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# Functionally distinct tree species support long-term productivity in extreme environments

Léo Delalandre, Pierre Gaüzère, Wilfried Thuiller, Marc Cadotte, Nicolas Mouquet, David Mouillot, François Munoz, Pierre Denelle, Nicolas Loiseau, Xavier Morin and Cyrille Violle

**Article citation details**
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**Review timeline**

| | |
|---|---|
| Original submission: | 27 July 2021 |
| Revised submission: | 25 October 2021 |
| Final acceptance: | 13 December 2021 |

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

# Review History

## RSPB-2021-1694.R0 (Original submission)

### Review form: Reviewer 1 (Kechang Niu)

**Recommendation**
Major revision is needed (please make suggestions in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**
Acceptable

**General interest: Is the paper of sufficient general interest?**
Good

**Quality of the paper: Is the overall quality of the paper suitable?**
Good

**Is the length of the paper justified?**
Yes

**Should the paper be seen by a specialist statistical reviewer?**
No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**
No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**
Yes

**Is it clear?**
Yes

**Is it adequate?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Comments to the Author**
In this study, Léo Delalandre et al. put forward a important question about functional significance of trait-distinct species in regulating ecosystem productivity. The study not only explicitly defined functional distinctiveness of species according species's occupation in multidimensional trait space, but also highlighted environmental context-dependent importance of species distinctiveness to productivity change using the ForCEEPS, getting interest and sound results.

I am happy to recommend the manuscript to be published by Proceedings B, but concerns more about how to explain the underlying mechanism of productivity change in response to loss of functionally distinct/common species,(i.e. productivity decline pronouncedly due to loss of distinct species and common species in harsh and benign environments, respectively). For instance, is this because functionally distinct species are often belong to abundant/dominant species in harsh environments but infrequent/rare species in benign sites? Or the intraspecific trait variation often larger in functionally distinct species relative to common ones. How about orders of species lost affects on performance of remained species, which is also dependent not only on species trait but also relative abundance. Such questions lead me wonder whether it is possible to explore potential mechanisms from this study.

PS: line 65 delete "limiting similarity". "Common species" often used to refer "common see"(i.e. frequently occupied in investigative plots) but in this study you may use it to indicate "ordinary' in multidimensional trait space, how about using better word to avoid confuse. Species lost in some plots locally did not necessarily result in extinct from regional species pool, be careful to using "extinction" .

## Review form: Reviewer 2

**Recommendation**
Major revision is needed (please make suggestions in comments)

**Scientific importance: Is the manuscript an original and important contribution to its field?**
Good

**General interest: Is the paper of sufficient general interest?**
Acceptable

**Quality of the paper: Is the overall quality of the paper suitable?**
Good

**Is the length of the paper justified?**
Yes

**Should the paper be seen by a specialist statistical reviewer?**
Yes

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**
No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**
Yes

**Is it clear?**
Yes

**Is it adequate?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Comments to the Author**
This is an interesting study that the authors simulated forest communities and used their models to compare if loss of functional distinct will have different effect on community productivity than that of functional common species have. They concluded that the functionally distinct species have larger effect on productivity in the stressed environment, but not in the milder environments. Overall, I think the idea is novel and the analysis make sense. However, I have a few major comments related with the traits and models they used. Without clearly understanding the issues related with these comments, I cannot fully believe the results.

1) The author emphasize "long term" in the title, as well as in the text line 107 "The loss of functionally distinct species reduces ecosystem functioning in the long term." But I am wonder which analysis/results match this long-term conclusion?

2) All the results in this simulation study depend on the models they used. I found the authors explained why the ForCEEPS model is useful with a long paragraph in the introduction. In addition, they explained the assumptions of the model with several lines in the method. However, there was nowhere explain HOW to use the model or HOW the model works. The very less information in the text only let the reader find more information from the references. The same for the FORCLIM model (by the way, what is the FORCLIM? The same as ForCEEPS, there should be a full name in the text). Here the authors need to clearly explain either in the text or put in the SI.

3) The authors didn't mention any information related with species abundance, but only species richness. Without any assumption of density, I can hardly agree with the results "Functionally

distinct tree species support long-term productivity in extreme environments". The species effect on productivity for sure depends on how many individuals of each species appearing in the community. We can imagine that although the functional distinct species might have larger effect size, if there are only very few of them in a community, they cannot support the ecosystem functioning. So here need a clear explanation why there is no density included.

