Review of "Light-demanding canopy tree species are no indicators of past human disturbance in the Yangambi rainforest (Democratic Republic of the Congo) "

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Review of "Light-demanding canopy tree species are no indicators of past human disturbance in the Yangambi rainforest (Democratic Republic of the Congo)"

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Keywords : Central African rainforest, forest composition, forest history, light-demanding canopy species, recovery from human disturbance hypothesis, Yangambi Biosphere Reserve, Annals of Forest Science, Open Peer Review Report, Open Peer Review

Original submission – R0

R0 - Authors

Cover letter R0

We are pleased to present our manuscript entitled 'Light-demanding canopy species are no indicators of past human disturbance in the central Congo basin' to Annals of Forest Science. We have verified that our manuscript (Research paper type) fits within the scope of Annals of Forest

Science. Our manuscript addresses the issue of forest dynamics and disturbance in the central Congo basin.

Two-thirds of the Congo basin forest is located in the Democratic Republic of Congo (DRC), the world's second richest country in extent of tropical forest and arable land. It is for this reason that DRC emerged as a "solution country" to the climate crisis in the wake of the 26th Conference of the Parties (CoP) of the Intergovernmental Panel on Climate Change (IPCC) in Glasgow. This newly achieved international status has been acknowledged by the IPCC by appointing the country as the host to organize the pre-CoP27 activities (September 2022), where notably Yangambi (our research site) has been chosen as the venue. However, it is a curious paradox that a country "of importance for climate change solutions" knows so little about its own ecosystem services.

Scientific research has shown that mature (old-growth) Congolese forests are an important carbon sink, whose protection can count as a nature-based-solution to climate change. Yet the drivers of this forest carbon sink are ill-understood. A particular point of discussion among scholars, is how pristine Congolese rainforests really are? Archaeological and linguistic research has shown that the central Congo basin rainforests have been inhabited for more than 2000 years by Bantu-speaking people, who introduced slash-and-burn farming in the region. This has led to serious questioning of the drivers of the observed carbon sink in alleged 'mature' African tropical forests. One school of scholars claims that these forests are really mature and that the sink is a result of a CO2 fertilization effect. Another school claims that these forests are in a late-successional stage due to slash-and-burn farming regimes in the past. Indirect evidence for this is thought to be visible in present-day taxonomic composition, with important numbers of individuals belonging to light-demanding species in the canopy. A solution to this debate will be crucial to better understand how tropical forests respond to climate change and, ultimately, to better constrain Land Surface Models (LSM) and Earth System Models (ESM).

Furthermore, many of the light-demanding species that are thought to be indicative of the forests' past, also happen to be of commercial value. Because some of these species seem to show a regeneration deficit, foresters are desperate to secure future timber stocks. As the present-day populations are thought to be a legacy of forest disturbance, some suggest that this very disturbance might be a good way to fight the regeneration deficit.

Clearly, a better understanding of Congo basin forests is needed to better inform models and forest management. However, serious knowledge gaps exist. Most studies often do not consider the forest as a whole, but rather focus on data from a few 'indicator species'. Furthermore, most studies on this subject were conducted in West-Central Africa (Cameroon, Gabon), where light-demanding species can be locally monodominant. Yet data for the vast central Congo basin (DRC) remain extremely limited. This is why we set up a forest monitoring experiment in the Yangambi reserve, located in the very heart of the Congo basin. We compare results of analysis focusing on indicator species, with results from a more holistic analysis considering all species. Our paper is 55 467 characters (including key message, abstract, spaces, references and captions). The manuscript has 74 references, 6 figures, 3 supplementary figures, and 1 appendix. We believe that the conclusions of our paper can be of interest to the diverse public of Annals of Forest Science. Therefore, we hope that our manuscript may be considered for peer-review.

We wish to express our gratitude in advance,

sincerely yours,

R0 - Reviewer 1 (Nadja Rüger)

Reviewer Recommendation Term: Major Revision

Level of interest: An article of importance in its field

Quality of written English: Acceptable

Declaration of competing interests: I declare that I have no competing interests

General comment

The manuscript uses forest inventory and tree ring data to show that the forests in the Yangambi Biosphere reserve (DRC) are not recovering from past human disturbance (as hypothesized for many areas in West-Central Africa), but likely represent undisturbed forests undergoing gap dynamics. The presented evidence includes continuous recruitment of light-demanding species,

the low share of light demanding species in terms of abundance and basal area, and the high similarity of species composition in areas of the forest where light-demanding species are aggregated and areas where they are not.

