is that the approach itself is a very conservative one which will tend to ‘average out’ differences across locations.

Response: This is a valid concern; but getting back to the definition of a metaweb as introduced originally by Dunne (2006; cited in the text at l. 50), a metaweb *by definition* averages out differences across location. Functionally, it serves as a “regional interaction pool”, and so captures the γ diversity of interactions, whereas local food webs (termed “metaweb realizations”) represent the α diversity of interactions. We have clarified this distinction when introducing the concept of a metaweb at ll. 45 to 58. We also provide some elements of answers to the legitimate question of “Why then do we need a metaweb?”, specifically at ll. 59 to 64. Furthermore, drawing on a recent review of network prediction challenges, we discuss at ll. 369 to 372 the fact that having a metaweb can be used to facilitate the prediction of local food webs; this last point, indeed, remains a formidable challenge that our method is not intended to solve.

Because the paper does not have an associated case study showing that it can actually detect differences in food web structure between places or times, the risk is that this is a method which allows an increase in the number of food webs - while at the same time predisposing them to all look identical.

Response: We would like to respectfully push back on the statement that the paper lacks a case study; indeed, the bulk of the manuscript *is* a case study,

specifically of producing a list of trophic interactions in a species pool for which we do not have this information. A case study like the reviewer asks, while undoubtedly interesting, would require several metawebs of mammals, which we do not have at the moment. The concern about all networks becoming identical is an interesting one. On one hand, we suspect this to be the case (see the discussion at ll. 38 to 40 showing the existence of various food web structural backbones). On the other hand, studies using metawebs have shown that they exhibit some degree of variation when spatially downscaled; this is the case for examples now listed at ll. 64 to 66. To check that different species pools would not result in networks with the same structure, we provide a simple simulation as Supp. Mat. 3 (cited at l. 273), wherein we sub-sample the Canadian and European species list, and show that there exists a distribution of network structure in a multi-variate space, both within and across regions. This result is reproduced in the figure in the margin.



The second issue is to do with when and how the phylogenetic signal would be most robust at predicting trophic interactions. Presumably systems dominated by generalists and with high phylogenetic overlap with the region generating the predictions will be very reliable in predicting food webs. However for areas with high endemism and limited species pools which may have favoured specialisation I am less convinced. Is it possible that some metric of phylogenetic relatedness across the metaweb should be reported in carrying out this kind of modelling .

Response: The information was present in the original manuscript, specifically at ll. 112 to 117. Quoting from the manuscript: “After taxonomic cleaning and reconciliation as outlined in the following sections, the mammalian European metaweb has 260 species, and the Canadian species pool has 163; of these, 17 (about 4% of the total) are shared, and 89 species from Canada (54%) had at least one congeneric species in Europe. The similarity for both species pools predictably increases with higher taxonomic order, with 19% of shared genera, 47% of shared families, and 75% of shared orders; for the last point, Canada and Europe each had a single unique order (*Didelphimorphia* for Canada, *Erinaceomorpha* for Europe)”. No changes were made.

As with the use of metawebs, my concern is that some of the most interesting ecology would be obscured by constructing food webs in this way.

Response: We hope that the clarification of the metaweb concept and its usefulness, and the demonstration of changes in Supp. Mat. 3, will have alleviated this concern.

What I would really liked to have seen was a case study which showed were a set of food webs had been able to show a clear ecological pattern (e.g. David Post’s lake food webs showing relationships with size and productivity), reconstruct those food webs using the modelling approach and show that the pattern was still evident, and not averaged away by the process of inferring the food webs.

Response: An important step of our pipeline is to compare our prediction to data from Strong & Leroux (2014) and GLOBI data (see at ll. 295 to 302), which is exactly similar to what the reviewer suggests. We reach a very good predictive

accuracy on these datasets (resp. 91% and 92%), suggesting that our method is able to make correct inference on the structure of the food web. In addition to Supp. Mat. 3 on structural variation, and Supp. Mat. 1 on the ability to estimate network properties from an RDPG, we are confident that this concern has been addressed.

Referee 3

In this study, the authors developed a data-driven framework for the prediction of unknown ecological networks. Specifically, as far as my understanding, the analytical procedure is as the following three steps. First, for a known ecological network (food web of European mammalian in this case), the latent generality trait (i.e., prey species composition) and vulnerability trait (predator species composition) are extracted by performing t-SVD of the interaction (adjacency) matrix. Then, the generality / vulnerability traits of species in the other community with an unknown network structure are estimated by mapping the extracted traits of the known community onto global phylogeny. Finally, left and right subspaces of the target community are probabilistically obtained based on the estimated generality / vulnerability traits: multiplying these subspaces yield the probabilistic network realization of the unknown community. Applying this framework to the established European food web and mammalian phylogeny, the authors reconstructed the hitherto unknown trophic network of Canadian mammals.

Response: We are grateful to the referee for a very succinct summary of our manuscript; although this information was present in the caption of Figure 1, we understand how valuable it can be to guide readers, and have adapted parts of it to add to the introduction.

Overall, I agree with the ecological importance of the topic covered in this study (i.e., how to infer the network structure of an ecological community where there is poor knowledge or lack of direct observations of species interaction). However, the text is hard to follow, and I feel there is room to revise, especially for its presentation.

