

# Landscape diversity promotes landscape functioning in North America

Corresponding Author: Professor Pascal Niklaus

**This file contains all editorial decision letters in order by version, followed by all author rebuttals in order by version.**

**Attachments originally included by the reviewers as part of their assessment can be found at the end of this file.**

Version 0:

Decision Letter:

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Dear Professor Niklaus,

Please allow us to sincerely apologise for the long delay in sending a decision on your manuscript titled "Landscape diversity promotes landscape functioning in North America". It has now been seen by 2 reviewers, and we include their comments at the end of this message. They find your work of interest, but some important points are raised. We are interested in the possibility of publishing your study in Communications Earth & Environment, but would like to consider your responses to these concerns and assess a revised manuscript before we make a final decision on publication.

In particular, please ensure that your revised manuscript meets the following editorial thresholds:

\*Clarify your experiment design and statistical analysis.

\*Consider the possible hypotheses of the potential impact of landscape diversity on the temporal stability of productivity.

\*Added detailed discussions on the possible mechanisms responsible for the observed result.

We therefore invite you to revise and resubmit your manuscript, along with a point-by-point response that takes into account the points raised. Please highlight all changes in the manuscript text file.

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**Important:** The response to reviewers must not include any figures, tables or graphs. If you wish to respond to the reviewer reports with additional data in one of these formats, please add them to the main article or Supplementary Information, and refer to them in the rebuttal. Due to current technical limitations, any figures, tables, or graphs embedded in your rebuttal will not be included in the peer review file, if published.

We are committed to providing a fair and constructive peer-review process. Please don't hesitate to contact us if you wish to discuss the revision in more detail.

Please use the following link to submit your revised manuscript, point-by-point response to the referees' comments (which should be in a separate document to any cover letter), a tracked-changes version of the manuscript (as a PDF file) and the completed checklist:

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We hope to receive your revised paper within six weeks; please let us know if you aren't able to submit it within this time so that we can discuss how best to proceed. If we don't hear from you, and the revision process takes significantly longer, we may close your file. In this event, we will still be happy to reconsider your paper at a later date, as long as nothing similar has

been accepted for publication at Communications Earth & Environment or published elsewhere in the meantime.

Please do not hesitate to contact us if you have any questions or would like to discuss these revisions further. We look forward to seeing the revised manuscript and thank you for the opportunity to review your work.

Best regards,

Huai Chen, PhD  
Editorial Board Member  
Communications Earth & Environment  
[orcid.org/0000-0001-7650-289X](https://orcid.org/0000-0001-7650-289X)

Joe Aslin  
Deputy Editor  
Communications Earth & Environment

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## REVIEWER COMMENTS:

### Reviewer #1 (Remarks to the Author):

This is a potentially interesting study using large-scale data for demonstrating the importance of landscape diversity on promoting ecosystem functioning. The study attempted to verify their findings by using different independent datasets, for example, FIA.

However, before I can go deep into the contents of the paper, I have some remarks for the authors to revise, particularly at the aspects of clarity:

#### Major remarks:

1. Fig.1 looks very confusing to me. You use blocks covering North America by combining ecoregions and space. However, you did not show these blocks on the map. Why? You should do that, otherwise, it is very abstract to understand the actual meaning of your quasi-experimental study design. Moreover, what is the 56 unique LC compositions? It looks like in some blocks, you should have more than two or three LC types, you should clarify, at least make an additional table for improving clarity.
- 2, what is the purpose of using quasi-experimental design? It looks very straightforward to use grids/blocks and conduct all the spatial analyses and interpretations using the grids that cover the North American territory.

#### Minor remarks:

- 1, Line 360: fitted-> treated
- 2, Line 362: why there is only a single inequality symbol ">" in the description of different LC types?
- 3, Line 366, you used rarified tree species richness, what is the baseline of the rarification?
- 4, Line 320: what is the meaning of landscape functioning? why not use ecosystem functioning? what are the differences?