Overall, I find the manuscript clear, well-written and the results and interpretations convincing and relevant. In some parts I would have wished for more information regarding the methodology (see below). For example, it remains unclear to me how the pockets were defined and how the tree species were classified.

Specific comments

L19: "different from other forests". It is unclear what "other forests" are. I suggest a more specific formulation, e.g. "different from the surrounding forest" throughout the manuscript.

L31-32: I suggest to omit "because … study".

L91: Why is Bourland et al. cited here? If it is cited because of the same methodology, then a different place would be more appropriate.

L106ff: Here more information is needed, e.g. it is important to state that the transects were 50 m wide. In general, I suggest to integrate the information from Supplementary Methods 1.2. There is some repeated material anyway. Also, I am curious how the species were classified into plant functional types in the cited literature, based on which characteristics. It would also be good to state somewhere that all species that are not listed in Appendix 1 are assumed to be shade-tolerant.

L144ff: I would need some visual information to understand this section, e.g. showing the density of tree of the different plant functional types along the transects. Moreover, it is unclear to me how the extent of the pockets beyond the 50-m wide transect was determined.

L196ff: I don't think it is common practice to refer to Results figures in the Methods section.

L227: POM is not explained.

L247: add "of species composition" after "hierarchical clustering analysis"

L258-259: I suggest to omit "Results of the … Yet"

L289ff: Two decimal places seem to suggest an unjustified degree of accuracy. One decimal place would be enough.

L296-297: "This indicates…" I suggest to move this to the Discussion because it is an interpretation of the results.

L302: add "%" after 5.9

L 305-309: move to Discussion

L305-306: "slower" instead of "less fast"

L 326: I suggest to start the Discussion with a short recap of the goals, the approach and the main findings of the study.

L328-329: again, I think this is too many decimal places

L333ff: Somewhere in this section it would be interesting to talk about the pockets of short-lived pioneers. These gaps must be quite recent and I assume there is information whether the forest was used for agriculture during the last decades.

L347-349: It is unclear why the pockets should represent aggregates of smaller gaps.

L356: Isn't "almost pure" and "monodominant" the same?

L373: add "due" before "to"

L383: I suggest to replace "contrasting" by "continuous"

L388: add "the shape of the" before "size distribution"

L391ff: I think it would make sense to state that decreasing diameter growth rates with size would also contribute to trees accumulating in intermediate diameter classes.

L446-448: I do not agree. Populations of LLPs may be very vulnerable to logging because the mature trees are the seed reservoir of the population and their sporadic recruitment often doesn't make up for the loss through logging (see Ohse et al. 2023).

L509: is there a website that could be cited?

Fig. 2: I would be curious to see the histograms for SLP and NPLD plots as well. The font of the lables is too small and the light-green text is invisible.

Fig. 6: the colors of the heat map are barely visible. Also, it would be good to have a color legend in the figure.

Cited literature:

Ohse, B., et al. 2023. Demographic synthesis for global tree species conservation. Trends in Ecology & Evolution 38: 579-590. DOI: 10.1016/j.tree.2023.01.013

R0 - Handling Editor / Editor in chief (Erwin Dreyer)

Decision letter R0: Major Revision

Dear Mr Nestor Luambua,

We have received the comments provided by an expert in the field about your manuscript (ANFS-D-23-00142), "Light-demanding canopy species are no indicators of past human disturbance in the central Congo basin". As we were unable to collect a second review despite numerous reminders, I decided to rely on this unique assessment, and on a detailed reading of the manuscript (while I am not an expert in tropical forest dynamics).

The topic is very interesting and fits very well into the scope of Annals of Forest Science. The demonstration made that forests in the central Congo basin differ largely from those in the western margins of the Basin in terms of dynamics is a very interesting and important topic. The data set gathered here, and the analyses developed for the demonstration sound very solid and comprehensive. The external reviewer did a nice job in analysing the manuscript and provide quite a number of useful suggestions and raised some concerns that need be addressed during the revision. Moreover, I share the feeling that the manuscript is nicely presented, and I commend the authors for the care taken in

During my reading, I was however rapidly struck by the fact that you published in Ecology and Evolution (November 2021) a paper with exactly the same goals and questions than in the submitted manuscript, and based also on the Yangambi rainforest (DRC). The earlier manuscript was based on a smaller set of species and concentrated only on light demanding species to make the demonstration. As a matter of fact, the demonstration remained inconclusive as was clearly expressed in the paper (this is a typical example of "negative" or "inconclusive" results that indeed deserve publication). The manuscript submitted here differs from the published mainly by the use of a larger range of species and plots including shade tolerant ones. Otherwise, the methods remain similar. Interestingly, the new manuscript was fully rewritten, and there is only little overlap in the text between the two documents).