4) The authors are quite confident of the selected 14 functional traits are better than the classical functional traits. My concern is I am not sure the traits used in this study can all be used as "functional traits'. I only found one sentence in line 137 said "The congruence of these parameters with classical functional traits was discussed in a previous study [33]", which I also don't find clear statement in the reference. I believe here the author need add the justification. e.g. DDMin: minimal required annual degree-days sum (°C), why this is a functional trait?

## Decision letter (RSPB-2021-1694.R0)

17-Sep-2021

Dear Mr Delalandre:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

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If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:
If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:
It is a condition of publication that you make available the data and research materials supporting the results in the article. Please see our Data Sharing Policies (https://royalsociety.org/journals/authors/author-guidelines/#data). Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

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All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Professor Gary Carvalho
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
In this manuscript, the authors evaluated how species loss may influence ecosystem functioning using a forest gap model, ForCEEPS. They compared three different scenarios of species loss, 1) functionally distinct species were lost first, 2) functionally common species were lost first, and 3) random loss. The found that functionally distinctive species loss led to stronger drop in primary productivity than the other two species loss scenarios in harsh environment, but common species loss led to stronger productivity drop than the other two scenarios of species loss in warm and wet environment. They concluded that functional distinctiveness can capture species diversity effects on ecosystem functioning, and the effect of functional distinctiveness varied along environmental gradient. Two reviewer reviewed this manuscript. They both have very serious concerns about the analytical methods, the results and the writing. First, the authors used the ForCEEPS model in this study. As pointed out by reviewer #2, the method section did not provide enough description about this model. More description about how the model works will help the readers understand the findings. Second, the authors should explore the mechanisms underlying the effect of functional distinctiveness in their analysis. Maybe the authors could try to demonstrate how functional distinctiveness may influence the complementary effect and sampling effect of species diversity on ecosystem functioning. Third, the authors used 14 plant traits in their analysis. as pointed out by reviewer #2, other traits may be also important for plant growth and hence ecosystem productivity, eg. the leaf life span and specific leaf area. I think the authors should consider to include more traits related to plant survival and growth in their analysis.

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
In this study, Léo Delalandre et al. put forward a important question about functional significance of trait-distinct species in regulating ecosystem productivity. The study not only explicitly defined functional distinctiveness of species according species's occupation in multidimensional trait space, but also highlighted environmental context-dependent importance of species distinctiveness to productivity change using the ForCEEPS, getting interest and sound results.

I am happy to recommend the manuscript to be published by Proceedings B, but concerns more about how to explain the underlying mechanism of productivity change in response to loss of functionally distinct/common species,(i.e. productivity decline pronouncedly due to loss of distinct species and common species in harsh and benign environments, respectively). For instance, is this because functionally distinct species are often belong to abundant/dominant species in harsh environments but infrequent/rare species in benign sites? Or the intraspecific trait variation often larger in functionally distinct species relative to common ones. How about orders of species lost affects on performance of remained species, which is also dependent not only on species trait but also relative abundance. Such questions lead me wonder whether it is possible to explore potential mechanisms from this study.

PS: line 65 delete "limiting similarity". "Common species" often used to refer "common see"(i.e. frequently occupied in investigative plots) but in this study you may use it to indicate "ordinary' in multidimensional trait space, how about using better word to avoid confuse. Species lost in some plots locally did not necessarily result in extinct from regional species pool, be careful to using "extinction" .

Referee: 2
Comments to the Author(s)
This is an interesting study that the authors simulated forest communities and used their models to compare if loss of functional distinct will have different effect on community productivity than

that of functional common species have. They concluded that the functionally distinct species have larger effect on productivity in the stressed environment, but not in the milder environments. Overall, I think the idea is novel and the analysis make sense. However, I have a few major comments related with the traits and models they used. Without clearly understanding the issues related with these comments, I cannot fully believe the results.

1) The author emphasize “long term” in the title, as well as in the text line 107 “The loss of functionally distinct species reduces ecosystem functioning in the long term.” But I am wonder which analysis/results match this long-term conclusion?

2) All the results in this simulation study depend on the models they used. I found the authors explained why the ForCEEPS model is useful with a long paragraph in the introduction. In addition, they explained the assumptions of the model with several lines in the method. However, there was nowhere explain HOW to use the model or HOW the model works. The very less information in the text only let the reader find more information from the references. The same for the FORCLIM model (by the way, what is the FORCLIM? The same as ForCEEPS, there should be a full name in the text). Here the authors need to clearly explain either in the text or put in the SI.

