



Peer Community In

Forest & Wood Sciences

Common gardens are essential tools to study forest tree adaptation: a case study with the European black pine

Laurent Bouffier  based on peer reviews by **Richard Whittet** , **Milan Lstiburek** and 1 anonymous reviewer

Guia Giovannelli, Clara Tallieu, Hendrik Davi, Frédéric Guibal, Caroline Scotti-Saintagne, Bruno Fady (2026) Adaptive effects of geographic origin on tree ring width and radial growth -climate relationships in *Pinus nigra* Arnold, the European black pine. HAL, ver. 2, peer-reviewed and recommended by Peer Community in Forest and Wood Sciences.

<https://hal.inrae.fr/hal-05528456>

Submitted: 05 August 2025, Recommended: 16 April 2026

Cite this recommendation as:

Bouffier, L. (2026) Common gardens are essential tools to study forest tree adaptation: a case study with the European black pine. *Peer Community in Forest and Wood Sciences*, 100188.

<https://doi.org/10.24072/pci.forestwoodsci.100188>

Published: 16 April 2026

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Common gardens (or tree provenance trials) consist of collections of trees from various geographical origins (provenances) planted across several test sites. These experimental plantations aim to study adaptation to different environmental conditions through both genetic differentiation and phenotypic plasticity (Leites and Benito Garzón, 2023). Improving our understanding of how different geographic origins of a forest tree species perform across contrasting environments is essential for selecting appropriate Forest Reproductive Material (FRM) for plantations.

A network of European black pine (*Pinus nigra*) common gardens was established in the 1970s across four bioclimatically contrasting sites, including sixteen provenances representing four subspecies (*P. n. laricio*, *P. n. nigra*, *P. n. pallasiana*, *P. n. salzmannii*). Giovannelli *et al.* (2026) conducted a retrospective analysis based on increment cores collected from 867 trees. Annual radial growth over more than 40 years was analyzed in relation to monthly climatic variables (minimum temperature, maximum temperature, and precipitation). The authors identified general trends: late spring minimum temperatures negatively affected annual growth, whereas early summer precipitation had a positive effect. However, climate effects varied both among provenances and between sites. In addition, phenotypic plasticity was high across the four sites, with some changes in the ranking of provenances. This study provides valuable insights for forest managers aiming to select the most

suitable provenance -or mixtures of provenances - depending on plantation location and expected future climate conditions.

Finally, I acknowledge the constructive exchanges between the reviewers and the authors, which contributed to improving the clarity and readability of the manuscript.

References:

Leites, L., Benito Garzón, M. (2023). Forest tree species adaptation to climate across biomes: Building on the legacy of ecological genetics to anticipate responses to climate change. *Global Change Biology*, 29, 4711–4730. <https://doi.org/10.1111/gcb.16711>

Guia Giovannelli, Clara Tallieu, Hendrik Davi, Frédéric Guibal, Caroline Scotti-Saintagne, Bruno Fady (2026) Adaptive effects of geographic origin on tree ring width and radial growth - climate relationships in *Pinus nigra* Arnold, the European black pine. HAL, ver.2 peer-reviewed and recommended by PCI Forest and Wood Sciences <https://hal.inrae.fr/hal-05528456>

Reviews

Evaluation round #2

DOI or URL of the preprint: <https://hal.inrae.fr/hal-05528456>

Version of the preprint: 2

Authors' reply, 14 April 2026

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Decision by Laurent Bouffier , posted 07 April 2026, validated 08 April 2026

Dear Authors,

Two reviewers have now evaluated the revised version of your manuscript, and both highlight its substantial improvement. You have addressed and incorporated most of the comments raised during the first round of reviews. I would like to thank you for this thorough work, which has significantly enhanced the clarity of the manuscript, with a focus on the relationships between radial growth and climate.

The statistical approach has been considerably simplified through the use of a single ANOVA. One reviewer expressed some reservations regarding the chosen statistical model. However, I find the authors' justification for not including a provenance effect nested within subspecies — given the presence of admixture in many provenances — to be acceptable. I agree with this reviewer that a full ANOVA model would be more powerful than response functions for analyzing G×E interactions. That said, G×E interactions no longer appear to be the primary focus of the manuscript, as the emphasis is now placed on rank changes between sites.

One reviewer has suggested a few minor editorial revisions. I encourage the authors to address these points, after which I would be pleased to recommend the manuscript in PCI FWS.

Best regards,

Laurent Bouffier

Reviewed by Richard Whittet , 27 March 2026

The manuscript is now much clearer and simpler and so it is easier to pick out the main messages, so I am very happy to recommend it. Well done to the authors. I have a few final (mostly editorial) comments for their consideration:

Line 212-213 Individual annual ring-widths (rw) were calculated as the mean of the two radii collected on each tree.

