




Is it possible to model and predict the growth of mixed-forests under a changing climate : some answers provided by the new model « PDG-Arena » developed on the CAPSIS platform.

Erwin Dreyer  based on peer reviews by **Harald Bugmann** and 1 anonymous reviewer

Camille Rouet, Hendrik Davi, Arsène Druel, Bruno Fady, Xavier Morin (2024) PDG-Arena: An ecophysiological model for characterizing tree-tree interactions in heterogeneous and mixed stands. bioRxiv, ver. 3, peer-reviewed and recommended by Peer Community in Forest and Wood Sciences. <https://doi.org/10.1101/2024.02.09.579667>

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This interesting preprint develops a new model with a quite strange name (see below why this name was used by the authors) that aims at describing the growth of mixed forests (it may also be used for monospecific forests with a regular or irregular structure). It is based on two main features: it is a process-based model that integrates a tree-tree interaction module. The model derives from the modelling framework « Physio-demo-genetics model PDG » developed earlier at INRAE-Avignon, and « Castanea », developed at Orsay and Avignon as a widely used stand-level process-based model. « Arena » underlines the competition between trees in mixed stands. The « PDG-Arena » model was developed on the Capsis platform (<https://capsis.irad.fr/capsis/presentation>), which is a shared platform for the development of tree growth models under a very open framework maintained by several French institutions.

The reviewers and the recommender saw two important strengths in the preprint : (i) PDG-Arena is definitely a significant improvement when compared to the existing models and may be used for accurately predicting the growth and dynamics of mixed stands ; (ii) it was validated against an impressive data set gained in a quite impressive network of mixed stands of beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) with a 5-year

growth analysis at individual tree level (based on two detailed surveys at individual tree level. PDG-Arena could properly predict the growth of these stands and showed significant improvements for the existing models.

During the review process, many important questions were raised, some directly related to the manuscript (which the authors addressed very convincingly during the revision of the first version of the preprint), and some referring to more general debates around predictive forest growth models able to integrate long-term changes. For instance, the long-lasting debate opposing the proponents of process-based forest growth models (that might require a large number of sometimes difficult-to-document processes leading to growth predictions, Forrester et al. 2016) and phenomenological models that directly link actual (recorded) growth and stand dynamics to climate and soil variables, is not yet settled. Both approaches display strengths and weaknesses. Similarly, the ability of both families of models to predict the impact of extreme events induced by climate change (like severe drought episodes associated to high temperatures likely to happen at higher frequencies in the near future) remains to be assessed and is the main challenge for this area of research.

A second question that raises large interest is whether mixed forest stands display a larger resilience to future climate changes than monospecific and homogenous stands. Camille Rouet and his colleagues present convincing results that this is the case (both using their model and from the recorded data). However, there is still debate whether the observed over-yielding in mixed forests under favourable conditions will be maintained under severe drought episodes and after a return to more favourable water availability and moderate temperatures (Jourdan et al, 2019; Jourdan et al, 2020).

The model is available for testing under the condition of participating to the CAPSIS community (which gives access to the shared resources available on the platform. The codes and data used to test the performance of the model can be accessed on the Zenodo data repository.

This preprint should open the way for fruitful cooperation and further improvements in a very important area for forest science in the near future.

References:

- Camille Rouet, Hendrik Davi, Arsène Druel, Bruno Fady, Xavier Morin (2024) PDG-Arena: An ecophysiological model for characterizing tree-tree interactions in heterogeneous and mixed stands. bioRxiv, ver.3 peer-reviewed and recommended by PCI Forest and Wood Sciences <https://doi.org/10.1101/2024.02.09.579667>
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Reviews

Evaluation round #2

DOI or URL of the preprint: <https://doi.org/10.1101/2024.02.09.579667>

Version of the preprint: 2

Authors' reply, 29 August 2024

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Decision by [Erwin Dreyer](#) , posted 24 August 2024, validated 26 August 2024

Dear Camille Rouet

The revised version of the preprint " PDG-Arena: An ecophysiological model for characterizing tree-tree interactions in heterogeneous and mixed stands" has been examined again by the two reviewers who did the first round of reviews. Their comments were very positive, and as can be seen in their brief assessments, they believe the preprint can now be recommended. I completely agree with their assessment and am ready to recommend the preprint after a small number of rather technical changes in the presentation of the text and the data set associated with the preprint.

