**Line references in Responses are based on the track change version**

**Reviewer: 1**

Comments to the Author

Overall comments:

This paper is well-written and is on a topic that will be of interest to almost all readers. The author’s objectives are pretty clearly spelled out and their methods are fairly appropriate. However, I do question how much of a real contribution this paper makes. There are some methodological modifications that could help alleviate some of these concerns.

1. Including dam rate as a variable greatly weakens the analysis, in my opinion, and paints an overall picture that bigger networks are inherently better. The result is that the reader can be left with an “I already know that” feeling. The authors go to great lengths to explain that the larger and more connected networks are also the most impacted. I think that a more valuable approach would be to consider this type of scenario (sans-dam rate variable) as a historical analog and instead provide a parallel analysis in which dams completely (or partially) sever connectivity. This would also provide the additional benefit of showing which networks are most impacted.

Response: We respectfully disagree that including dam rate as a variable greatly weakens the analysis. In our view, this variable is necessary because it *penalizes* networks with more abundant dams and thus reduces connectivity scores for dammed networks. Therefore, although we explain that larger networks tended to have higher connectivity scores, this is despite dams and reflects the overall size and structural complexity of these networks. This does not necessarily mean that large, complex networks are inherently better, but rather that only large, complex networks have the capacity to support large-scale migrations and range shifts. We acknowledge that smaller networks are still ecologically important for many reasons, particularly because they tend to have fewer dams (e.g., lines 443-453).

We considered the suggestion for a historical analogue analysis without dams. However, we note that the original lake-stream networks are already based on the spatial arrangement of lakes and streams without the influence of dams (aside from the fact that dams created some lakes or altered the hydrology of some lakes and streams - correcting for these effects would not be possible at the continental scale). As such, our approach was designed to show which networks are most impacted (dam rate variable), as you suggest. We specifically added a line in the discussion that our analysis indicates not only which networks are most impacted, but also those likely to benefit from restoration (lines 457-459).

Finally, we also considered a parallel analysis in which dams completely or partially sever connectivity. Although we agree that this is useful, this essentially has already been done (Cooper et al. 2017; <https://doi.org/10.1016/j.scitotenv.2017.02.067>). The dam dataset used in their study also served as the basis for dams in our dataset (LAGOS-US-NETWORKS). We added a citation to the Cooper paper in line 120. Given that this study focused on stream reaches (i.e., links), it therefore made sense for us to focus more on lakes (explained in more detail in lines 144-151). This is part of why we chose the hub lake approach - if these important nodes are compromised, by definition, these networks become fragmented. Therefore, identification of hub lakes shows which networks are susceptible to fragmentation based on their structure. However, we agree that the presence of dams at or near hub lakes would be especially important for (or detrimental to) network connectivity, so we added information on this in lines 149-151.

2. The ecological justification for using lakes as hubs is weak, yet the entire paper is premised on the idea that this is a valuable and worthwhile analysis. The authors rightly point out that geometrically lakes resemble nodes and stream reaches as links, but is that ecologically meaningful? The authors could and should do more to justify their use of this approach, especially in the introduction. Are there groups of species (either taxonomic or functional groups) that are more likely than others to benefit from this approach?

Response: We had to designate either lakes or streams as nodes to apply a graph theory framework. This is not to say that hubs must always be lakes; we acknowledged that other studies may choose the opposite based on their unique circumstances or objectives (lines 147-149). Our previous response further justifies our decision for lakes as hubs in our particular study.

In the methods, we provided further justification for how our connectivity variables are relevant for both slow- and fast-dispersing taxa, as well as how this is essentially what is commonly done in coarse-filter studies focused on structural connectivity (lines 235-239)

3. Many of the results focus on whole network comparison (comparisons between basins). I find these to be some of the least interesting results and a stronger focus on individual hub lakes (node strength) would be more interesting, from my perspective. What can we do to preserve these lakes? Which lakes are most detrimental if lost? The flip side is which lakes could have connectivity restored? Link importance is also ignored in this study but is also quite important. The authors are already quite familiar with many of the tools that can be used to rank node importance (e.g. Santiago Saura’s Conefor software or the iGraph package in R).

Response: Although whole network comparisons may be less interesting results, no studies have described freshwater network structure and connectivity at the conterminous US scale based on both lakes and streams and thus we felt it necessary to report this information.

In essence, hub lakes are highly important nodes based on multiple network structure variables (must be articulation point, have high betweenness centrality, and have high vertex strength). Therefore, by identifying hub lakes, we have identified highly important nodes - nodes that if maintained/restored would benefit network connectivity - but also nodes that if compromised damage network connectivity. Although we mainly focused on the number and location of hubs nationally and within networks, we also reported the dammed/undammed status of hubs (lines 358-361).