Line 292-295. Hard to read at first, could split it up to specify that you are presenting range in site, then ssp., then provenance

Line 305. Empty parentheses

Figure 3. Sorry I didn't pick up on this earlier but I might suggest transposing this table so that sites are on the vertical and climate variables are on the horizontal – it would make it easier to compare across sites.

Table 5. Just a suggestion to improve column names. First assumption when looking at it is that they refer to specific years, 7 and 16. Also a typo in Levens Blokc/Prov

463. Edit for clarity: significant positive influence of [high/low] spring temperatures and [high/low] early summer precipitation

465. Italicise name

476. Reword to 'winters that are too warm'

492-494. Is it relevant to compare studies directly (i.e. "lower than ours") where they contain completely different taxa and designs? It would be better to frame this by saying something like: "other studies have generally found that large site effects rendered provenance effects very small. In this study, despite there also being substantial differences among sites, we detected significant differences among provenances that have biologically plausible interpretation" – which would set you well to provide interpretation in the rest of the discussion.

Reviewed by anonymous reviewer 1, 20 March 2026

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Evaluation round #1

DOI or URL of the preprint: <https://hal.inrae.fr/hal-05195614>

Version of the preprint: 1

Authors' reply, 26 February 2026

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Decision by Laurent Bouffier , posted 20 October 2025, validated 20 October 2025

Editorial decision for Round #1

The submitted preprint presents a very large dataset from four European black pine (*Pinus nigra*) common gardens. Radial growth measurements from increment cores are used to assess variations in climate–growth relationships and to estimate genetic, plasticity, and GxE effects.

I warmly thank the authors for submitting their preprint to the Peer Community in Forest & Wood Sciences, and I thank the three reviewers for the quality of their evaluation. Based on the comments of the reviewers as well as my own reading of the manuscript, my editorial decision is to invite the authors to undertake a major revision of their manuscript.

This is undeniably a very rich dataset. However, the three reviewers have identified major issues regarding the statistical analyses. I fully agree with their concerns and strongly encourage the authors to address them thoroughly. In particular, for the general analysis based on the 7 provenances (Equation 2), a Provenance x Site interaction would likely be more appropriate than a nested effect to evaluate plasticity. It is also highly probable that residual variance differs among sites. This should be tested, and the statistical model adapted accordingly.

The selection of trees for core sampling must be clearly justified and discussed. As highlighted by Reviewer 3, the sampling strategy may have introduced bias. The number of trees with ring measurements should be added to Table 1. The data available in Fady et al. (2024) correspond to a larger dataset than the one used in this preprint. I strongly recommend adding a dedicated Readme file dedicated to this preprint, allowing readers to easily extract the subset of data used to reproduce the analyses or test alternative statistical models. For example, I was unable to find the ring measurements in Cestas (01-4200-09-02) for all 300 trees sampled (15 provenances x 20 trees).

The manuscript is generally well written, but I agree with Reviewer 2 that the results section is very dense. I encourage the authors to rewrite it, potentially using appendices to improve readability.

This preprint has the potential to become a very nice contribution to the literature. I really encourage the authors to undertake the revisions requested by the three reviewers. Once revised, the manuscript will be submitted to the same reviewers before any decision.

I look forward to reading the revised version.

Reviewed by Milan Lstiburek, 17 October 2025

I fully agree that this is an important and timely investigation. The introduction is well-written and logically structured, concluding with clearly stated objectives. For readers less familiar with *Pinus* species, the authors might consider briefly noting whether genetic correlations between radial growth and climate variables have been reported in other *Pinus* species. This could provide a useful reference framework (null hypothesis) for the study.

While I fully acknowledge the practical complications inherent in provenance experiments, my main concerns relate to the Materials and Methods section. I believe it is critical to address the following points to strengthen the results and the general implications of this study for *Pinus nigra*.

1. Mortality

Information is needed on the number of surviving trees per provenance and site, as well as their spatial distribution. A map showing mortality patterns would help assess potential survivorship bias and spatial clustering, which could influence growth responses and ranking.

2. Statistical testing

The analysis includes 16 provenances (across four subspecies) with variable presence across the four sites. With 16 provenances, there are 120 possible pair-wise comparisons. The authors need to justify the use of non-parametric testing and specify which post-hoc procedure was used following the Kruskal-Wallis test.

For the climate-growth analysis (e.g., Table 4), the authors conduct a very large number of correlation tests (monthly variables x sites x groups). There is no mention of any adjustment for multiple testing, raising the risk of Type I errors. The authors should justify whether and how they addressed this issue.

