

**Point-by-point responses to Reviewer comments and additional edits for
NCOMMS-19-28516A by Yeakel et al.**

Reviewer Comments:

Reviewer 1:

General Comment: The authors have done a great job in revising the manuscript. I agree that it is reasonable to keep the model simpler at this stage (inclusion of the engineering impact). It was a pleasure to read this interesting piece of work and I believe that a better understanding of ecosystem engineering at the network level is so far lacking therefore this contribution is a necessary step.

General Response: We thank Dr. Sanders very much for his constructive feedback regarding our manuscript.

Reviewer 2:

General Comment: It is the second time that I review this manuscript. The authors have made a very thorough revision and written an equally thorough Response to reviewers. The main concerns in the first round of review included insufficient and/or unclear Introduction and Method description, inconsistencies in some graphs and between some sections, and unconvincing/speculative result mechanisms; the authors have addressed all these concerns to great satisfaction. After the second round of review, I have only 11 comments, which are all minor and easily addressed. The resulting revision would be very minor and do not, in my opinion, necessitate another round of peer review. I can now wholeheartedly recommend this manuscript for publication in Nature Communications.

Manuscript and review summary:

This manuscript presents an ecological network assembly model, able to include feeding interactions, service interactions, and interactions mediated through ecosystem engineering. The authors analyze the model's performance, i.e. the realism of the generated network structure; they explore how structure and stability are affected by service interactions (mutualisms); and, finally, how engineering affects stability (primary and secondary extinctions; persistence; species richness at steady state).

There are four main claims. Firstly, the assembly model results in interaction networks with structures consistent with empirical observations. Secondly, increasing the frequency of mutualisms, in networks with feeding and service interactions, results in a more nested interaction structure at steady-state species richness and a lower average persistence of species in the network. Thirdly, ecosystem engineering tends to decrease primary and secondary extinctions (somewhat dependent on the frequency of engineering and service interactions). Fourthly, engineering redundancies (more than one species engineer the same entity) increases steady-state species richness through the facilitation of colonization.

To my knowledge, the main claims are novel, particularly with regards to the effects of ecosystem engineering, and are well supported by the presented data. The paper is timely and connects to the growing interest in non-trophic interactions and how they affect network structure and dynamics. The paper will certainly interest researchers in network ecology and is likely to influence thinking in the field.

For the reasons outlined above, I recommend the paper to be considered for publication in Nature communications. Due to its timeliness, novelty, and likelihood to garner interest, it is a very good fit for the journal.

Additional points:

- The manuscript is clearly written.
- I do not consider any further “experiments”, i.e. simulations, to be necessary.
- The manuscript cannot be shortened much.
- The authors have done themselves justice without overselling their main claims.
- As far as I can tell, they are fair in their treatment of previous literature and discuss their claims appropriately in the context of previous literature.
- The authors have provided sufficient methodological detail for the experiments to be reproduced.
- There are no statistical analyses of the data, only summary statistics. Statistical analyses are not strictly necessary here.
- There are no special ethical concerns.

General Response: We thank Dr. Curtsdotter very much for her incredibly helpful and detailed feedback on our manuscript. We would like to note that her efforts were above and beyond what is typically expected of a reviewer, and our manuscript has benefited immensely in both its clarity and content. Our sincere gratitude!

Specific Comments

Assembly without ecosystem engineering

Comment 2.1: Lines 162-163: Though the use of the term “basal resource” has been much clarified through the author’s revision, I suggest changing “basal resource” to “abiotic basal resource” to preclude any misunderstanding.

Response 2.1: We have incorporated the suggested edit.

Comment 2.2: Lines 176-178: Please specify here that a species’ competition strength is penalized by the number of its potential resources (i.e. number of resources in the pool) and the number of realized consumers (i.e. number of predators in the local community). I am aware that this is stated explicitly in the Methods, but I strongly recommend including it here in the main text, as these pieces of information are critical for understanding the effects of (low levels of) engineers on extinction rates. The suggested mechanisms for

these results (lines 395-422), do not make sense without this information. I had a whole comment written up about it, before something clicked in my head and I remembered this small but critical detail...

Response 2.2: Yes - thank you for pointing out this omission. We have now included this clarification. We note that for need interactions, the realized and potential interactions are the same, so we have not included that distinction with respect to services. The sentence now reads:

Line 169: *"A species' competition strength is determined by its interactions: competition strength is enhanced by the number of need interactions (where the number of potential and realized interactions are equivalent) and penalized by the number of its realized resources (i.e. those resources present in the local community, favoring functional trophic specialists) and realized predators (i.e. those predators present in the local community).."*

Comment 2.3: Lines 205-209: I suggest the authors to add one sentence to spell out to the reader what the point is of the comparison between their assembly model and the niche model. In the Response to Reviewers they state that this is to show that their assembly model produces structures relevant to the real world and to provide a reference point to studies using the niche model. I would simply like to see the author's to spell this out in the main text to the benefit of the reader, as it is not obvious how the comparison of network structures generated by two different models fit into the preceding comparisons of the assembly model network structure and empirical network structure. (This suggestion is similar to my original comment (2.8 in the Response to Reviewers), but I want to make clear that I agree with the author's in a) keeping the comparison in the manuscript, and b) keeping the vast majority of the comparison in the Supplementary (Appendix 3).)