I am really convinced that publication of this second manuscript is be fully justified, as this illustrates quite nicely the facts that (i) conclusions in ecology (and particularly in forest ecology) depend strongly on data sampling and that (ii) it is sometimes very important to revisit earlier questions with new samples. I therefore believe there is no issue in publishing this second contribution to that interesting question.

However, this needs be made much clearer in the introduction and the construction of the manuscript. The current version is build like a fully new analysis with no reference to the earlier paper until the M&M section. This is counterproductive as it casts some doubts about the validity of the results. I would rather suggest to construct the present manuscript in direct continuity with the earlier one, and using as main driver for the present manuscript: the earlier analysis of the question yielded inconclusive results, which is the reason for coming back to the same question with a different sampling strategy. Doing so would fully justify a new paper on the topic and make this new paper really interesting. This requires a revision of the introduction, which should rapidly refer to the earlier paper and develop how the weaknesses in the earlier sampling would be compensated in the new demonstration, which indeed leads to new and more solid conclusions. I believe that the title should also include the fact that this new manuscript is revisiting an older question with new data.

As stated by the external reviewer, the text is in general clearly written, although it is in places redundant, while several details are missing in the method description.

Although I am not a specialist of such spatial analysis, I made a number of comments about clarity and logic of the text. There are many places where an effort is required to clarify the approach. A

few examples (see my comments in the text): do you use 10 "new" plots or the 43 plots that altogether make the experimental design? Why detail the procedure for ring with analysis when you solely rely on the count to assess tree age? Why not construct the discussion around the 4 hypotheses presented in the introduction and answer them?

We have therefore reached the conclusion that your manuscript may be accepted for publication after a very careful revision and a new round of external reviews. Below, please find the reviewers' comments for your perusal.

With kind regards, and looking forward to the revised version.

Revised Version R1

R1 – Authors

Author's response to editors' and reviewers' comments R1

We thank the editor and the referee for their helpful reviews. Our revisions addressing your comments have substantially improved the paper, though none of its results or conclusions have changed. To address the review comments properly, and to improve the clarity of the manuscript, we have reorganized the materials and methods section. The main structural changes are the following:

- We have integrated the supplementary methods within the methodology section to avoid redundancy.
- To make the materials and methods section clear, we have added a separate sub-section to describe the inventory of focal species in Moni river transects (Luambua et al 2021) and we have shortened the study area sub-section.
- We reworded the "Identifying the location and estimating the size of pockets of light-demanding trees" section to be more clear.

Some paragraphs from the introduction, results and discussion sections were also rewritten substantially to address review comments.

Answers to Editor in chief / Handling Editor

The topic is very interesting and fits very well into the scope of Annals of Forest Science. The demonstration made that forests in the central Congo basin differ largely from those in the western margins of the Basin in terms of dynamics is a very interesting and important topic. The data set gathered here, and the analyses developed for the demonstration sound very solid and comprehensive. The external reviewer did a nice job in analysing the manuscript and provide quite a number of useful suggestions and raised some concerns that need be addressed during the revision. Moreover, I share the feeling that the manuscript is nicely presented, and I commend the authors for the care taken in.

During my reading, I was however rapidly struck by the fact that you published in Ecology and Evolution (November 2021) a paper with exactly the same goals and questions than in the submitted manuscript, and based also on the Yangambi rainforest (DRC). The earlier manuscript was based on a smaller set of species and concentrated only on light demanding species to make the demonstration. As a matter of fact, the demonstration remained inconclusive as was clearly expressed in the paper (this is a typical example of "negative" or "inconclusive" results that indeed deserve publication). The manuscript submitted here differs from the published mainly by the use of a larger range of species and plots including shade tolerant ones. Otherwise, the methods remain similar. Interestingly, the new manuscript was fully rewritten, and there is only little overlap in the text between the two documents).