### Reviewer #2 (Remarks to the Author):

#### General comments for the authors

In their paper "Landscape diversity promotes landscape functioning in North America," the authors showed that landscape-level diversity, measured as the number of land-cover types (different ecosystems), is positively related to landscape-wide remotely sensed primary production across North America. They found that more land-cover types were associated with higher productivity stability and accelerated 20-year greening trends, particularly at high latitudes. Also, species diversity was correlated with landscape-level productivity, but the effect of species diversity and landscape diversity were independent.

I congratulate the authors for the innovative approach to diversity-ecosystem functioning at the landscape level and for the care in challenging their dataset with additional analyses using complementary databases from different locations, combining landscape effects with local levels of diversity (e.g., tree species richness). Although I find the study innovative and with results that complement biodiversity and ecosystem functioning studies, some points need to be carefully reviewed, especially regarding the terms used to describe the experimental design and how the statistical analyses were conducted. For example, the definition of experimental blocks and the way the block was considered in the general linear mixed models do not seem to be the most appropriate. Furthermore, the use of ANOVA Type I to summarize the results needs justification, as the use of ANOVA Type II may be a viable alternative. Finally, I suggest some improvements in other parts of the text, such as the legend and order of the figures, correction of the reference numbering, and improvement in the discussion. Overall, this is a very interesting study with a lot of potential. The manuscript is solid and provides information that will advance our understanding of the relationship between landscape diversity and ecosystem functioning. However, some specific issues need to be addressed:

#### Major comments:

##### Experimental design

I) The way the plots are distributed in a quasi-experimental set-up does not adhere to the principles of a block experimental design. In a block design, each block contains exactly one replicate of all the treatments in the experiment, and a single replicate from each of the treatments is assigned to each block (Gotelli and Ellison 2013). This block design principle does not seem to be applied in this study experimental design.

NJ Gotelli and AM Ellison. 2013. A Primer of Ecological Statistics. Sinauer, Sunderland, MA.

##### Statistical analysis

II) Why did the authors choose to use ANOVA Type I instead of Type II? If there's no clear evidence of an interactive effect of the predictor variables being evaluated, nor a specific interest in the sequence of their analysis, perhaps an ANOVA Type II analysis would be a more beneficial option. Unless the authors are interested in some specific pattern, it's essential to justify the use of such an analysis.

III) Even though the experimental blocks are not real blocks, it's worth considering including the block as a random effect, along with the LC composition. Do the authors have an a priori hypothesis about potential effects of the 'blocks'? If not, this absence of a hypothesis would be another reason to include the block as a random effect in the analysis.

IV) It is also not clear how the authors selected four types of landscapes out of six possible types (grasslands, shrubland, forest, wetland, urban, and agricultural areas) for the analysis and visualization of the results. This is particularly significant

as in Figure 3, that there are a maximum of four types of landscapes on the x-axis (Landscape diversity), but the authors mention in the text (L59-60) that they considered six types in the study.

#### Discussion and hypothesis

V) Little was discussed in the main text about the analyses and results of the temporal stability of productivity. Considering the study's aims and the analysis of 20 years of data at the landscape level, this discussion would certainly be important. Thus, I suggest including the possible hypotheses of the potential impact of landscape diversity on the temporal stability of productivity, as this is a crucial aspect that should not be overlooked. Additionally, it is important to discuss the possible mechanisms responsible for the observed result.

VI) Some reference numbers do not correspond with what was described in the text. There seems to be an error in the numbering of the references from a certain number (perhaps from reference 20 onwards). Please double-check the order of the citations in the text.

#### Specific comments

L47-48: The reference "20" does not correspond to what was described in the sentence.

L68-73: This excerpt also describes the methods used, in this case, how the response variables were obtained. This diverges from the rest of the paragraph, which begins to report the results. Therefore, I suggest moving this excerpt to the previous paragraph.

L68-71: Reference 25 does not correspond to what was described in the sentence, but rather to 24. It seems that there was an error in the numbering of the references from a certain number (perhaps from reference 20 onwards). Please double-check the order of the citations in the text.

L72-73: Please add a brief definition of EVIs'.