We did not consider link importance in this study for several reasons, but mainly because it was beyond our scope. Our paper is focused on identifying corridor networks (inherently consisting of both nodes and edges) that can support freshwater connectivity. In our network connectivity score calculation, we considered variables related to both nodes and edges. A secondary focus was identifying important nodes (i.e., hub lakes) for maintaining networks. This decision was based on the fact that previous freshwater connectivity studies have focused mostly on streams rather than lakes and rarely both (lines 120-124, 131-139, 144-151). The Cooper et al. 2017 paper we mentioned above is an example of this, as it focused on only streams and link importance. Notably, lakes in freshwater networks are commonly dammed and thus represent locations where connectivity is easily compromised.

4. The justification for using terrestrial protection for aquatic protection is a little weak. I understand that this is commonly done, but there could also be instances in which aquatic protection is decent despite poor terrestrial protection and visa versa. Obviously the reasons for doing this have a lot to do with the scale of the study and lack of aquatic protection datasets, but it would be helpful to have some additional sentences to explain this.

Response: We added some more text to the introductory paragraph about protected areas (lines 164-182). We mention how most past research has focused on representation of fresh waters in protected areas and shown mixed/limited benefits for freshwater biodiversity, but has not focused on freshwater connectivity, which is a component of the Aichi biodiversity Target 11. Whereas other studies have shown that Target 11 has been partially achieved for fresh waters, no studies have looked at connectivity explicitly. We sought to fill this research gap by focusing on connected networks and critical nodes for network connectivity (hubs).

We also explain in the methods how we nuanced the idea of “protection” for fresh waters to incorporate both protection of waterbodies themselves and watersheds, as well as different levels of legal protection (lines 296-308).

Detailed comments are included in the manuscript.

Response: We appreciate both the high-level, general comments in addition to the detailed line comments.

Line 27: Maybe this kind of terminology could be incorporated into the title?

Response: We agree that this would make the title more descriptive. We added the phrase “lake-stream networks” to the end of the title.

Lines 37-39: Dammed and undammed connectivity aren’t really compared in this analysis, correct?

Response: Not explicitly, but we quantify the prevalence of dams across all networks and added a reference to a previous study that compared dammed and undammed connectivity using essentially the same dam dataset (Cooper et al. 2017) (explained in more detail in responses to general comments above).

Lines 49-50: Check the number of keywords against journal requirements.

Response: The journal allows 6-12 keywords/phrases and we currently have 10.

Line 97: Check journal requirements. Subheadings in the introduction are rare in most journal papers.

Response: Although the journal does not prohibit subheadings in the introduction and we simply intended to help guide the reader, we have removed this and other subheaders in the introduction.

Lines 150-152: However, I would argue that freshwater ecology is ahead of terrestrial ecology in that it considers habitat restoration in a major way. In contrast, most terrestrial corridor efforts are focused on identifying the “best route” with less of a focus on what is needed to make the corridor feasible for the species to more through.

Response: Although the specific text in question here has been removed for text flow purposes, we agree with the overall point about differences in connectivity restoration in freshwater vs. terrestrial. We added text in the discussion about restoration of more natural hydrology for conservation purposes (lines 534-544)

Line 161: Usually you wouldn’t have this as a subheading. Check journal requirements.

Response: See response to comment about original line 97.

Line 199: How were nodes weighted? Or were they unweighted?

Response: We clarify this point in lines 224-228.

Lines 201-204: Needs expansion.

Response: We clarify in the reference to Table 1 that this table contains individual variable descriptions and justifications (line 228). We also provided more details about variables in lines 235-239.

Lines 201-204: Vertex strength needs to somehow be described in this section somewhere.

Response: We agree that vertex strength is an important variable; however, lines 235-239 describe the network variables and vertex strength is a lake-scale variable that was only used to identify hub lakes. We clarified in the section on hub lakes that we were referring to vertex strength when we previously referred to and defined node strength (lines 274-281).

Lines 205-207: Which variables? Please provide much more detail. Some variables are also dependent on an average dispersal distance. Did you use any variables that required parameterization?

Response: We clarified and provided more information on the ecological relevance of specific variables (including the average lake distance variable, which is relevant to average dispersal distance) and added another reference to Table 1 for the full descriptions (see lines 224-239). We did not use any variables that required parameterization, but added text in the discussion that this could be an option with specific taxa of interest (lines 577-580).