Response 2.3: Thank you for this feedback. We have modified this section to read:

L203: *"In Supplementary Note 3 we include a brief comparison of assembly model food webs with those produced by the Niche model \cite{Williams2000}. While the aims of these approaches are quite distinct, we provide this comparison as a reference point to traditional food web models, and to emphasize that both approaches result in food webs with similar structures (Supplementary Figures 2,3)."*

Comment 2.4: Lines 236-238: Here the authors write "The dominance of functional specialists early in

the assembly is primarily due to the initial colonization by autotrophs." In my first review, I asked whether this did not make the result an artifact, as there is only one abiotic basal resource for the autotrophs to feed on, so they cannot be anything but functional specialists. In the Reponse to Reviewers, 2.12, the authors agreed there was an issue here, and that their analysis was missing the point. One of the changes they made to address this, was to include only consumers in the analysis of specialism/generalism. If

they included only consumers, then the importance of functional specialists early in assembly cannot be driven by the autotrophs; unless for some reason herbivores are allowed only one autotroph prey? Is this paragraph perhaps an overlooked remnant from the first version of the manuscript? Also, if the autotrophs have been excluded from this analysis, please state that in the text, for example around lines 213-219.

Response 2.4: We agree with the Reviewer and note that the description of concern was indeed left over from the previous version of the manuscript. We have amended the following sentences to read:

Line 218: *“Only trophic links between species are considered here, such that we ignore links to the abiotic basal resource in our evaluation of trophic generality.”*

Line 239: *“The dominance of functional specialists early in assembly is primarily due to the initial colonization by consumers with few resources.”*

Figures in main text

Comment 2.5: In Figure 4, there is a brief explanation of how the extinction rates and persistence are calculated. However, these metrics now occur already in Figure 3. I suggest to move or add this description to the figure text of Figure 3.

Response 2.5: We have now amended Figures 3 and 4 to be consistent in how they define primary and secondary extinction rates and persistence.

Comment 2.6: In Figure 4d, I suggest inverting the color scale (but keep the response variable as it is now). For these figures, the authors followed my suggestion to inverse the response variable for more intuitive reading. However, in doing so they seem to also have inverted the color scale, such that lighter colors indicate higher values and darker colors lower values. Unfortunately, in all the other subplots, in the same and other graphs, lighter colors indicate lower values and dark colors higher values. This singular deviation in the otherwise consistent color coding makes reading the subplot non-intuitive and opens up for misinterpretation unless the reader is careful. Now, this is obviously not a major issue, and I feel almost petty in pointing it out, but I also feel somewhat responsible for the issue as it happened as part of the authors, on my suggestion, trying to make the graph more intuitive to interpret!

Response 2.6: :) We appreciate the Reviewer’s attention to detail and have reversed the color scheme accordingly.

Supplementary Information

Comment 2.7: I suggest that the authors, simply for greater transparency for the less mathematically minded, change equation S2 to $pm = \eta S(S+M)^2 = \eta S(1+\eta-\eta e)^2$, to clarify the definition of realized and potential links. If I got the initial step wrong, i.e. how the realized and potential links were defined, please correct it, of course.

Response 2.7: We have included the suggested intermediate calculation.

Comment 2.8: In Appendix 2, I suggest including the Reponse to Reviewers 2.16 and 2.46. With regards

to 2.16, the authors have improved the main text in this point, but the authors Response clarifies it further. I do not recommend putting this explanation in the main text, but it would be a valuable contribution to the Appendix. With regards to 2.46, it states explicitly how the replicates were created. Though in retrospect it seems obvious, it wasn't after my initial read of the manuscript, so for transparency I would included it in the Appendix.

Response 2.8: Agreed. Supplementary Note 2 now includes these clarifications.

Supplementary figures

Comment 2.9: There are some inconsistencies in the figure text and labels in Figure S5. In the plot a-axis

titles for mutualism it says "Mutualism in-degree (service receivers)" and "Mutualism out-degree (service donors)". Similarly, in the the figure text it says "mutualism in-degree (the number of service receivers a species has) and out-degree (the number of service providers a species has)". However, this definition of mutualism in- and out-degree clashes with the later sentence in the figure text: "As the mutualism in-degree increases, so does the number of service donors that are needed for the receiving species to remain in the community." Furthermore, the results show that species persistence decreases with a species' mutualism in-degree, while it is unaffected by mutualism out-degree. This would be consistent with the definition of mutualism in-degree being number of service donors a species has (i.e. the opposite of the definition in the figure labels and text); the more donors it has the greater is the risk for secondary extinction. This is exactly the argument the authors make in the main text, when referring to Figure S5. I'm guessing the authors got the definitions confused when labeling the figure and writing up the figure text, so it's an easy fix.

Response 2.9: We thank the Reviewer for catching this and have fixed the discrepancy.

Comment 2.10: I suspect the first sentence of S6 figure text is a mistake. It says that the pool consists of

200 non-engineering species, but it shows the result for networks with modifiers and engineers in it, so the pool must contain engineers.

Response 2.10: Correct - this mistake is now fixed.

Comment 2.11: In figure S9, subplot d has been updated with the inverse of the response variable, but

the figure text has not been updated to reflect this change. According to the color bar, the response variable is S^*/S_u^* , but in the figure text the description is still for S_u^*/S^* .

Also, comment 7, about the color scheme of Figure 4d, applies equally to Figure S9d.

Response 2.11: Another great catch. This has now been fixed and the color scheme has been updated.

Additional changes to the manuscript:

- 1) The title has been changed to that suggested by the editor
- 2) The abstract has been shortened to 164 words
- 3) The third paragraph of the introduction has been partly removed and partly merged with the second paragraph, as it was largely repetitive and ill-placed.
- 4) Minor changes to grammar throughout and general formatting to conform to NatComm guidelines