3. Model assumptions and diagnostics

The linear models (Eq. 1 and 2) assume homogeneity of error variance across groups. This assumption should be formally tested. If violated, remedial measures (e.g., data transformation, generalized models) should be implemented to address the issue. These diagnostics, and any corrective actions, should be described either in the main manuscript or, if extensive, in an appendix.

4. Sampling protocol

The decision to sample only healthy, dominant, cylindrical trees surrounded by four codominant neighbors is understandable in terms of minimizing competition. However, this non-random sampling limits the general-

izability of the findings. The rankings of provenances could differ if suppressed or average trees had been included. Acknowledging this limitation in the discussion would strengthen the interpretation of the results.

5. Tree age and spacing

Tree age should be incorporated as a covariate, particularly for traits such as total circumference or diameter at age 39. While the authors separate early and late growth phases, this may not fully account for confounding due to age-related variation or spacing differences among sites. Incorporating spatial autocorrelation using tree coordinates or including a competition index as a covariate could offer valuable insights and help account for these effects.

6. Model specification for provenance x site interactions

Eq. 2 nests provenance within site, which limits the formal testing where provenance rankings vary significantly across sites. A more appropriate model would include a direct interaction term (site x provenance).

7. Documentation of the statistical models

I strongly recommend including the full specification of the statistical models (including random and fixed effects, and any post-hoc procedures) in an appendix.

I would be pleased to review a revised version of the manuscript. At that point, I will focus more closely on the study's findings and their practical implications. For now, I prefer to wait until the main analytical concerns have been addressed.

Reviewed by Richard Whittet , 15 September 2025

Review of Low genetic diversity and high phenotypic plasticity for growth traits and growth-climate relationships in *Pinus nigra* Arnold, the European black pine

The authors present findings from a sampling campaign in four contrasting provenance tests of *Pinus nigra* and subsequent analyses of growth data. The results are summarised at subspecies and provenance levels and are interpreted reasonably in the discussion. Site effects were dominant (as would be expected), and this is described as phenotypic plasticity. The correlations between climate and growth seem logical and these vary slightly between sites with different limiting factors, which is interesting. I suspect foresters will be most interested in subspecies differences so it is important that this is well covered (it is, though see some extra suggestions in my minor comments).

This is an impressive dataset that appears to have been very carefully compiled. The introduction and discussion sections are clear and concise. The manuscript should eventually be published but a lot of improvements (especially in the results) are required beforehand to get the most value out of the data and communicate it well.

The level of detail about sampling and data analysis is unsatisfactory. Important omissions are how sampling was carried out within sites (number of blocks etc), and how the models were fitted. These matters will need to be resolved for the reader to fully understand the results. The GxE work needs significant improvement – I think the test performed was highly likely to produce 'significant' results which may not be very important in reality – a good figure showing rank or variance changes across sites would be more useful than a test statistic.

The results section is very long, difficult to read and many of the findings are not revisited in the discussion. Because there are a lot of results, many of which are quite similar (different growth metrics summarised by different groups), it is hard to write the results in a way that is not very repetitive. But I think this makes it more important to present them succinctly and efficiently. Table 4 is probably the most important in the paper, and is the one that the discussion focusses on. Could the number of other figures and tables be reduced to concentrate on the most important messages? Or could the entire paper be shorter? For example, focussing only on an overall subspecies analysis, and then the 7-provenance dataset but writing a basic summary of the full dataset to use as supplementary material?

Editing is required throughout to improve the English. I have highlighted examples in the attached PDF but have not elaborated on each one of these with a comment.

Title and abstract

Does the title clearly reflect the content of the article? ☒ Yes, ☐ No (please explain), ☐ I don't know

Title. Do small differences in provenance means necessarily mean there is low genetic diversity? Maybe the diversity is within rather than between populations? Could edit to 'adaptive differentiation among provenances', or similar? Also worth being clear that this is work done in experiments and not in-situ.

Abstract is too long! Simplify after having completed other revisions.

Introduction

Are the research questions/hypotheses/predictions clearly presented? ☐ Yes, ☒ No (please explain), ☐ I don't know

Does the introduction build on relevant research in the field? ☒ Yes, ☐ No (please explain), ☐ I don't know

72-74. Long sentence

76. Rarely completely free of confounding effects. Could reword to say they are minimised

123. Remove 'Yet' to avoid starting a paragraph with a conjunction

124. Necessary to say what the reference is to within the parentheses? Would suggest either just include the citation, or elaborate properly.