I am really convinced that publication of this second manuscript is be fully justified, as this illustrates quite nicely the facts that (i) conclusions in ecology (and particularly in forest ecology) depend strongly on data sampling and that (ii) it is sometimes very important to revisit earlier questions with new samples. I therefore believe there is no issue in publishing this second contribution to that interesting question.

However, this needs be made much clearer in the introduction and the construction of the manuscript. The current version is built like a fully new analysis with no reference to the earlier

paper until the M&M section. This is counterproductive as it casts some doubts about the validity of the results. I would rather suggest to construct the present manuscript in direct continuity with the earlier one, and using as main driver for the present manuscript: the earlier analysis of the question yielded inconclusive results, which is the reason for coming back to the same question with a different sampling strategy. Doing so would fully justify a new paper on the topic and make this new paper really interesting. This requires a revision of the introduction, which should rapidly refer to the earlier paper and develop how the weaknesses in the earlier sampling would be compensated in the new demonstration, which indeed leads to new and more solid conclusions. I believe that the title should also include the fact that this new manuscript is revisiting an older question with new data.

We sincerely thank you for your thorough reading of our manuscript and especially for your very positive comprehension of what we want to show. We fully agree that what you suggest will greatly improve the paper. Following your specific recommendation in the pdf, we rephrased the penultimate paragraph of the introduction, explicitly referring to our earlier paper, its conclusion and its shortcoming:

"Therefore, our overall ambition is to test the validity of the 'recovery from human disturbance hypothesis' beyond West-Central Africa. Specifically, data supporting the hypothesis for the vast central Congo basin (representing more than half of the Central African rainforest area), remain extremely limited (White et al. 2021). This is why we set up a monitoring experiment in the Yangambi reserve, located in the heart of the Democratic Republic of Congo (Luambua et al. 2021). In a former study, we showed that the abundance of light demanders in Yangambi cannot be unambiguously attributed to past human disturbances (Luambua et al. 2021). We used a methodological approach that focused on the spatial distribution of the most abundant light demanders, following earlier studies that concentrated on localising and measuring a few light-demanding 'indicator' species (Bourland et al. 2015; Morin-Rivat et al. 2017; Vlam et al. 2017). Yet our former study was inconclusive, just because we tried to draw conclusions on only a subset of species in the forest, ignoring ecological characteristics of the other species (Luambua et al. 2021). Therefore, here we test a few of the assumptions behind the hypothesis by focussing on all species in the forest of Yangambi." (lines 91-104). We also integrated this information in the Key message and in the abstract.

We changed the title to avoid overgeneralization of the results. The former title was: "Light-demanding canopy species are no indicators of past human disturbance in the central Congo basin". While the new title is: "Light-demanding canopy species are no indicators of past human disturbance in the Yangambi rainforest (Democratic Republic of Congo)". This new title is closer to the title of the previous paper: "Spatial patterns of light-demanding tree species in the Yangambi rainforest (Democratic Republic of Congo)".

However, we are not sure if and how we can rephrase the title so that it refers to the fact that this new manuscript is revisiting the older question, and at the same time reflect sufficiently on the new insights? In fact, the present paper is far more conclusive than the old one and this is reflected in the titles of both papers. The previous paper had a title that suggested a mere descriptive analysis of "Spatial patterns of light-demanding tree species in the Yangambi rainforest (Democratic Republic of Congo)", while the present paper has a title summarizing the main finding that "Light-demanding canopy species are no indicators of past human disturbance in the Yangambi rainforest (Democratic Republic of Congo)".

As stated by the external reviewer, the text is in general clearly written, although it is in places redundant, while several details are missing in the method description. Although I am not a specialist of such spatial analysis, I made a number of comments about clarity and logic of the text. There are many places where an effort is required to clarify the approach. A few examples (see my comments in the text):

do you use 10 "new" plots or the 43 plots that altogether make the experimental design?

The additional plots were only used for the clustering analysis. We now rephrased this:

"To determine whether plots within pockets of tree functional types are significantly different from one another, we performed a hierarchical clustering analysis of species composition. To strengthen the clustering analysis, we combined the 10 Moni River plots installed for the purpose of this study, with additional data from 33 plots that were previously installed in mature mixed, mature

monodominant, or pioneer forest in the vicinity of the Moni River catchment (YGB-05 through -31 and YGM-08 through -12) (Kearsley et al. 2013, 2017a, b). This resulted in a full dataset of 43 plots for clustering analysis (10 Moni River plots, plus 33 additional surrounding plots)." (lines 257-264) (answer repeated below).