3) The authors didn’t mention any information related with species abundance, but only species richness. Without any assumption of density, I can hardly agree with the results “Functionally distinct tree species support long-term productivity in extreme environments”. The species effect on productivity for sure depends on how many individuals of each species appearing in the community. We can imagine that although the functional distinct species might have larger effect size, if there are only very few of them in a community, they cannot support the ecosystem functioning. So here need a clear explanation why there is no density included.

4) The authors are quite confident of the selected 14 functional traits are better than the classical functional traits. My concern is I am not sure the traits used in this study can all be used as “functional traits’. I only found one sentence in line 137 said “The congruence of these parameters with classical functional traits was discussed in a previous study [33]”, which I also don’t find clear statement in the reference. I believe here the author need add the justification. e.g. DDMin: minimal required annual degree-days sum (°C), why this is a functional trait?

## Author's Response to Decision Letter for (RSPB-2021-1694.R0)

See Appendix A.

# RSPB-2021-1694.R1 (Revision)

## Review form: Reviewer 1

**Recommendation**
Accept as is

**Scientific importance: Is the manuscript an original and important contribution to its field?**
Good

**General interest: Is the paper of sufficient general interest?**
Good

**Quality of the paper: Is the overall quality of the paper suitable?**
Good

**Is the length of the paper justified?**
Yes

**Should the paper be seen by a specialist statistical reviewer?**
No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**
No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**
Yes

**Is it clear?**
Yes

**Is it adequate?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Comments to the Author**
The authors have clarifed all of my conerns, I have no more comments

## Review form: Reviewer 2

**Recommendation**
Accept as is

**Scientific importance: Is the manuscript an original and important contribution to its field?**
Good

**General interest: Is the paper of sufficient general interest?**
Excellent

**Quality of the paper: Is the overall quality of the paper suitable?**
Good

**Is the length of the paper justified?**
Yes

**Should the paper be seen by a specialist statistical reviewer?**
No

**Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.**
No

**It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.**

**Is it accessible?**
Yes

**Is it clear?**
Yes

**Is it adequate?**
Yes

**Do you have any ethical concerns with this paper?**
No

**Comments to the Author**
The author addressed most of my questions very well. I think the manuscript is quite nice now. I have no further comments.

# Decision letter (RSPB-2021-1694.R1)

13-Dec-2021

Dear Mr Delalandre

I am pleased to inform you that your manuscript entitled "Functionally distinct tree species support long-term productivity in extreme environments" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Professor Gary Carvalho
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

# Appendix A

Dear Editor,

Thank you very much for your comments and suggestions on our manuscript entitled "Functionally distinct tree species support long-term productivity in extreme environments". Based on the comments by the Associate Editor and the two reviewers, we added a more thorough description of the model, we have performed a supplementary analysis to understand the mechanisms explaining the role of functionally distinct species in sustaining productivity at both ends of the environmental gradient, and we included more justification for using ForCEEPS parameters as proxies for functional traits. We provide hereafter a line-by-line response (blue text) to each point raised by the Associate Editor and the two reviewers.

Thanks to these revisions, the manuscript, and especially the discussion on the mechanisms underlying the effects of distinct species, has been greatly improved. We hope this new version will be suitable for publication in the *Proceedings B* and we look forward to hearing from you.

Sincerely,

Léo Delalandre, on behalf of all co-authors.

**Associate Editor**

In this manuscript, the authors evaluated how species loss may influence ecosystem functioning using a forest gap model, ForCEEPS. They compared three different scenarios of species loss, 1) functionally distinct species were lost first, 2) functionally common species were lost first, and 3) random loss. The found that functionally distinctive species loss led to stronger drop in primary productivity than the other two species loss scenarios in harsh environment, but common species loss led to stronger productivity drop than the other two scenarios of species loss in warm and wet environment. They concluded that functional distinctiveness can capture species diversity effects on ecosystem functioning, and the effect of functional distinctiveness varied along environmental gradient.

Two reviewer reviewed this manuscript. They both have very serious concerns about the analytical methods, the results and the writing. First, the authors used the ForCEEPS model in this study. As pointed out by reviewer #2, the method section did not provide enough description about this model. More description about how the model works will help the readers understand the findings.