128. Replace 'genetic diversity for' with 'variation in', which might be more precise – you go on to say that it is among populations so the reader can infer that it is assumed to be adaptively significant

134. If relevant to mention programmes elsewhere, the UK breeding programme focussing on laricio too, see Lee, S.J. and Connolly, T., 2004. Selection of parents for the Corsican pine breeding population in Britain. Forestry, 77(3), pp.205-212.

135. Restoration

136. No need to write 'in this context'

Materials and methods

Are the methods and analyses sufficiently detailed to allow replication by other researchers? ☐ Yes, ☒ No (please explain), ☐ I don't know

If applicable (for empirical studies), are sample sizes are clearly justified? ☐ Yes, ☒ No (please explain), ☐ I don't know

Are the methods and statistical analyses appropriate and well described? ☐ Yes, ☒ No (please explain), ☐ I don't know

155. It would be useful to know how the experiments were planned. Were they established in a coordinated way (i.e. as part of a series), or was each one quite different?

169-170. Slightly more information about how the genetic groups were defined would be helpful. Are they admixed because it the home site is a natural 'hybrid' zone or because of tree planting?

176. I think it would make more sense to describe the data collection before the climate data

189. Monthly, rather than annual?

193. How were the 20 trees/provenance sampled? Was the block design used?

194. Better description of the instrument required?

221. What does 'more integrated' mean?

226. Explicitly mention that the sites with two adjacent tests are Pomet and Verdun to remind the reader

250. What is the P? Provenance, or provenance nested within subspecies? Or are there two different model structures?

251. Without knowing how the blocks were sampled, it's hard to determine whether this is the appropriate model – i.e. whether it is legitimate to treat provenance and block as random effects. Judging by the experiment designs, the number of trees sampled per block, or number of blocks sampled could be very different across sites. Can more information be included about this? It also makes it difficult to verify whether the approach of

adjusting means by block is correct

261. Is the statistical significance of differences among sites relevant and meaningful? It could be interesting if there were significant differences in climate:growth relations (slopes), but it's not very interesting for trait means.

Results

In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? ☐ Yes, ☐ No (please explain), ☒ I don't know

Are the results described and interpreted correctly? ☐ Yes, ☐ No (please explain), ☒ I don't know

266. What does 'high quality' mean?

Table 3. Add standard error or standard deviation?

Table 3. How did the rectangular spacing at Cestas influence RW? Were there larger differences between the two radii at this site? If so, how did that influence the mean or the variability? Did it change with age?

274. Does this mean that where the late spring maximum temperature was LOW, the growth was LOW? Sentence is quite hard to read at the moment, and suggests the opposite. Again with the winter maximum temperature. It is the use of the word maximum which is confusing, so please revisit this section and make sure it is precise.

320-348. I think there is too much unnecessary written interpretation here. For example, is it relevant to work out the average variance explained (lines 346-7) for different traits and sites? I think they are very different things that should not be compared in this way. And so, it is also confusing to read the range in var exp by block. The section would work better with a figure to replace Table 5 which is not very easy to read. A stacked bar chart (one for each trait), where the residual was also shown would be efficient, and the text could be very minimal.

Figure 3b. Would a colour-blind person be able to read this? It is also quite hard to use this picture to compare provenances across sites, and awkward to join the provenance names with the colours. Consider redrawing to something that is more compact and easier to read.

370. Did the block effects become non-significant because the variance was dominated by the site effect?

Table 6 (and 5). Is there something to say about the differences in effect size between D15 and D38? The provenance effect becoming more visible at some sites and less visible at other sites? This is also true of rw15 and rw38 from the single-site analyses – generally, the provenance effect is larger for the later of the two sampling instances.

Table 7a. Reorder table so it is easier to see the min, mean and max together? Do minimum and maximum provide the most useful summary? Maybe 25 and 75th percentiles would be more representative, avoiding extreme values.

408-411. How is 'best' and 'worst' defined? In terms of growth?

Table 7b. This seems like an overly stringent definition of GxE yet hasn't been described very well (only in the table caption?). I am not sure that I understand it but "Probabilities that the matrices of mean values for seven provenances are identical" will surely produce 'significant' results in most cases. It might be acceptable for well-replicated clonal lines in an annual crop but not in mature forestry experiments where the data are naturally very 'noisy'. I suggest re-thinking this, presenting the finding in a different way – possibly visually. If a test statistic is desired, then can it be extracted from the models you have fitted (e.g. % variance explained by provenance:site interaction?)

Figure 5. Why does circumference have its own summary figure but the other traits do not?

431. I don't understand this section about neutral vs adaptive. Is it appropriate to compare these two things? It seems quite tenuous to me.