Lines 207-211: In general, this explanation needs to be explored much more than it is as currently written.

Response: We addressed much of this in the previous responses to other comments in this paragraph, but nonetheless please see the text in lines 222-241.

Lines 242-243: I’m not sure that this has really been sufficiently demonstrated. Given that many of these hubs are reservoirs and may have invasive species, altered temperatures, and altered flow regimes

Response: the key word here is “conceptually”, but we added the phrase “per graph theory” to emphasize that this has not necessarily been established (line 270). The discussion section starting on line 481 addresses previous studies of hubs in fresh waters, to which we added that our study is novel for its large spatial scale and widespread flexibility in biodiversity research. This discussion section also contains references to two freshwater studies that show the importance of hubs in patterns of biodiversity (Muirhead and MacIsaac 2005, Bishop-Taylor et al. 2015), but we note that these are landscape to regional scale studies. We also noted in lines 462-464 and 534-537 in the discussion the point about invasives, temperatures and hydrology.

Lines 262-264: GAP status is terrestrial, right? How do you justify using terrestrial protection when it may differ from freshwater protection?

Response: The text we added above about past research on freshwater representation in protected areas should help address this point (line 169). Here, we added that we are considering a range of definitions of “protection” to account for the fact that terrestrially-minded protected areas are not necessarily set up for freshwater ecosystems and that our focus is on connectivity in relation to protected areas, building off past work and investigating this aspect of Aichi Target 11 (lines 165-182).

Lines 299-301: It would be nice to actually see this reduction in numbers. See for example Dilts et al. 2016 that quantified different proposed renewable energy build-out scenarios as well as a scenario that excluded current land use (historical analog). A similar setup could be used to quantify stream networks including and excluding dams.

Response: As explained above, the Cooper et al. (2017) study essentially performs this based on dams and stream networks in the conterminous US. They showed the degree of network fragmentation that has occurred nationally due to the presence of dams and compared that to a scenario with no dams. Because this was already done, we do not see the need to repeat this analysis with virtually the same dam dataset; however, our approach using hub lakes similarly demonstrates which nodes, if removed or dammed, are likely to result in network fragmentation based on underlying network structure (lines 149-151).

Line 342: This isn’t really the most informative finding. See the earlier comment about issue with not including dams as fragmenting the networks directly. I think that you end up painting an overly optimistic connectivity picture if you do not consider dams in the network analysis.

Response: As explained in the previous response, we did not fragment networks based on dams because this would essentially repeat the analysis of Cooper et al. (2017). Instead, we analyzed overall structural connectivity of networks, which we quantified using the variables reflecting network size, complexity and susceptibility to fragmentation (described in more detail in Table 1 and lines 230-239). Although our analysis scored larger networks more highly because large networks span the climatic gradients necessary for ecological resilience under climate change, it is important to report that these large networks are heavily dammed (and thus scores are penalized for having large numbers of dams). In other words, the biggest networks are ecologically important, but their connectivity is heavily compromised. We address this notion further in the discussion section beginning on line 442, but specifically in lines 453-456.

Table 2: Sacramento/San Joaquin?

Response: We changed the network previously named San Francisco Bay to Sacramento/San Joaquin, as suggested.

Figure 3 caption: This is the first time that this is described, yet it is an important concept. Could you please define this earlier in the paper.

Response: In the methods, we used “node strength”, which means vertex strength. To avoid confusion, we switched that term to “vertex strength”. We define/describe the variable in lines 279-281 and have updated previous references of “node strength” to “vertex strength” throughout the manuscript to maintain consistent wording.

Figure 3 caption: I’m wondering if this needs to be a criterion or if it instead can be an outcome? I could envision some lakes in the middle of a long stream network that could be very important even if they are just located on a single stream stretch.

Response: We made articulation points a hub criterion because compromising them results in network fragmentation. Although we agree that a lake within a long stretch of streams may be ecologically important in some circumstances, that lake does not hold together and connect many subnetworks the way an articulation point does. If we made articulation points a descriptor of hubs rather than an input variable, we would essentially be reporting which hubs are articulation points and which are not. This would lead to the general conclusion that articulation point hubs are more important for network connectivity than non articulation point hubs. Therefore, we think it makes sense for articulation point to be a hub criterion rather than descriptor.

**Reviewer: 2**

Comments to the Author

1. Table 1 should be reformatted to make it easier to connect the “Description” and “Ecological Justification” with the appropriate “Variable name.”

Response: We removed some words to make the table more readable and inserted more spaces between rows. Our revision has both a track-changed and clean copy of the table.