Why detail the procedure for ring width analysis when you solely rely on the count to assess tree age?

Ring widths were used to estimate the number of missing rings for cores where the pith is missing: "After extracting the cores, they were prepared with a sander (Festool ROTEX RO 150 FEQ) and scanned at 1200 dpi with a high-resolution digital scanner (EPSON Expression 11000XL). Ring widths were measured in two radii per individual, using DHXCT2016 software developed at Woodlab-UGent. In cases where the pith was absent on the core, the distance between the oldest visible ring and the pith was estimated using the degree of arc in this oldest ring (Hietz 2011; Hubau et al. 2019). The number of missing rings close to the pith was estimated as the ratio of the missing distance to the pith and the average ring width of this sample. The age of the tree was therefore considered to be the number of rings counted from the pith to the bark. We used histograms to visualize age distribution of the two functional types." (lines 247-255). (answer repeated below).

Why not construct the discussion around the 4 hypotheses presented in the introduction and answer them?

We actually did this. Each of the subtitles in the discussion is a summarized answer on one of the four research questions from the introduction.

Research question (i) (introduction lines 106-107): do light demanders occur in large 'pockets' occupying large areas of forest?

Discussion subtitle 4.1: Pockets of light-demanders are small and do not occupy large areas of forest

Research question (ii) (introduction lines 107-108): Are light demanders abundant?

Discussion subtitle 4.2: Light-demanding species are not abundant in the pockets

Research question (iii) (lines 108-109): Do they exhibit a regeneration deficit?

Discussion subtitle 4.3: Light-demanding species do not exhibit regeneration deficit

Research question (iv) (lines 109-110): Is species composition in pockets of light demanders different from the surrounding forests?

Discussion subtitle 4.4: Pockets of light-demanders do not differ from surrounding forests

If you prefer, we could change the subtitles in the discussion to represent the research questions rather than formulate them as answers?

Answers to Reviewer 1

The manuscript uses forest inventory and tree ring data to show that the forests in the Yangambi Biosphere reserve (DRC) are not recovering from past human disturbance (as hypothesized for many areas in West-Central Africa), but likely represent undisturbed forests undergoing gap dynamics. The presented evidence includes continuous recruitment of light-demanding species, the low share of light demanding species in terms of abundance and basal area, and the high similarity of species composition in areas of the forest where light-demanding species are aggregated and areas where they are not.

Overall, I find the manuscript clear, well-written and the results and interpretations convincing and relevant. In some parts I would have wished for more information regarding the methodology (see below). For example, it remains unclear to me how the pockets were defined and how the tree species were classified.

We sincerely thank the reviewer for the recommendation and for the positive and constructive comments. We have now improved the methodology section, with special attention to section (2.3) Identifying the location and estimating the size of pockets of light-demanding trees.

We also explained the criteria used in literature to classify tree species in plant functional types. This was previously hidden in a supplementary methods document, but now this is integrated in

section (2.2) Inventory of focal species in Moni river transects (Luambua et al 2021). We refer to our responses below for more information.

Specific comments

Abstract

L19: "different from other forests". It is unclear what "other forests" are. I suggest a more specific formulation, e.g. "different from the surrounding forest" throughout the manuscript.

Thanks for the suggestion. We rephrased here (and elsewhere): "(iv) Is species composition in pockets of light demanders different from the surrounding forests?" (lines 25-26)

L31-32: I suggest to omit "because … study".

We omitted this and rephrased: "We conclude that light-demanding canopy species do not indicate past human disturbance in Yangambi and that they are an intrinsic component of old-growth forests rather than a transient feature of successional forests." (lines 37-39)

Introduction

L91: Why is Bourland et al. cited here? If it is cited because of the same methodology, then a different place would be more appropriate.

We deleted this citation here, keeping only the citation to our previous study (lines 95-96).

Methods

L106ff: Here more information is needed, e.g. it is important to state that the transects were 50 m wide. In general, I suggest to integrate the information from Supplementary Methods 1.2. There is some repeated material anyway. Also, I am curious how the species were classified into plant functional types in the cited literature, based on which characteristics. It would also be good to state somewhere that all species that are not listed in Appendix 1 are assumed to be shade-tolerant.