Discussion

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? ☒ Yes, ☐ No (please explain), ☐ I don't know

Are the conclusions adequately supported by the results (without overstating the implications of the findings)? ☐ Yes, ☐ No (please explain), ☒ I don't know

476-477 . "Provenance effect on phenotypic trait variance were generally higher than subspecies effects" is quite interesting. Are there other economically important traits that vary more clearly among the subspecies?

521. Are there other considerations would influence deployment of lesser-used subspecies or deployment in mixture? Do you know whether it is a practical or realistic suggestion? For example, is much known about the differences in supply chain for FRM, the silviculture, or the quality of the forest products? It is fine if these things are unknown but worth mentioning things other than pest and disease susceptibility, to give some more integrity to the statement.

544. Hear Hear! We need more common gardens. This is a very good opportunity to synthesise the 'limits of the study' as per the subheading, and given that you have made applied statements about wider use. What changes would you make in the design of the next round of *P. nigra* tests in order for their results to better inform end users?

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Reviewed by anonymous reviewer 1, 27 August 2025

Title and abstract:

Does the title clearly reflect the content of the article? ☒ Yes, ☐ No (please explain), ☐ I don't know
Does the abstract present the main findings of the study? ☒ Yes, ☐ No (please explain), ☐ I don't know

Introduction

Are the research questions/hypotheses/predictions clearly presented? ☒ Yes, ☐ No (please explain), ☐ I don't know

Does the introduction build on relevant research in the field? ☒ Yes, ☐ No (please explain), ☐ I don't know

Materials and methods

Are the methods and analyses sufficiently detailed to allow replication by other researchers? ☒ Yes, ☐ No (please explain), ☐ I don't know

If applicable (for empirical studies), are sample sizes are clearly justified? ☒ Yes, ☐ No (please explain), ☐ I don't know.

Are the methods and statistical analyses appropriate and well described? ☐ Yes, ☒ No (please explain), ☐ I don't know **See comments below**

Results

In the case of negative results, is there a statistical power analysis (or an adequate Bayesian analysis or equivalence testing)? ☒ Yes, ☐ No (please explain), ☐ I don't know

Are the results described and interpreted correctly? ☐ Yes, ☒ No (please explain), ☐ I don't know. **See comments below**

Discussion

Have the authors appropriately emphasized the strengths and limitations of their study/theory/methods/argument? ☐ Yes, ☒ No (please explain), ☐ I don't know. **See comments below**

Are the conclusions adequately supported by the results (without overstating the implications of the findings)? ☒ Yes, ☐ No (please explain), ☐ I don't know

Principio del formulario

I wish to remain anonymous

Final del formulario

"Low genetic diversity and high phenotypic plasticity for growth traits and growth-climate relationships in *Pinus nigra* Arnold, the European black pine"

Comments:

The study uses tree ring data obtained from several common garden tests of *Pinus nigra* provenances including different subspecies to evaluate variation in climate-ring growth relationships depending on phylogenetic or geographic origin, and plantation habitat. The annual growth ring data is also used to estimate intraspecific genetic variation and phenotypic plasticity on radial growth traits, testing also for genotype by environment interactions and ranking the growth performance of subspecies and provenances across the common garden tests.

In general, the study is very well justified, and the sampling protocol was set up appropriately, aligned to the objectives and goals of the study. However, from my point of view, there is a major issue regarding the models used for the statistical analyses, which have some implications on the description and interpretation of some results, particularly those related with the comparison of variance components, phenotypic plasticity and genotype by environment interaction. Thus, even though the study contains important and useful experimental data, in my opinion, the manuscript requires some revision, particularly in the statistical analysis and results interpretation.

1. To estimate block, subspecies and provenance effects (i.e., variance components) on radial growth traits, the proper model (Equation 1) should include both the Subspecies (Sp) and the Provenance within subspecies [P(Sp)] components simultaneously as a full model. The way it was done, estimating each component as separate, alternative models, is biased towards the model using the Provenance effect, because it implicitly includes both variance components [Sp + P(Sp)], so it is not strange that results show more variation across provenances than across subspecies.

2. Similarly, the proper statistical model to test for environmental effects on provenance variation (equation 2), and at the same time test for genotype by environment variation (and also for phenotypic plasticity) should include "P + PxS" instead of "P(S)", since the same seven provenances are being tested across all test sites in the model. By including the PxS component, the significance of genotype by environment interaction can be tested directly. Moreover, if PxS is significant, it would be a direct indication that phenotypic plasticity differs among the provenances included in the analysis, and phenotypic plasticity for provenances can be interpreted from stability analysis models.

3. Other minor editing details are marked directly on the PDF manuscript file.

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