L147 and Figure 4: Figure 4 was cited after Figure 5. Please consider changing the order of each figure.

Also, in Fig 4., what do the abbreviations H and E mean? The meaning of these abbreviations is not stated in the figure caption.

L182-186: This discussion is not clear for me. Could the authors detail it more and make it clearer, please?

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Decision Letter:

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Dear Professor Niklaus,

Your manuscript titled "Landscape diversity promotes landscape functioning in North America" has now been seen by our reviewers, whose comments appear below. In light of their advice we are delighted to say that we are happy, in principle, to publish a suitably revised version in Communications Earth & Environment.

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Communications Earth & Environment

Joe Aslin  
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Communications Earth & Environment  
<https://www.nature.com/commsenv/>  
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#### REVIEWERS' COMMENTS:

##### Reviewer #1 (Remarks to the Author):

I commend the authors to take care of my and other reviewer's comments, by trying their best to revise the paper and providing their tracks of revision in their responses. I think the paper now is more readable and interesting. That means it is publishable now. Congratulations!

##### Reviewer #2 (Remarks to the Author):

I am pleased with the authors' efforts to revise this manuscript and integrate the comments provided in my first review. All of my comments were replied to or incorporated to my satisfaction.

My only additional suggestion is related to one of my previous comments regarding the study's nonadherence to the principles of a block experimental design. The authors explained that some B-EF experiments have used incomplete block designs, as they did in the present study. Thus, why not recognize in the main text that the author used an incomplete block design, as other important studies have done before?

I congratulate the authors for such exciting research.

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However, before I can go deep into the contents of the paper, I have some remarks for the authors to revise, particularly at the aspects of clarity:

### Major remarks:

1. Fig.1 looks very confusing to me. You use blocks covering North America by combining ecoregions and space. However, you did not show these blocks on the map. Why? You should do that, otherwise, it is very abstract to understand the actual meaning of your quasi-experimental study design. Moreover, what is the 56 unique LC compositions? It looks like in some blocks, you should have more than two or three LC types, you should clarify, at least make an additional table for improving clarity.

RESPONSE: We now re-created the map to more clearly show the combination of spatial grid and ecoregion, which we use as blocks, by delineating the units using thicker black lines.

We also created a supplementary table listing all the blocks, the length of the LC type richness gradient (abbreviated "LCR" in the manuscript), and the specific LC compositions present in the respective blocks.

Indeed, the number and identity of LC types differs between blocks. In each block, we used the LC types that allow us to create a LCR gradient with all the LC type combinations replicated 20 times. In each block, we selected LC combinations up to a maximum LCR of 4. When not all possible LC combinations could be realized, we either dropped the respective LCR level, or dropped the LC type that prevented adequate replication from the set. In other words, there sometimes was a trade-off between selecting a longer LCR gradient using a set of fewer LC types, or having more LC types (and therefore more LC combinations) but a shorter LCR gradient.

2. what is the purpose of using quasi-experimental design? It looks very straightforward to use grids/blocks and conduct all the spatial analyses and interpretations using the grids that cover the North American territory.

RESPONSE: It is an established convention in experimental biodiversity research that the different species combinations are used as statistical replicates for the test of species diversity. This way, effects of diversity per se can be separated from effects of particular species compositions. In analogy, we therefore used the different LC combinations as statistical replicates for the test of effects of LCR.

With the quasi-experimental design we chose, within each block, all possible LC type combinations occur, and each is replicated the same number of times ( $n=20$ ). This allows us to isolate effects of LC type richness from effects due to the presence of a particular LC type. When we would use all available data, this would not be the case.

We understand that this dataset could also be analyzed differently, but our aim here was, especially for reasons of comparability and integration into the vast body of existing biodiversity-ecosystem functioning literature, to adopt an approach that is as similar as possible to the one used in species diversity experiments.

### Minor remarks:

1, Line 360: fitted-> treated

RESPONSE: We now write “was included in the model as random term”

2, Line 362: why there is only a single inequality symbol ">" in the description of different LC types?