We thank the editor for the time spent on the evaluation of our work. We apologize for the lack of details provided in the original version. We indeed only cited several published articles that described the models due to space constraints, but we recognize that this can be too succinct for the reviewers and future readers. We have now added a full description of the model in Appendix 1 (reproduced from Functional Ecology with the permission of the authors and in agreement with the copyright policy of Funct. Ecology) and referred to it in the main text. Thank you for this suggestion.

Second, the authors should explore the mechanisms underlying the effect of functional distinctiveness in their analysis. Maybe the authors could try to demonstrate how functional distinctiveness may influence the complementary effect and sampling effect of species diversity on ecosystem functioning.

This is an excellent suggestion. Obviously, such an analysis could be considered in itself as another article, a follow-up of our current work demonstrating the role of distinctiveness on ecosystem productivity. Nonetheless, we have explored this issue by applying the partitioning of biodiversity effects proposed by Loreau and Hector (Partitioning selection and complementarity in biodiversity experiment. Nature 412:72-76) to our simulated data. This led to interesting findings that certainly reinforce our original ones: distinct species sustain productivity by the selection effect on one extreme of the gradient, and by the complementarity effect on the other. Given space constraints (we reached the upper limit) and the pioneering aspect of these additional findings, we propose to present them in an Appendix (Appendix 3, containing Methods + Results), and we referred to it in the discussion **(lines 294 to 303):**

*In cold sites, distinct species were the most abundant and productive of the community because of their response to the abiotic environment. On the contrary, at the other extreme of the environmental gradient (i.e. in warm-dry sites), although distinct species sustained productivity too, they were neither more abundant nor more productive than ordinary ones. We further performed a partitioning analysis of biodiversity effects (Appendix 3) which tends to show that distinct species might have sustained productivity in warm-dry sites through complementarity with the other species, and not by being the dominant ones in such environments. Even if the relatively low number of sites along our environmental gradient does not allow for generalization, this result opens an interesting direction for future research.*

Third, the authors used 14 plant traits in their analysis. as pointed out by reviewer #2, other traits may be also important for plant growth and hence ecosystem productivity, eg. the leaf life span and specific leaf area. I think the authors should consider to include more traits related to plant survival and growth in their analysis.

Thank you for pointing out a lack of explanation regarding the definition of the parameters we used. In particular: (1) SLA or leaf life span contain information that is, to a large extent, conveyed by the parameters of the model; (2) many trait dimensions mechanistically related to plant survival and growth are included in the modelling framework, and all of them were taken into account by the 14 parameters that we used for our analyses. We modified the methods

(*Species pool and species traits*, **lines 134 to 142**) to provide more information on this point. Please find below a more complete justification of our choices.

(1) The relationships between these parameters and functional traits have been extensively assessed (Morin et al., 2021), including Specific Leaf Area (SLA). We detailed this in response to the comment 4) made by referee 2 (see below); in particular, in (Morin et al., 2021)'s table that we have included below, LMA significantly correlates with ForCEEPS parameter G (Spearman's r = 0.557; p.value = 0.011). Consequently, the information carried by SLA (or by LMA) is in fact already included in the model, to an important extent, through the parameter G. In addition, we provide a supplementary analysis showing that, when the distinctiveness ranking is computed on traits linked to growth and leaf economics strategy (Specific Leaf Area, nitrogen content and plant height), it correlates with the ranking computed on the 14 parameters of the model used as traits (Fig. S4A). This further indicates that the distinctiveness we computed based on ForCEEPS parameters is tightly correlated to the distinctiveness based on broadly-used functional traits proposed by the editor. Again, this is an important suggestion that helps root our study in the theoretical corpus of functional ecology, and we warmly thank the editor and the reviewers for their comments.

(2) Traits related to survival and growth present in the model and used in our analysis cover a wide range of ecophysiological processes.

- The parameters that determine species establishment and survival at the site scale encompass at least four major dimensions: (i) response to water availability (***DrTol****: Drought tolerance index*), and (ii) nitrogen availability (***NTol****: Soil nitrogen requirements*); (iii) browsing tolerance (***Brown:*** *Browsing susceptibility of seedlings*); (iv) temperature requirements (***DDMin****: Minimal required annual degree-days sum;* ***WiTN****: Monthly minimum winter temperature tolerated for regeneration;* ***WiTX****: Monthly maximum winter temperature tolerated for regeneration*).