Detailed suggestions:

Preprint text:

1. Please provide a revised version without correction marks for the final recommendation and link. The correction marks were indeed very useful for assessing the changes made during the revision, but are no longer useful (the current version 2 on BioRxiv is fine).
2. A last proofreading of the V2 on BioRxiv would be useful to correct very minor typos along the text and produce the final, recommended version.
3. Please add to the preprint the reference to the data set under the classical format of a reference citation. The data set is a production per se and needs to be identified and referenced like other productions.
4. In the list of data files, there is an incomplete reference to a code page (which is probably obsolete and of no use. Please remove it (or we can do it for you).
5. Please provide in the preprint an account for the different contributions of the co-authors (using the CreDIt taxonomy) and

Data and code sets:

Thank you for completing the data set and clarifying its presentation. I would nevertheless recommend a few additional changes:

1. Please provide a full title to the data set, and author names (i.e., all contributors to the data set). The title and author list may differ from those of the preprint. This, together with the DOI of the data set, will make it fully citable and easily findable.
2. The presentation text detailing the presented data and codes could be slightly extended and completed to better introduce the different formats and files (there are many...). This might help potential reusers of the data set and the codes. The model code is also presented on a different page with a different DOI: please provide a title and the list of the authors and cite it in the reference list of the preprint.
3. Please clarify the relationship to the Capsis platform: is there information available on this platform that is of importance for running the model? Please clarify this relationship.
4. It will always be possible to complete the data sets with additional data in the future (crown section data for instance).

We thank you very much for processing these last steps and are ready to prepare the final recommendation immediately after these last changes have been made.

With best regards and looking forward to the very final version of the preprint and the associated data.

Erwin Dreyer, recommender of this preprint in Peer Community of Forest and Wood Sciences.

Nancy, August 23, 2024.

Reviewed by [Harald Bugmann](#), 10 August 2024

I greatly appreciate the considerable efforts that the authors have spent to deal with my review comments. Their responses and the corresponding changes to the text are very good and convincing. Some issues will always remain, both with the model as well as with the data (we never have the "ideal" model, and data have their own pitfalls), but the authors have done a very good job clarifying what they have done, and in many instances even changing their approach (e.g. re. LAI). I think the manuscript is ready to go now. Congratulations! :-)

Reviewed by anonymous reviewer 1, 02 July 2024

I thank the authors for the detailed replies and have no further questions or comments on the manuscript.

Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.1101/2024.02.09.579667>

Version of the preprint: 1

Authors' reply, 21 June 2024

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Decision by [Erwin Dreyer](#) , posted 20 April 2024, validated 22 April 2024

A revision of the preprint is required before recommendation may be considered.

Dear authors

Your preprint presents a new extension to the well known process-based forest growth model "Castanea" developed several years ago and quite widely used. This new version aims at addressing mixed forest stands with two or three dominant or co-dominant species and taking this mixture explicitly into account for the simulations. The preprint is quite nicely and clearly presented, presents in details the additional processes integrated in this new model with respect to the older "Catanea" version, and aims at testing its performance by comparing its output with that of Castanea, and with real growth in 19 mixed stands. This is a beautiful and interesting exercise.

The preprint has been reviewed by two specialists in this field who provided numerous insightful comments about the construction of the preprint, the output of the new model (does it produce more accurate predictions?), and the discussion (are the most important shortcomings of the model predictions identified and discussed?). The reviews are very detailed, and the reviewers (an anonymous reviewer and Harald Bugmann from ETH) provided a very detailed (and in places critical) examination of the preprint.