We now integrated all text from the supplementary Methods into the main text, avoiding repetitions. The transects are now described in the second paragraph of section 2.2: "Therefore, for the previous study, we installed eight parallel transects oriented perpendicular to the Moni River (Fig.1) (Luambua et al. 2021, 2022). Each of these transects is 5 to 8 km long, east-west oriented and separated by ~450 m. Transects were installed by cutting all non-woody vegetation and lianas over a width of 2m. The transects together cover a total length of ~50 km (Luambua et al. 2021). Along the transects, a focal species inventory was carried out over an area of 25 m on the two sides of the transects' baseline (so transects are 50 m wide), covering a total area of ~250 ha (Luambua et al. 2021)." (lines 134-140).

We also included definitions of SLPs, LLPs and NPLDs in the third paragraph of section 2.2: "SLPs and LLPs are heliophilous species that develop optimally, during all of their lives, in bright light conditions, with relative illuminance of at least 30% (Meunier et al. 2015). SLPs have a short lifespan of less than forty years; while LLPs have a longer lifespan. NPLDs are semi-heliophilous species whose seedlings develop optimally in average light conditions, with relative illuminance between 10 and 30% (Meunier et al. 2015)." (lines 145-149).

L144ff: I would need some visual information to understand this section, e.g. showing the density of trees of the different plant functional types along the transects. Moreover, it is unclear to me how the extent of the pockets beyond the 50-m wide transect was determined.

We significantly rewrote this section to better clarify our method of Kernel Density Estimation (this is now section 2.3 Identifying the location and estimating the size of pockets of light-demanding trees). In the results (section 3.1), we explain that "KDE identifies circular hotspots, which is why the pockets extend beyond the transects." (lines 290-291).

We also added a new **Fig.3** showing a detailed representation of some of the pockets: "A detailed representation of some of these pockets, shows the repartition of trees along the transect and the location of pockets of tree functional types, determined by KDE (Fig.3)." (lines 291-294).

L196ff: I don't think it is common practice to refer to Results figures in the Methods section.

We no longer refer to result figures in the Methods section, only to maps (Fig.1-2).

L227: POM is not explained.

POM is now defined at first use: "On each tree, the point of measurement (POM) of the diameter was marked with paint. For trees with buttresses or any deformations at 1.30 m, the POM was taken about 50 cm above the deformation." (lines 210-212).

L247: add "of species composition" after "hierarchical clustering analysis"

We added "of species composition" after "hierarchical clustering analysis" (line 258).

L258-259: I suggest to omit "Results of the … Yet"

This entire paragraph was much simplified as a response to another reviewer: "As species composition can vary within plots, a preliminary subplot-level test revealed a lack of intra-plot heterogeneity. Therefore, full plots were used as sites in the main clustering analysis." (lines 265-267).

Results

L289ff: Two decimal places seem to suggest an unjustified degree of accuracy. One decimal place would be enough.

We have now used a single decimal place to estimate percentages.

L296-297: "This indicates…" I suggest to move this to the Discussion because it is an interpretation of the results.

We rephrased this paragraph: "In our dataset, LLPs are scarce, representing 3.5% of all individuals and 14.6% of the basal area within the group of full inventory plots installed in LLP pockets (Fig.4). Furthermore, they are more abundant in the highest diameter classes, taking up >40% of the basal area in the DBH classes from 80cm onwards within these LLP pockets (Fig.4). LLPs are even scarcer in the mixed old-growth forest outside the pockets (Fig.4), where they represent only 1% of stems and 2.2% of basal area, and where they also do not dominate the basal area in the larger DBH classes." (lines 301-307)

L302: add "%" after 5.9

corrected (line 310).

L 305-309: move to Discussion

We have removed these sentences from Results.

L305-306: "slower" instead of "less fast"

this sentence is removed.

Discussion

L 326: I suggest to start the Discussion with a short recap of the goals, the approach and the main findings of the study.

We now start the discussion with a short recap of the aim and research questions: "The aim of this study was to test the 'recovery from human disturbance hypothesis' for the Yangambi rainforest, focussing on the following specific research questions: (i) do light demanders occur in large 'pockets' occupying large areas of forest? (ii) are light demanders abundant in their pockets? (iii) do light demanders exhibit a regeneration deficit? (iv) is species composition in pockets of light demanders different from the surrounding forests? The sections below answer these questions one-by-one, ending with a discussion on the implications of our findings." (lines 333-339).