- The other parameters that we used are involved in growth (***G****: Optimal growth, and* ***S****: Allometry between diameter and height*), succession dynamics (***Amax****: Maximum age*), and competition for light (***Amax****: Maximum age;* ***HMax****: Maximum height;* ***La****: Shade tolerance of adults;* ***Ly****: Shade tolerance of seedlings;* ***A1max and A2****: Crown size allometry parameters*).

The parameters that we used are causally involved in the dynamics simulated by the ForCEEPS model (see Appendix 1, which we added in response to your comment 1 and referee two's comment 2), and thus provide valuable information about the processes at stake in the forest community simulated, by mechanistically linking their physiology and environmental requirements to their persistence and their coexistence depending on the environment. We believe that the modification to our method section lines 134 to 142 and the Appendix 1 provide enough justification for the choice of the traits used in our model.

**Referee 1:**

In this study, Léo Delalandre et al. put forward a important question about functional significance of trait-distinct species in regulating ecosystem productivity. The study not only explicitly defined functional distinctiveness of species according species's occupation in multidimensional trait space, but also highlighted environmental context-dependent importance of species distinctiveness to productivity change using the ForCEEPS, getting interest and sound results.

I am happy to recommend the manuscript to be published by Proceedings B, but concerns more about how to explain the underlying mechanism of productivity change in response to loss of functionally distinct/common species,(i.e. productivity decline pronouncedly due to loss of distinct species and common species in harsh and benign environments, respectively). For instance, is this because functionally distinct species are often belong to abundant/dominant species in harsh environments but infrequent/rare species in benign sites? Or the intraspecific trait variation often larger in functionally distinct species relative to common ones. How about orders of species lost affects on performance of remained species, which is also dependent not only on species trait but also relative abundance. Such questions lead me wonder whether it is possible to explore potential mechanisms from this study.

Thank you for your reading and positive comments. We agree that our description and analysis of the mechanisms underlying the patterns that emerged from the simulations are not precise enough. We modified several elements in the text and the appendix to overcome this lack of information:

- We modified and completed table 1 (Correlation between species distinctiveness and productivity in the 11 sites), to add the correlation between species distinctiveness and their biomass in the 11 sites. This table permits to conclude, as you wrote, that: "functionally distinct species […] often belong to abundant/dominant species in [cold, but not warm-dry] environments"**.** Note that the table contained an error that is now fixed (the results remain ultimately unchanged). The figure can be reproduced and all the changes can be tracked in the code available on GitHub: https://github.com/LDelalandre/Project-1_Distinct-sp_BEF)

- To go further in understanding the mechanisms underlying the effects of distinct species at both ends of the gradient, we performed a supplementary analysis using the partitioning of biodiversity effects into selection and complementarity effects proposed by Loreau and Hector (Partitioning selection and complementarity in biodiversity experiment. Nature 412:72-76). We included it as an appendix (Appendix 3), and refer to it in the discussion **(lines 298 to 308).**

- We added more explicit description of this in the text, e.g., **lines 294 to 301**, by explicitly mentioning that "In cold sites, distinct species were the most abundant and productive of the community because of their response to the abiotic environment", and that "distinct species might have sustained productivity in warm-dry site through complementarity with the other species, and not by being the dominant ones in such environments."

PS: line 65 delete "limiting similarity".

Done.

"Common species" often used to refer "common see"(i.e. frequently occupied in investigative plots) but in this study you may use it to indicate "ordinary' in multidimensional trait space, how about using better word to avoid confuse.

Thank you for this wise advice. We changed *common* for *ordinary* in the whole manuscript.

Species lost in some plots locally did not necessarily result in extinct from regional species pool, be careful to using "extinction".

This is a good point, thank you. We changed this term for "removal" (**line 240**), and "species richness gradient" (**line 248**).

**Referee 2:**

This is an interesting study that the authors simulated forest communities and used their models to compare if loss of functional distinct will have different effect on community productivity than that of functional common species have. They concluded that the functionally distinct species have larger effect on productivity in the stressed environment, but not in the milder environments. Overall, I think the idea is novel and the analysis make sense. However, I have a few major comments related with the traits and models they used. Without clearly understanding the issues related with these comments, I cannot fully believe the results.

Thank you for your insightful reading of our manuscript. Please find our responses to your four comments below.

1) The author emphasize "long term" in the title, as well as in the text line 107 "The loss of functionally distinct species reduces ecosystem functioning in the long term." But I am wonder which analysis/results match this long-term conclusion?