Interestingly, the comments raise the long lasting debate between defenders of (as explicit as possible) process-based models and of more empirical (phenomenological) models, and show that this debate is still very active and up-to-date. This point is particularly questioned by Harald Bugman in his analysis about the shortcomings he identified in the presented PDG-Arena model. Well, as a (former) tree ecophysicologist, I would favor process-based models, but indeed, as the applications take into account local diversity in forest structure and composition, such models are getting more complicated, require more parameters and loose flexibility. Anyway, the preprint is not aimed at solving this debate but at presenting PDG-Arena in details with a nice attempt to exemplify its actual performance in real situations. But it might be better taken into account in the discussion of the preprint.

I went myself (as a non expert) through the preprint and provided a few comments that might be found in the attached copy of the pre-print). I found that the presentation and structure of the preprint in in most instances quite clear and providing many data and approaches that contribute to a critical appraisal of the performance of the model. This really justifies recommendation of the preprint, however after a very careful revision. I had also a look at the data presented in the Zenodo repository. Although they are easily accessed, I had the feeling that they would require a careful description of the differetn data sets (I was unable to find it) in order to facilitate potential reuse.

My decision is therefore that the preprint requires a revision based on the suggestions made by the two reviewers and myself for clarity, and for a potential extension of the discussion to handle some critical issues behind such detailed modelling procedures. In addtion, we expect you prepare a detailed letter indicating how the suggestions and comments of the reviewers were addressed during the revision process. A final decision would then be taken based on this new version. [Download recommender's annotations](#)

Reviewed by [Harald Bugmann](#), 14 April 2024

General comments

In this manuscript, the authors develop the well-known physiological model CASTANEA/PDG further to be able to evaluate tree mixtures and the impacts of this diversity on productivity. The resulting model is called PDG-Arena (note that it is not explained anywhere why this is "Arena"). The authors are using this model to simulate 39 forest plots ($r = 10$ m, i.e. merely 314 m² each) from three sites that feature different mixtures (as well as monospecific plots). They use a smart design to "regularize" the measured plots towards uniform distributions of trees in horizontal space as well as mimicking single-species plots where in reality there are mixed-species plots; this allows them to disentangle the diversity effects nicely.

The results suggest that (1) PDG-Arena performs somewhat better than CASTANEA for these plots, and (2) that there is a small positive biodiversity effect indeed.

The development of PDG-Arena is described coherently and in a transparent manner. Yet, there is some discrepancy between the plea of the authors that mechanistic, ecophysiologicaly-based formulations need to be sought, and the fact that multiple simplifying assumptions are made that are countering this endeavor somewhat; for example that trunks are ignored for the calculation of radiation although it is known that they can absorb a considerable fraction of the sunlight, and are also important for backscattering; or the assumption that there is no differentiation between trees (in terms of sizes or species) regarding rooting behavior, which likely has strong implications for water competition in real stands. Undoubtedly any model needs to be based on simplifying assumptions. Some of them are addressed in the Discussion section (e.g. the rooting problem), but they are not put in context with the results of the study, unfortunately. Others are not addressed at all.

There are larger worries regarding the data used for benchmarking the simulations. The description of the data is not very clear. I presume that an initial inventory of the 39 plots was made in 1996 (this is why the simulations are starting in 1996), but no further inventories were executed (this is not clarified anywhere). It then appears that the growth of the trees was analyzed using dendrochronology (l. 213). It would be important to know whether all 1177 stems (l. 277) were cored indeed (this would be a huge amount of work!), or whether this was done only for a subset of the trees; but this is not stated anywhere. More importantly, tree height was

assumed to be constant (l. 208), i.e. no height increment was simulated over 17 years (1996-2013), whereas growth was assumed to be BAI times tree height, which induces a strong bias in the simulation results as well as in the data (assuming that woody increment was calculated from the data using the same assumption - this is not stated anywhere, though). But if height was constant indeed, why not compare BAI (obs) against BAI (sim)? This would be a much more straightforward comparison (let's not even think about issues such as form factors etc.).