Response: Based on comments by all three reviewers, we have greatly improved the presentation of the manuscript, and we hope that it will prove appropriate in its revised form. We paid specific attention to smoothing out some transitions in the methods. Most importantly, we now emphasize at ll. 131 to 133 that SVD is a general case of PCA, a method with which ecologists are very likely familiar. We hope that this will help develop a better instinct for how our method operates.

For example, the authors used RDPG (random dot product graph) to obtain the latent feature subspaces, but I didn't know anything about this method, so I couldn't understand how it relates to SVD from the text alone. Thus, I suggest the authors add the text that explains the concept of the RDPG (e.g., this assumes that interaction occurs more often between the species with similar functional traits) and that SVD is a promising method to provide these functional traits from the observed network data. Similar incomprehensible points may be found in the Methods.

Response: We thank the reviewer for pointing out this issue; RDPG is a simple trick to transform the three matrices \mathbf{U} , $\mathbf{\Sigma}$, and \mathbf{V}' of the SVD into two, defined as $\mathbf{L} = \mathbf{U}\sqrt{\mathbf{\Sigma}}$ and $\mathbf{R} = \sqrt{\mathbf{\Sigma}}\mathbf{V}'$, so that the underlying original matrix can be reconstructed through the matrix multiplication $\mathbf{L}\mathbf{U}$. We have added this information at ll. 196 to 198. In particular, we realized that we had re-used L and R for both the the SVD and RDPG subspaces, and have changed the notation to remove the ambiguity. As we clarified across the manuscript following comments from reviewer 1, the “traits” here are more accurately described at latent variables, but their similarity is indeed a predictor of the expected similarity of interactions.

In addition, I am wondering if all the results are described correctly. Specifically, the authors assert that the reconstructed Canadian food web recovers over 95% of known interactions by comparing databases of recorded pairwise interactions. However, I found no corresponding description in “Results and discussion of the case study” section (and also “Data cleanup, discovery, validation, and thresholding” section). Thus, if the result exists, please add it to the appropriate part and otherwise remove the description from the abstract.

Response: These results were already present in the text, but we have clarified their presentation at ll. 295 to 302. The taxonomic breakdown of which taxa are shared, was present in the original submission, see ll. 112 to 117.

Minor comments:

L119–120: The logic is unclear. Is there any assumption that a list of prey and predator species tend to be similar among closely related species? Please clarify.

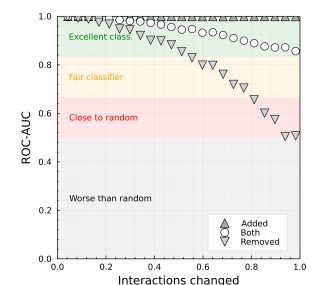
Response: This is correct; we have clarified this concept at ll. 22 to 23.

L143 & 296: ‘a’ RDPG -> an RDPG?

Response: We thank the reviewer for this comment; it turns out that since RDPG starts with the sound “ä”, “an” RDPG is the correct form. We have corrected throughout.

L150–153: Did you use all the data in the European metaweb for an interaction presence/absence classification analysis? If this is true, overfitting may occur in determining the threshold for interaction probability. Thus, I suggest the authors adopt some approaches to avoid overfitting, such as the cross-validation methods.

Response: We did indeed use all the data from the European metaweb in order to produce the left and right sub-spaces for the transfer step. Based on this comment, we have produced Supp. Mat. 1, in which we show that even with up to 40% of interactions withheld, the binary classifier remains highly accurate; furthermore, we show that the threshold identified responds to network completeness of sampling, and that for reasonably well sampled networks (as the European metaweb is, see ll. 88 to 94 and references), the structural properties of the reconstructed network are within a very narrow range of what they actually are. We are therefore confident that the risk of overfitting is minimal. An example of the results from Supp. Mat. 1, specifically showing that RDPG maintains a ROC-AUC even with extreme data perturbations, is presented in the margin.



L247–249 & top panels in Fig. 6. I consider these results are algebraically self-evident. Specifically, 1st left and right singular vectors correspond to the direction with the highest variance for the row- and column-wise elements, respectively. That is, elements with greater contribution to these 1st singular vectors tend to have larger values for the row or column vector in the original matrix. Therefore, I think these results provide no novel information, and a simple statement of this should suffice.

Response: We do feel like these results can guide the reading of the manuscript; furthermore, the situation would look a lot different from an entirely modular network (for example), and so we have made no changes to the manuscript.

L301–304. In addition to the authors' mention, I think biased information of species interactions toward specific behaviours or ecological relationships may significantly limit such approaches. As you know, there are various types of ecological relationships, such as competition, mutualism, etc. However, for many of them, species interactions have not yet been studied as much as for trophic relationships (e.g., Kéfi et al. 2012, Ecol Lett). Furthermore, a recent study implied that, even in a community that has been studied as a prey-predator system, various unanticipated interactions (these might not be trophic ones) play a significant role in its dynamics (Kawatsu et al. 2021, Ecol Lett). Applying the approach proposed in this paper to such a system would result in biased predictions. Please discuss this point in the manuscript.

Response: We focused the case study of food webs, because the European metaweb was available and of a sufficiently high quality to establish the robustness of the method. That being said, our discussion of metawebs at ll. 64 to 66 now includes non-trophic examples. We have cited the references suggested by the reviewer in the introduction (ll. 82 to 86).