L328-329: again, I think this is too many decimal places

We have reduced it to 1 decimal place (lines 344-345).

L333ff: Somewhere in this section it would be interesting to talk about the pockets of short-lived pioneers. These gaps must be quite recent and I assume there is information whether the forest was used for agriculture during the last decades.

We added a few lines on the SLP gaps at the start of discussion section 4.1: "The two SLP pockets identified are large (Fig.1) and the abundance of short-lived pioneer trees indicates recent forest disturbance. The largest of them was clearly a wind-throw event, while the other one was a farmland (Fig.1) (Luambua et al. 2021)." (lines 341-343).

L347-349: It is unclear why the pockets should represent aggregates of smaller gaps.

We rephrased this: "The 'pockets' of light-demanders in the Moni transects (Fig.1) fall within the range of the intermediate gaps, indicating that small gaps are probably not detected by the KDE approach, focussing on just a few indicator species." (lines 362-365).

L356: Isn't "almost pure" and "monodominant" the same?

The two terms are close, but by "monodominant stand" we mean a stand where one taxon dominates (at a certain percentage, e.g. 60-80% of individuals), whereas "almost pure stand" is an

almost monospecific stand (around 100% of individuals belong to a single species). By "almost pure monodominant stand" we mean a monodominant stand that tends towards a pure stand.

L373: add "due" before "to"

We have added "due" as requested. (line 390).

L383: I suggest to replace "contrasting" by "continuous"

We rephrased: "However, LLPs in our study site show a DBH distribution that is contrasting with the age distribution (Fig.7)" (lines 401-402).

L388: add "the shape of the" before "size distribution"

We've added "the shape of the" as requested. (line 407).

L391ff: "Long-lived pioneers typically have high juvenile growth rates, which produce bell-shaped size distributions: fast juvenile growth quickly removes recruits from the lower size classes and increases stem counts in higher size classes." I think it would make sense to state that decreasing diameter growth rates with size would also contribute to trees accumulating in intermediate diameter classes.

We rephrased it as follows: "The decrease in diameter growth rates with size for LLP species contributes to trees accumulating in the intermediate diameter classes, producing bell-shaped size distributions." (lines 410-411)

L446-448: I do not agree. Populations of LLPs may be very vulnerable to logging because the mature trees are the seed reservoir of the population and their sporadic recruitment often doesn't make up for the loss through logging (see Ohse et al. 2023).

we agree and we added this notion: "Our results, together with previously published analysis, show that such practices are not needed in the intact (unlogged) Yangambi rainforest, as the populations of the present LLPs are likely stable as an inherent element of the mature rainforest. On the contrary, populations of LLPs may be very vulnerable to logging because the few large individuals are the seed reservoirs of the population and their sporadic emergence to large sizes often doesn't make up for the loss through logging (Ohse et al. 2023)." (lines 470-476).

It is true that most light-demanding species are also exploited timber species (Ouédraogo et al., 2011). Some previous literature (e.g. Morin-Rivat et al., 2017), based among other things on the regeneration deficit deduced from the size distribution of trees, proposed to create openings in the forest canopy to allow light to reach the ground and thus promote the regeneration/recruitment of light-demanding species in order to guarantee the stock of wood to be exploited in the future. In this study, we carried out an analysis of unharvested natural forests. The age distribution shows that LLPs do not have a regeneration deficit. They are stable in an unharvested natural forest because they regenerate naturally following the gap dynamics. There is therefore no need to create openings in the canopy to boost the regeneration of LLPs. However, in a logging context, LLP populations can indeed be very vulnerable if loggers have not taken care to leave certain mature trees as "seed trees" as required by regulations. The loss of volume due to logging is often not compensated before the next rotation, mainly because of the short rotation duration (see Ohse et al. 2023). Ohse et al (2023) propose that the logging rotation duration should be determined by the "age at minimum commercial size", which is probably correlated with reproductive age. They also suggest increasing minimum cutting diameters to improve regeneration for certain species.

References

L509: is there a website that could be cited?

We have corrected this error by referring to the Thornton 1983 book (line 379).

Figures

Fig. 2: I would be curious to see the histograms for SLP and NPLD plots as well. The font of the labels is too small and the light-green text is invisible.

This is now **Fig.4**. We plotted histograms for all tree functional types and we changed the font of all text to black for visibility.