The simulation results nicely show the patterns hypothesized by the authors. Yet, they left me concerned. On the one hand, the effects induced by moving from CASTANEA to the three simulation studies with PDG-Arena (using three assumptions re. stand structure) are really very minor (Tab. 3 of the manuscript), with the r^2 always being >0.965 . Hence we are talking about minute effects here. On the other hand, the performance of any of the simulations appears poor to very poor (Tab. 4 of the manuscript) compared to measured (?; cf. above - what was actually measured, and how?) wood volume increment. Clearly PDG-Arena has the best performance, but this does not exceed an r^2 of 0.5 and does not go below an error of 34%, which is clearly not satisfactory. Thus, the question arises whether these results can actually be trusted. It appears that both models would need to undergo additional development to be able to represent stand growth over a period of 17 years accurately, particularly since the initial situation was taken exactly from the measurements (inventory).

In that same context, the authors mention that LAI data are from the recent drought period (l. 216 and 418) whereas the inventory data are from nearly 30 yrs ago. This may explain the divergence between LAI values of ca. 3 (single-sided, I presume) and the very high BA values (ca. 50-60 m²/ha), which are hard to reconcile and may lead to strong inconsistencies in a model that is driven by radiation, and thus LAI. It is not clear whether LAI was set to a constant across the simulation time, using the 2022/2023 values. This would be a highly debatable assumption.

Importantly, one aspect that would be key for simulations across multiple years with a dynamic model is not addressed in the results shown in this study at all: it appears that all that is tested is diameter increment (and indirectly, volume increment using a static tree height), but not the development of any other tree characteristics such as height, the height of the crown base, leaf mass or leaf area, let alone allocation to belowground compartments (for which admittedly there would most likely not be any data). It would have been highly insightful to compare the simulated stands at the end of the inventory period (2013 - was there really no inventory carried out at that point in time?) against measurements. Focusing the comparison on simulated GPP among models and woody increment between models and a tree ring reconstruction leaves many questions unanswered. The inference drawn in this manuscript re. biodiversity effects is only believable if PDG-Arena is shown to realistically reflect the dynamics of these 39 plots, but the manuscript falls short in this regard, I am sorry to say.

The Discussion is relatively short and not structured very well. This should be reconsidered.

Detailed comments (by line numbers of the manuscript)

Abstract: is basically fine, but contains a few typos. Pls check (I cannot refer to line numbers here).

9: replace "if" by "even though".

119: "dynamic" -> "dynamics".

127: excess comma after "multi-layer".

138f.: cumbersome wording; better "are expressed on a per area basis, e.g. gross primary production is expressed as gC/m²". The use of "soil" and "surface" is confusing in this context.

Fig. 1: The caption needs to be re-worked. The use of "hold" (and "held") should be replaced by verbs such as "calculate" or "perform"; si en français on peut dire "tenir/tenu" (honnêtement, je ne sais pas), ça ne se traduit pas en "hold/held". Also, "a trees crowns" is not correct grammar. Either "a tree's crown", or "the trees' crowns", or something similar.

142: wording issue - "the projected area of the individual crowns" (again, avoid "surface" here). I think this would say it all, and the comparison to the stand area is simply not needed.

159: omit second occurrence of "water" (not needed).

186: "operates two executions" is cumbersome wording. Replace by something like "evaluates light conditions using SamsaraLight in two steps for every simulation year".

188: "radiations" -> "radiation" (twice). This is probably the same thing as "les précipitations", which is simply "precipitation" in English. No plural possible here.

189: omit "every year".

193: "a" -> "the" (it is not a model, but "the model" here).

197: I was confused by the word "parameter" here. These are variables that should change dynamically in the model, right? A parameter is a constant. I appreciate that later we are told that h and hcb are held constant in the simulations, but here they should still be called "variables".

273: "at plot" -> "at the plot".

277: were indeed all 1177 trees cored? Was this done in 2014, and this is the reason why the time series extends to 2013 only? Or was a second (?) inventory done in 2013 (cf. l. 281)? This should be clarified. If the reader does not understand the data, the benchmarking cannot be understood fully either.

279: so was tree height kept constant across time? This is not clear either.

281: How many field inventories have been made? Just one in 1996? If more are available, why weren't they used for the benchmarking of the models (cf. General comments)?