RESPONSE: There are two groups of three LC types each. For clarity, we now write “the first group, consisting of forest, agriculture and wetland had systematically larger EVI values than the second group, which consisted of grassland, shrubland, and urban.”

3, Line 366, you used rarified tree species richness, what is the baseline of the rarification?

RESPONSE: The problem this solves is that not all forest inventory plots have the same area. Because by sampling a larger area one generally finds a higher total species richness (one of the most universal principles in ecology), we rarefied the species richness of large inventory plots to the number of tree individuals one would expect on the smaller standard plot size.

This is explained in the methods (line 332) where we write “The FIA inventory plots varied in size, and we therefore down-sampled species richness (SR) by rarefying SR to the number of individuals expected in a standard area of 0.1 ha. Rarefied SR values averaged 4.68 across all plots”. In the revised text, we then further write: “For the analyses of the effects of local tree-species richness (SR) on the EVI of the landscape plot, we used the logarithm of rarefied species richness multiplied with the percentage forest cover as predictor“. Here, the point is that the larger the forest area in the plot, the larger the observed effect on the whole landscape plot's EVI will be – hence, the modeled effect of forest species richness needs to be multiplied with the forest area concerned. Here is a specific example: given a certain effect of tree species richness on the productivity of the respective forest area (e.g. a 20% increase in forest productivity per unit land), the observed "signal" this causes at the whole landscape plot level will be twice as large in a single-LC landscape in which the entire area of the landscape plot is covered with forest than in a two-LC landscape in which only about half of the landscape plot's area is covered by forest.

4, Line 320: what is the meaning of landscape functioning? why not use ecosystem functioning? what are the differences?

RESPONSE: Throughout the paper, we use the term ecosystem functioning when we refer to plot-scale species diversity experiments, and landscape functioning when we refer to landscape plots. Importantly, landscapes typically contain multiple different ecosystems. We use these different terms to more clearly distinguish these different spatial and organizational scales.



## Reviewer #2 (Remarks to the Author):

### General comments for the authors

In their paper “Landscape diversity promotes landscape functioning in North America,” the authors showed that landscape-level diversity, measured as the number of land-cover types (different ecosystems), is positively related to landscape-wide remotely sensed primary production across North America. They found that more land-cover types were associated with higher productivity stability and accelerated 20-year greening trends, particularly at high latitudes. Also, species diversity was correlated with landscape-level productivity, but the effect of species diversity and landscape diversity were independent.

I congratulate the authors for the innovative approach to diversity-ecosystem functioning at the landscape level and for the care in challenging their dataset with additional analyses using complementary databases from different locations, combining landscape effects with local levels of diversity (e.g., tree species richness). Although I find the study innovative and with results that complement biodiversity and ecosystem functioning studies, some points need to be carefully reviewed, especially regarding the terms used to describe the experimental design and how the statistical analyses were conducted. For example, the definition of experimental blocks and the way the block was considered in the general linear mixed models do not seem to be the most appropriate. Furthermore, the use of ANOVA Type I to summarize the results needs justification, as the use of ANOVA Type II may be a viable alternative. Finally, I suggest some improvements in other parts of the text, such as the legend and order of the figures, correction of the reference numbering, and improvement in the discussion.

Overall, this is a very interesting study with a lot of potential. The manuscript is solid and provides information that will advance our understanding of the relationship between landscape diversity and ecosystem functioning. However, some specific issues need to be addressed:

### Major comments:

#### Experimental design

I) The way the plots are distributed in a quasi-experimental set-up does not adhere to the principles of a block experimental design. In a block design, each block contains exactly one replicate of all the treatments in the experiment, and a single replicate from each of the treatments is assigned to each block (Gotelli and Ellison 2013). This block design principle does not seem to be applied in this study experimental design.

NJ Gotelli and AM Ellison. 2013. A Primer of Ecological Statistics. Sinauer, Sunderland, MA.