2. The term “vertex strength” is used in the caption for Figure 3 but I could not find anywhere in the body of the manuscript where this term is defined or described.

Response: In the methods, we used “node strength”, which means vertex strength. To avoid confusion, we switched that term to vertex strength. We define/describe the variable in lines 279-281.

3. Lines 255-257: I do not understand what this sentence is trying to communicate. It begins with “…although we did not differentiate between natural lakes and reservoirs…” suggesting that the remainder of the sentence will be about some difference between lakes and reservoirs. However, the remainder of the sentence reads “…we reported differences in the prevalence of hubs between natural lakes and reservoirs for waterbodies ≥ 4 ha.” Hubs occur between lakes (natural or otherwise). So, are the relevant differences due to lake size (1 ha versus 4 ha)? Or are the differences between the prevalence of natural lake hubs versus reservoir hubs?

Response: We clarified that we compared natural lake hubs versus reservoir hubs in our results. We also added a sentence indicating that the 4 ha cutoff was due to the data source used, but that lakes < 4 ha were unlikely to be reservoirs (lines 284-293).

4. I don’t understand how the terms “freshwater networks” and “freshwater corridor networks” are being used in this manuscript. When/how does a “freshwater network” become a “freshwater corridor network?”

Response: We clarify in line 114 that freshwater networks consist of lakes, rivers and streams. We also clarify in line 188 that a corridor network consists of several local corridors.

5. I am unclear how PCA results were converted to connectivity scores, and how breakpoints were determined: <2 = low, 2-4 = medium, and >4 = high. Were all variables in Table 1 included in the PCA?

Response: We clarified in lines 252-254 that we used all variables in Table 1 in the PCA. We also clarified in lines 372-373 that cutoffs for low, medium and high connectivity scores were based on visual inspection of the score distribution (histogram; Fig. S2). We used the first two principal components to calculate connectivity scores (i.e., two dimensions with the Pythagorean theorem to calculate the distance from the origin along these two axes) (line 261). We did not deem it necessary to explain this level of mathematical detail, as PCA is an inherently multi-dimensional analysis in which points are plotted and integrated within a multi-dimensional place

6. Are dams factored into connectivity scores? Dam rate is one of the variables described in Table 1. However, in the Discussion (lines 414-417) the authors point out that the largest freshwater corridor networks contain abundant dams and may therefore limit “functional connectivity.” This suggests to me that dams are not fully considered in the computation of “structural connectivity” scores.

Response: We clarified in the previous response that we used all variables in Table 1 in the PCA, including dam rate. We mention in Table 1 and lines 256-259 of the methods that we used the dam rate variable to penalize networks for connectivity barriers, resulting in lower connectivity scores.

7. Do the methods for characterizing “protected” lakes or lake hubs take into account water withdrawals? Many of the western networks are highly stressed by water withdrawals, even as some of these, like the Colorado River, are characterized by a high amount of “protection.”

Response: This is a good point. Although we mentioned in the methods that we assumed static hydrology (line 248), we agree that water withdrawals and droughts can alter network connectivity, even when waterbodies are “protected”. We added lines expressing this in the discussion (lines 523-527).

8. The majority of lake hubs identified in this manuscript were reservoirs (77.7% of those that could be classified as either reservoirs or natural lakes; lines 318-319). I am not sure I am entirely comfortable labeling artificial lakes (reservoirs) as important hubs for freshwater network connectivity. Reservoirs exist because they are dammed, which disrupts freshwater network connectivity (acknowledged by the authors in lines 419-422). Reservoirs can also facilitate biological invasions (lines 424-425). I would add that reservoirs also disrupt stream network continuity by altering water temperatures, stream flow dynamics, and movement of sediment and woody debris. If a particular hub reservoir was to no longer exist, the restored river channel in that location would presumably be just as important as a hub, just not a lake hub, and the overall connectivity of the freshwater network would be enhanced. Thus, one could argue that to promote freshwater network connectivity, reservoir hubs should be removed, not protected. The fact that this is unlikely to occur (lines 426-429) doesn’t not negate the possibility that reservoirs may do more to disrupt freshwater network connectivity than to enhance it.

Response: This is also a good point. We added more discussion of the ecological impacts of impoundments at network hubs in lines 463-464. In this discussion, we point out how our analysis shows where additional impoundments are likely to cause more damage (i.e., at or near hubs). We also added more discussion on what connectivity restoration should look like - an emphasis on natural hydrologic regimes and mitigation of the negative effects of impoundments, particularly in a climate change context (lines 534-544).