Since we simulated forest dynamics along 2,000 years and measured ecosystem property at the end of the temporal series, we considered that we focused on long-term ecosystem productivity, as opposed to productivity measured a few years after an experiment is performed. To make more explicit the temporal spanning of the simulations, we added a figure in the appendix (Appendix 2, Fig. S3) showing accumulated biomass along the 2,000 years in the 11 sites. We highlighted long-term equilibrium at the end of 2,000 years.

2) All the results in this simulation study depend on the models they used. I found the authors explained why the ForCEEPS model is useful with a long paragraph in the introduction. In addition, they explained the assumptions of the model with several lines in the method. However, there was nowhere explain HOW to use the model or HOW the model works. The very less information in the text only let the reader find more information from the references. The same for the FORCLIM model (by the way, what is the FORCLIM? The same as ForCEEPS, there should be a full name in the text). Here the authors need to clearly explain either in the text or put in the SI.

Thank you for bringing up that point: we agree that the description of the model should be directly accessible to the reader. We added an appendix (Appendix 1, reproduced from Functional Ecology with the permission of the authors and in agreement with the copyright policy of Funct. Ecology) describing the model in detail, as you suggested. We also added a sentence referring to that appendix in the text (lines **125-126**). In addition, we added the full names of the ForCEEPS and FORCLIM models (line **82** and **121**).

3) The authors didn't mention any information related with species abundance, but only species richness. Without any assumption of density, I can hardly agree with the results "Functionally distinct tree species support long-term productivity in extreme environments". The species effect on productivity for sure depends on how many individuals of each species appearing in the community. We can imagine that although the functional distinct species might have larger effect size, if there are only very few of them in a community, they cannot support the ecosystem functioning. So here need a clear explanation why there is no density included.

Thank you for this suggestion. We agree that this was not clear enough in the text. The strength of our approach is that we did not manipulate species abundance, only their distinctiveness, while abundance is an emerging property of our simulations, which can, indeed, explain the large effect size of distinct species in extreme sites. And it does, at least in cold sites, but not in warm-dry sites, which is a very promising finding. We added several elements in the text (from Methods to Discussion) to develop this argument, including:

**Lines 147, 148**, where we precise that functional distinctiveness is measured irrespective of species abundance in our study.

**Lines 270 – 273**, where we say that "*the correlation between species productivity in monoculture and their distinctiveness was significantly positive in the three coldest sites*

*(Bever, Grande Dixence, and Davos – Table 1). In all the other sites, there was no correlation between species functional distinctiveness and either biomass or productivity.*"

**Lines 294 – 296**, where we say that "*In cold sites, distinct species were the most abundant and productive of the community because of their response to the abiotic environment. On the contrary, at the other extreme of the environmental gradient (i.e. in warm-dry sites), although distinct species sustained productivity too, they were neither more abundant nor more productive than ordinary ones.*"

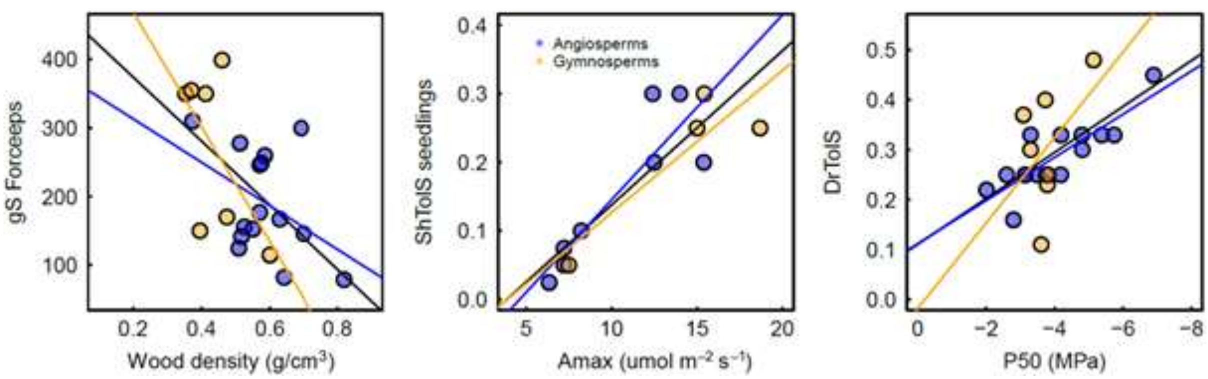
4) The authors are quite confident of the selected 14 functional traits are better than the classical functional traits. My concern is I am not sure the traits used in this study can all be used as "functional traits'. I only found one sentence in line 137 said "The congruence of these parameters with classical functional traits was discussed in a previous study [33]", which I also don't find clear statement in the reference. I believe here the author need add the justification. e.g. DDMin: minimal required annual degree-days sum (°C), why this is a functional trait?