**RESPONSE:** We agree that in many designed studies, each blocks contain a complete set of the exact same treatments. However, there also are block designs in which this is not the case (so-called incomplete block designs), and they are not uncommon in biodiversity research. Many species diversity experiments replicate the diversity gradients in the different blocks using different species sets, or different species combinations.

One of the most famous and very extensively studied example is the Jena Experiment, which is one of the largest and longest-running biodiversity-ecosystem functioning experiments. It consists of four different blocks that capture spatial variation within the field site (e.g. due to edaphic conditions varying with distance from the nearby Saale river). In

Jena, within each block, diversity levels are realized with different species combinations, i.e. the combinations are not replicated across blocks.

Another important example is the BIODDEPTH study (Hector et al. 1999 Science 286 1123-1127), which basically consists of a set of seven separate biodiversity experiments, each implemented in a different country using a different sets of species; in the statistical analysis, the term “site” conceptually served as “block”.

Our present design is similar to the one of the BIODDEPTH study, with separate diversity experiments realized in each “block”, each using the LC types prevailing in the respective block. The blocks serve to capture large-scale spatial variation due to different environmental conditions and the differences between blocks due to different LC types present. In our statistical models, we therefore first remove differences in average productivity values among blocks, and then test for productivity increases along the LC type richness (LCR) gradients within blocks.

We have chosen an analogue design as a vast body of literature bases on the experimental studies mentioned above. Having a similar design allows to more directly compare our work to this literature, and vice versa.

Another way to analyze our data would be by meta-analysis, in which we consider the different diversity gradients in the different blocks as separate experiments; we have done this to verify our analysis: we first extracted the effect sizes found in each block, and then combined them by meta-analysis. The slope of the productivity—LCR relationship we obtained essentially remained the same. We therefore stick with the more straightforward analysis in a large linear mixed model, first fitting block (site differences), followed by land-cover type richness.

## Statistical analysis

II) Why did the authors choose to use ANOVA Type I instead of Type II? If there's no clear evidence of an interactive effect of the predictor variables being evaluated, nor a specific interest in the sequence of their analysis, perhaps an ANOVA Type II analysis would be a more beneficial option. Unless the authors are interested in some specific pattern, it's essential to justify the use of such an analysis.

RESPONSE: This indeed is an important point. Our models do not contain interactions, and essentially consist of the term LC type richness (LCR) fitted after block. Since the effect of LCR is adjusted for the effect of block in the Type I analysis, the test for effects of LCR is identical to a Type II test. In some models we also include a contrast between inherently very productive and inherently less productive LCs to remove this systematic (non-random) difference from the residual. This contrast is orthogonal to LCR, and therefore again the results of Type I and Type II analyses do not differ.

III) Even though the experimental blocks are not real blocks, it's worth considering including the block as a random effect, along with the LC composition. Do the authors have an a priori hypothesis about potential effects of the 'blocks'? If not, this absence of a hypothesis would be another reason to include the block as a random effect in the analysis.

RESPONSE: We understand this argument. In our original analysis, we included block as fixed effect, because we simply wanted to adjust the data for all spatial (block) differences before testing for the effect of LCR. The advantage of this approach is that no assumptions

are made about the statistical distribution of block effects. In the revised manuscript, we now include block as random effect, as suggested. The results stay essentially the same.

IV) It is also not clear how the authors selected four types of landscapes out of six possible types (grasslands, shrubland, forest, wetland, urban, and agricultural areas) for the analysis and visualization of the results. This is particularly significant as in Figure 3, that there are a maximum of four types of landscapes on the x-axis (Landscape diversity), but the authors mention in the text (L59-60) that they considered six types in the study.

RESPONSE: We distinguish six different LC types. However, we only use mixtures of up to four different LC types. The reason for this limit is that (1) LCR levels above 4 are only found in very few blocks, and (2) inspection of the satellite images revealed that landscape plots with higher LCR levels tend to be in highly disturbed areas, with some LCs that only occur in very small patches that sometimes are not easily attributable to a particular LC type. With LCR levels 1 to 4, this problem does not occur.