Fig. 6: the colors of the heat map are barely visible. Also, it would be good to have a color legend in the figure.

This is now **Fig.8**. We increased the contrast of the heatmap to improve visibility and we added a color legend in the figure.

Cited literature

Ohse, B., et al. 2023. Demographic synthesis for global tree species conservation. Trends in Ecology & Evolution 38: 579-590. DOI: 10.1016/j.tree.2023.01.013

We now cite this publication in line 476.

R1 - Handling Editor / Editor in chief (Erwin Dreyer)

Recommendation R1: Accept with minor modifications

Dear Mr Nestor Luambua,

I thank you warmly for the careful revision made for your manuscript (ANFS-D-23-00142R1), 'Light-demanding canopy species are no indicators of past human disturbance in the Yangambi rainforest (Democratic Republic of Congo)', submitted to Annals of Forest Science.

The revised version very nicely addressed all comments and suggestions made by the external reviewer and myself acting as handling editor of this submission. The external reviewer was unable to provide a novel assessment of this revision, and I read carefully the new version. I found the new version much clearer with respect to the earlier paper and to the addition provided here and its consequences for the main conclusion. This shows nicely how science evolves (new data help clarify earlier questions) and shows also the difficulties forest ecologists are confronted to when they try to reconstruct the demographic dynamics in complex forests like the tropical forests.

I have only one major concern: despite its importance and the nimber of experimental monitoring operations made at Yangambi forest, what is its representativity? Can your results be generalised to the Central Congo basin, or is there still a need to confirm such results in other parts of the forest?

As a conclusion, I believe the manuscript is almost ready for publication. Please address my comments and send us the revised version, which would then undergo a last step of quality control before going to production.

Further comments are listed in the attached copy of the manuscript and are mostly suggestions about writing and presentation. Below, please find the reviewers' comments for your perusal.

With kind regards.

Revised Version R2

R2 – Authors

Author's response to editors' and reviewers' comments R2

We thank the editor and the referee for their further helpful comments. This new revision has not altered any of our results or conclusions. Some sentences have been deleted and some words changed, taking your (pdf) comments into account. We added a paragraph at the end of the discussion to address your major question.

Answers to Editor in chief

The revised version very nicely addressed all comments and suggestions made by the external reviewer and myself acting as handling editor of this submission. The external reviewer was unable to provide a novel assessment of this revision, and I read carefully the new version. I found the new version much clearer with respect to the earlier paper and to the addition provided here and its consequences for the main conclusion. This shows nicely how science evolves (new data help clarify earlier questions) and shows also the difficulties forest ecologists are confronted to when they try to reconstruct the demographic dynamics in complex forests like the tropical forests.

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As a conclusion, I believe the manuscript is almost ready for publication. Please address my comments and send us the revised version, which would then undergo a last step of quality control before going to production.

Once again, we would like to thank you sincerely for your thorough reading of our manuscript and for your comprehension of what we want to show. We believe that one of the major contributions of the revisions of this paper, is that we down-tuned on the generalization of our results. As our paper presents a case study, we now humbly present our results as being representative for the Yangambi forest in the first place. However, we do agree that the discussion needs a careful reflection on if and how we can proceed to generalize our results. In line with the idea that science is an ever-evolving process, we believe that a recommendation for further and more in-depth research is a logical answer to your question. We therefore added the following paragraph at the end of the discussion (lines 463-475):

"Our study area is representative for a large area of the Congo basin, because it is situated in the transition zone between two widely distributed forest types: evergreen and semi-deciduous forests (Réjou-Méchain et al. 2021). However, more sites within these species-rich forests should be investigated using a holistic approach based on synecology of functional groups, before conclusions can be generalised or extrapolated to the entire Congo basin (Liira et al. 2019). We recommend to further test the 'recovery from human disturbance hypothesis' through analysis of full inventory plots, with a special focus on recruitment, growth, and mortality of trees within all functional groups (SLP, LLP, NPLD, ST) and all life stages (from young seedlings to old mature trees). We specifically recommend investing in permanent inventory plots following the ForestGEO protocol (Davies et al. 2021). Such plots are large (10 ha or more), include small trees (DBH < 10 cm) in the inventory and are therefore labour- time- and cost-intensive to install and remeasure. However, data of such plots is key to understand why tree species coexist (Davies et al. 2021)."

R2 – Editor in chief (Erwin Dreyer)

Decision R2: Accept with minor modifications