You are perfectly right to point out that the parameters we used are not all functional traits, and that our justification was not precise enough. Yet, we believe that several elements, listed below, can justify that we approximated species functional traits by ForCEEPS parameters.

1) Functional traits are "morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance." (Violle et al., 2007). ForCEEPS parameters affect species growth, reproduction, and survival, either directly ("intrinsic parameters", mentioned line **137**, e.g. G, optimal growth), or indirectly ("response-to-drivers parameters", mentioned line **135** e.g. Ly, shade tolerance of seedlings, DrTol, drought tolerance, or DDmin, minimal required annual degree-day sum, all of which impact species growth and survival depending on the environmental conditions). In that respect, it seems reasonable to state that the parameters of the model are more than proxies of functional traits: they directly relate to the ecophysiological processes that functional traits approximate, and are thus functional *sensu Violle et al. (2007).* For a thorough description of how the parameters affect species growth, reproduction, and survival, see Appendix 1, which we added in response to your comment 2.

2) The correlations between ForCEEPS parameters and species functional traits were extensively assessed in another recent study (Morin et al., 2021). We reproduce figures from this article and its appendix below to illustrate that point with some examples. For instance, species optimal growth parameter G (referred to as gS by Morin et al.) is negatively correlated with wood density (Pearson's r = -0.574, p.value = 0.005, table S9 above). As wood density informs on carbon invested per volume of stem, the documented trade-off between growing fast and investing carbon in dense tissues is successfully reproduced. Similarly, shade-tolerance

of seedlings (La, called ShTolSseedlings in the figure and table below) positively correlates with light-saturated net photosynthesis (Amax), and drought tolerance (DrTol) with embolism resistance (P50) (figure 7 and table S9 below), both of which are expected from ecophysiological knowledge of tree species. For a detailed discussion of these relations and their ecophysiological underpinnings, see (Morin et al., 2021), paragraph 5.3 of the discussion (*Mechanistic relevance of ForCEEPS parameters)*. As an illustration, the following figure and table are extracted from (Morin et al., 2021), and text in italic is reproduced from the article:




*"FIGURE 7 Correlations between key ForCEEPS parameters and ecophysiological traits extracted from the literature (see Appendix E). Blue dotsand line: Angiosperms; orange dots and line: Gymnosperms. Associated statistics are presented in Table S9".*

*"Table S9: Correlations between ForCEEPS parameters and ecological traits at the interspecific level. Upper table: Pearson's r ; lower table: associated p-value."*

| | Wood density (g/m3) | LMA (g/m2) | Na (g/m2) | Amax (umol/m2/s) | P50 (Mpa) | Ψ_tlp (Mpa) | Ψclose (Mpa) | SM_Ψclose (Mpa) | SM_Ψtlp (Mpa) |
|---|---|---|---|---|---|---|---|---|---|
| Pearson's R (All species) | | | | | | | | | |
| $g_s$ | -0.574 | 0.557 | 0.249 | 0.408 | 0.297 | 0.203 | 0.173 | -0.257 | -0.284 |
| $DrTol_s$ | 0.290 | 0.407 | 0.339 | 0.538 | -0.605 | -0.287 | -0.262 | 0.577 | 0.607 |
| $Nreq_s$ | 0.143 | -0.531 | -0.501 | -0.666 | 0.048 | 0.359 | 0.161 | 0.023 | -0.018 |
| $ShTol_s$ | -0.073 | 0.136 | 0.365 | 0.719 | 0.011 | -0.264 | -0.150 | -0.098 | -0.055 |
| $ShTol\_seedling_s$ | -0.094 | 0.189 | 0.306 | 0.869 | 0.024 | -0.362 | -0.217 | -0.145 | -0.083 |
| Pearson's R (angiosperm) | | | | | | | | | |
| $g_s$ | -0.431 | -0.174 | 0.000 | 0.509 | 0.646 | 0.134 | 0.077 | -0.745 | -0.707 |
| $DrTol_s$ | 0.621 | 0.582 | 0.451 | 0.191 | -0.838 | -0.645 | -0.581 | 0.728 | 0.811 |
| $Nreq_s$ | -0.171 | -0.508 | -0.430 | -0.478 | 0.125 | 0.432 | 0.258 | -0.019 | -0.079 |
| $ShTol_s$ | -0.110 | 0.263 | 0.346 | 0.712 | -0.002 | -0.167 | -0.059 | -0.036 | -0.019 |
| $ShTol\_seedling_s$ | 0.024 | 0.149 | 0.121 | 0.875 | -0.001 | -0.371 | -0.239 | -0.128 | -0.061 |
| Pearson's R (gymnosperm) | | | | | | | | | |
| gS | -0.590 | 0.673 | 0.075 | -0.135 | -0.665 | 0.379 | 0.246 | 0.757 | 0.739 |
| DrTolS | 0.250 | 0.536 | 0.465 | 0.784 | -0.458 | 0.253 | 0.171 | 0.522 | 0.509 |
| NreqS | -0.598 | -0.219 | -0.811 | -0.937 | 0.050 | 0.545 | 0.540 | 0.235 | 0.100 |
| ShTolS | 0.218 | -0.047 | 0.667 | 0.863 | 0.006 | -0.589 | -0.543 | -0.290 | -0.158 |
| ShTol_seedlingS | 0.374 | -0.222 | 0.627 | 0.886 | -0.038 | -0.536 | -0.504 | -0.228 | -0.102 |