To provide an example: In a block in which five LC types are used in the construction of the diversity gradient, we would have 5 different 4-LC-combinations: assuming the LC types are labeled A-E, these combinations would be ABCD, ABCE, ABDE, ACDE, BCDE. In a block with just the 4 LC types A-D, there would only be one LC mixture: ABCD.

In the revised manuscript, we now include a supplementary table that lists the specific LC compositions in all blocks.

#### Discussion and hypothesis

V) Little was discussed in the main text about the analyses and results of the temporal stability of productivity. Considering the study's aims and the analysis of 20 years of data at the landscape level, this discussion would certainly be important. Thus, I suggest including the possible hypotheses of the potential impact of landscape diversity on the temporal stability of productivity, as this is a crucial aspect that should not be overlooked. Additionally, it is important to discuss the possible mechanisms responsible for the observed result.

RESPONSE: Thank you, this is an interesting aspect. In our study, we cover two dimensions of temporal variability: first, we find that mixed-LC landscape plots show less inter-annual variability in productivity. Second, we observe an increase in productivity through time, and an increase in biodiversity effect through time, especially at high latitudes. With the data we have available, we unfortunately cannot address the underlying specific mechanisms. One reason is that with the satellite remote sensing product we used we only are able to assess the productivity of the entire plot, but we cannot break down this productivity into contributions by the individual LC patches. For this reason, we preferred not to emphasize this particular aspect too much. However, we plan to study this in more detail in future work.

VI) Some reference numbers do not correspond with what was described in the text. There seems to be an error in the numbering of the references from a certain number (perhaps from reference 20 onwards). Please double-check the order of the citations in the text.

RESPONSE: Thank you for your observation. Indeed, there seem to have been a problem with our reference manager, which did not update the references correctly. This is now resolved in the revised manuscript.

## Specific comments

L47-48: The reference “20” does not correspond to what was described in the sentence.

L68-71: Reference 25 does not correspond to what was described in the sentence, but rather to 24. It seems that there was an error in the numbering of the references from a certain number (perhaps from reference 20 onwards). Please double-check the order of the citations in the text.

RESPONSE: (see above)

L68-73: This excerpt also describes the methods used, in this case, how the response variables were obtained. This diverges from the rest of the paragraph, which begins to report the results. Therefore, I suggest moving this excerpt to the previous paragraph.

RESPONSE: The first (previous) paragraph describes the design variables (plot selection and diversity gradients). We chose to then start a new paragraph because the following paragraph (line 68 onward) describes the response variable and how it was generated and used. The separation thus is not by method and results, but rather by topic, which we feel follows the general reporting style of this article.

L72-73: Please add a brief definition of EVIgs'.

RESPONSE: We modified this section, which now reads: “We then integrated EVI' values over the growing seasons (see Methods), yielding EVI<sub>gs</sub>.”

L147 and Figure 4: Figure 4 was cited after Figure 5. Please consider changing the order of each figure.

RESPONSE: Thanks for reporting this, we have now re-numbered to figures as suggested.

Also, in Fig 4., what do the abbreviations H and E mean? The meaning of these abbreviations is not stated in the figure caption.

RESPONSE: Thanks for reporting this inconsistency, we corrected the figure to use the LC labels we use in the rest of the manuscript.

L182-186: This discussion is not clear for me. Could the authors detail it more and make it clearer, please?

RESPONSE: This paragraph indeed was very short. We now write:

"Second, and related to the first phenomenon, a redistribution of resources from LC types in which these occur at high abundance to other LC types resembles a mixing process that spatially "averages out" differences in resource levels between LC types. For example, some LC types like urban areas heat up more strongly than others like forest. In a mixed-LC-type landscape, local temperature extremes will thereby be moderated, with adjacent forest leading to lower maximum temperatures in urban areas, and urban areas leading to higher minimum temperatures in forest. Similar reasoning applies to other mobile resources such as nutrients. An interesting possibility therefore is that such a landscape-wide mixing could be beneficial *per se* for landscape functioning because it reduces potentially negative impacts of extreme variation".