289: Although I am intrigued by the approach taken here to generate synthetic stands that systematically miss certain aspects (compared to reality) such as species or species interactions, I found the description very difficult to follow and am not really sure I have understood. The setup O is straightforward, and in the setup RS tree positions were "regularized" (not sure this is a proper English term, but I understand). But what is the essence of the difference between RS and RN? This remains elusive to me, even after repeated reading of l. 293-297. Pls re-consider.

333: "informs" -> "inform".

334: it is not about the "presence" of physiological processes, but their importance. Pls adjust.

344: not clear what "modalities" is referring to here - the different sets of simulations, I guess? The term has not been used before, I think, and therefore should be avoided.

349-351: yes I agree, but the differences are really minute (cf. General comments).

352: "Modeling" -> "Model" ("modeling" refers to the process of developing the model).

398: "of" -> "or".

404-407: yes I agree, but on a (very) low level. Are the differences trustworthy if model performance is so low (cf. General comments)?

417: why is Bauges singled out here? cf. l. 217.

432: fix reference (parenthesis issue).

445: excess comma after "fluxes".

448-450: this is - theoretically - possible; however I have the strong feeling that the smallest fraction of the poor model performance is due to the climate interpolation. I am not convinced that this has deserved such prominence here.

466: perhaps have a separate section "Conclusions"?

467: "accurately simulate"... based on this study? I think this is an overstatement.

Reviewed by anonymous reviewer 1, 11 March 2024

The authors built a new model by introducing tree species interaction into CASTANEA. Trees compete for water and light. Models with and without interaction are tested against each other for several sites with beech and fir. Including interaction between trees improved the performance of the model when compared with measurements.

Interaction between trees, of the same or different species, is an area where we have little knowledge. At the same time it is the belief that mixing tree species is a way to increase the resilience of forest ecosystems. Having a model that can reliably represent tree interaction is therefore very valuable, especially since there

are not many of these models. Hence, the presented model and the promising results of this paper add an important tool to the toolbox of forest resilience researchers.

Some questions/remarks, in no particular order:

1) Competition for water and light is implemented, but there is no competition for nutrients, even if the authors themselves mention it in the introduction as being important (line 45). Shortly mentioning why this has not been done (and maybe possible consequences?) would be helpful. Maybe either in relation to mentioning 'limiting resources' (line 436), or when discussing possible improvements of the model (lines 451-465)?

2) What is meant by global change? (e.g. line 49)

3) If there is limited water available, is all water divided equally among the trees? Or is water uptake connected to transpiration? In other words, how does competition for water take place? (section 2.1.2)

4) There is no vertical or horizontal differentiation of soil water availability (lines 160-164). For the lack of horizontal differentiation an explanation is added, but not for the lack of vertical differentiation (although it is discussed in the discussion). I suggest either discussing/mentioning both here (lines 163-164), or neither (and discuss both in the discussion).

5) Calling mixing two different tree species „biodiversity“ is a bit of a stretch. After all, one can think of many more factors being of importance for biodiversity that all contribute to „maintaining key ecosystem services“ (line 5-6). I'm fully aware that it is difficult to quantify biodiversity or to somehow distill it out of model results and I agree that using the number of different tree species is a good first step/approximation, but I would be careful with the terminology. I propose to change the ‚net biodiversity effect (NBE)‘ to net mixing effect, or something along those lines, or otherwise clearly state that number of tree species is used as a proxy for biodiversity.

6) Since the paper introduces a new model, I think it would be nice to shortly discuss the limits/opportunities of the model. For what kind of setups can it be used? What are the size limitations of the plots? Can it be used for more than two different tree species? Can trees completely cover each other (undergrowth)? Etcetera

I didn't specifically check for typos/grammar, but here are the ones I came across:

Abstract: the model builds upon a validated...

Line 31: „different nature“, different than what?

Line 52: confounding factorS

Line 56: To what does „this approach“ refer? I assume a modelling approach or something like that?

Line 62: community compositionS

Line 74: When it comes to simulatING

Line 218: proportional

Line 333: to inform us

Line 398: more OR less

Line 562: attenuation coefficientS

Line 570: through the canopy