3) Ecophysiological trade-offs documented for functional traits are found in ForCEEPS parameters. For instance, late-successional species are generally characterized by a slow growth (G) and a long lifespan (LS), which are negatively correlated (see Appendix 2, Figure S1 of our manuscript). A more complete discussion of these correlations is provided in (Chauvet et al., 2017).

4) The use of ForCEEPS parameters as surrogates for species functional traits was performed in several studies using that model. Examples include (Gauzere et al., 2020), and (Chauvet et al., 2017).

5) In addition, we provide a supplementary analysis that shows that, when distinctiveness is computed on traits linked to growth and leaf economics strategy (Specific Leaf Area, nitrogen content and plant height), it correlates with distinctiveness computed on the 14 parameters of the model used as traits (Fig. S4A). This further indicates that the distinctiveness we computed based on ForCEEPS parameters is tightly correlated to the distinctiveness based on broadly-used functional traits.

For these reasons, we believe that the approximation of species functional traits by ForCEEPS parameters is justified. We completely agree that the justification was not explicit enough in our manuscript. We changed the text in that sense in the methods (lines **134** to **142**) and in the discussion (lines **335** to **339**).

Finally, thank you very much for pointing out a problem in the References: we mentioned a study that has been published recently, and in two places in the text, we still referred to the bioRXiv version of that article. We corrected it (the two occurrences were in the Methods section, line 122, paragraph *Forest succession model*, and line 13, paragraph *Species pool and species traits*, in the version we submitted*)*. The article is the following:

Morin X, Bugmann H, Coligny F de, Martin-StPaul N, Cailleret M, Limousin J-M, et al. Beyond forest succession: A gap model to study ecosystem functioning and tree community composition under climate change. Functional Ecology 2021;35:955–75. https://doi.org/10.1111/1365-2435.13760.

Literature cited in this document:


Chauvet, M., Kunstler, G., Roy, J., & Morin, X. (2017). Using a forest dynamics model to link community assembly processes and traits structure. *Functional Ecology*, *31*(7), 1452–1461. https://doi.org/10.1111/1365-2435.12847

Gauzere, P., Morin, X., Violle, C., Caspeta, I., Ray, C., & Blonder, B. (2020). Vacant yet invasible niches in forest community assembly. *Functional Ecology*, *34*(9), 1945–1955. https://doi.org/10.1111/1365-2435.13614

Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, *412*(6842), 72–76. https://doi.org/10.1038/35083573

Morin, X., Bugmann, H., Coligny, F. de, Martin-StPaul, N., Cailleret, M., Limousin, J.-M., Ourcival, J.-M., Prevosto, B., Simioni, G., Toigo, M., Vennetier, M., Catteau, E., & Guillemot, J. (2021). Beyond forest succession: A gap model to study ecosystem functioning and tree community composition under climate change. *Functional Ecology*, *35*(4), 955–975. https://doi.org/10.1111/1365-2435.13760

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x