

Dear colleagues

We have revised and finalized the manuscript titled “Interplay between fecundity, sexual and growth selection on the spring phenology of European beech (*Fagus sylvatica* L.)”, by Sylvie Oddou-Muratorio, Aurore Bontemps, Julie Gauzere, & Etienne Klein (available at bioRxiv, doi: <https://doi.org/10.1101/2023.04.27.538521>).

We would like to express our gratitude to the referees and to the recommender for their overall positive feedback on the previous version of our manuscript. In this revised version, we have addressed most of their suggestions.

First, we have reorganized the order of presentation in all sections, and rewritten extensive parts of the Introduction and Result sections, following the suggestions of both referees and of the recommender to improve the clarity and readability of the text. The new order begins with Fecundity selection, followed by Sexual selection, and then Growth selection. This order is now the same in the Abstract, Material and Methods and Results sections. This also keeps fecundity and sexual selection together, both of which are estimated on adult trees in situ, while growth selection is estimated on seedlings ex situ. We also redrawn the Figure 1 to give a better view of the context of the study.

Second, we have provided a stronger rationale for examining selection in two plots at different altitudes (see new Table 1 at the end of the introduction), and have discussed these results separately from the first ones (third paragraph of the discussion). Briefly, we have different expectations for fecundity selection on spring phenology at these two plots, which are located at extreme positions along the altitudinal range of European beech on the northern slope of Mont Ventoux. On the one hand, at low altitude, the main adaptive challenge is the high risk of water stress; moreover, we showed in a previous study that both early or late budburst may enhance survival and fecundity in this plot (Bontemps et al. 2017). On the other hand, at high altitude, the main adaptive challenge is the short growing season, which should result in intense fecundity selection for early phenology. Our results were consistent with these expectations. We hope to better convince the referees and the recommender that it is important to show and discuss how selection varies with the environment.

Finally, in the Discussion, we have reorganized the analysis of fecundity and sexual selection (first and second paragraphs, respectively), resulting in a more balanced consideration of the importance of these two types of selection (as suggested by referee 1). We have also added a preliminary summary of the main results (L512-520). We revised the third paragraph to better emphasize environmental variation in selection and to improve the discussion of how this study sheds light on the ability of beech populations on Mont Ventoux to adapt to ongoing climate change.

Specific answers to the comments of the referees and of the recommender are detailed below ((the initial comments are in black, our reply in green). We hope that the new revised version of our manuscript will be considered suitable for recommendation by PCI Evol Biol. The revised manuscript is 8733 words long, includes 73 references, five figures and five tables. All the supplementary tables and figures are grouped in a single file also available on BioRxiv. The data and R codes for analyses are available at : <https://doi.org/10.57745/ZVPNXX>

Sylvie Oddou-Muratorio, Aurore Bontemps, Julie Gauzere, & Etienne Klein

Recommender

The pre-print of Oddou-Muratorio and colleagues presents a thorough analysis of fecundity, sexual and growth (viability) selection in two European beech stands at contrasted altitudes. This study builds on previous work to show how selection gradients for spring phenology can be modulated by sexual selection and how environmental differences (i.e., altitudinal differences) can also have a major impact on the potential for contemporary evolution in a keystone forest tree. Two reviewers have provided positive evaluations of the pre-print. However, I agree with them in that the pre-print is hard to follow at parts (in particular the Results section), and that the art of Figure 1 can be improved, to give a better view of the context of the study. I found also interesting the reviewer suggestion of using path analysis to take into account the temporal succession of sexual, fecundity and viability selection; an idea worthwhile of further exploration.

I read carefully the pre-print myself and came out with some comments that hope will also be useful to the authors to produce an updated pre-print:

In terms of improving the comparison with other studies and understanding better the context, it would be useful that the two stands are described not only by reporting the altitude but also giving some climate (and other environmental) characteristics. It would also help if TBB (time to budburst) was translated into degree-days, a common measure that standardises for temperature differences at different locations or years. For example, in lines 135-137, the difference in number of days to budburst at the lower vs the higher plot could be due just to different temperature accumulation at the two altitudes (and that would explain also why the pattern changes in a common garden where trees were grown in the same environment). To make the translation between time in days to degree-days would help also to evaluate whether there are different local adaptation patterns at the two altitudes.

SOM et al. E1) Table 1 has been added, providing detailed information on the climate at each plot, including the growing degree-day. Additionally, sentence L132-135 has been added to better explain the difference in the number of days to budburst at the lower versus the higher plot when measured in situ or in the common garden.

Line 222. Can you report exclusion probabilities for the 13 SSR loci? Also, line 231, I find unusual to consider “no unsampled parents” when in continuous forest tree populations is common to have a large amount of external gene flow. Can you provide a rationale for this?

SOM et al. E2) the exclusion probability is now reported L332.

The editor's concern regarding the sampling of the whole breeding male population (BMP) to assign paternity in a non-isolated population is valid. This approach may lead to the wrongful assignment of a given offspring to an unrelated sampled male that matches by chance, while the true father remains unsampled (cryptic gene flow), resulting in a false-positive paternity rate, which is a type I error. Therefore, it may be more appropriate to independently estimate the size of the BMP (N_{BMP}) and consider a percentage of non-sampled potential fathers in the CERVUS assignment procedure. However, a previous study (Oddou-Muratorio et al. 2003) demonstrated that overestimating N_{BMP} can lead to a higher likelihood of failing to detect the true father, even if it was sampled (type II error) *. To avoid a high rate of Type II error while considering the risk of scoring error rate, we chose to neglect the risk of Type I error due to subsampling of the BMP. This choice is supported by the high exclusion power of our microsatellite markers.

[*This is likely because CERVUS calculates the threshold paternity score value above which paternity can be granted at a given level of Type I error based on simulations assuming panmixia. However, non-sampled males outside the plots are likely to have lower contributions than sampled males within plots because the probability of pollen dispersal usually rapidly decreases with distance.]

Line 306. Can you provide the equation for this model?

SOM et al. E3) the problem is that the BestFec-Model is selected in the result section, so we cannot provide its equation in the material and method section. However, we added in the text the additional quadratic term to be included L299-300.

I understand (as also suggested by one of the reviewers) that the common garden was probably established with other objectives, but that it came handy to test for viability selection in this study. If this is the case, can you provide a reference to the full analysis of the common garden? In particular the part related to the drought treatment is not very well described in the pre-print (although it is important for the interpretations and conclusions developed in the Discussion section). Also, the reader is left wondering about the genetic components that could be computed using the family structure of the common garden (e.g., genetic selection gradients computed using bivariate models or heritability estimates).

SOM et al. E4) Two previous studies (Gauzere et al., 2016, 2020) analyzed the portion of the common garden that was not subjected to drought treatment to infer the genetic components of maternal variance for several functional traits. This information is now explicitly mentioned in L190-193. Furthermore, L187-190 provides additional details on the drought treatment.

In this study, we investigated the relationship between growth and budburst in seedlings using a simple statistical framework, a classical regression model with family and block effects. Indeed, since the common garden already allows for the separation of environmental and genetic factors affecting growth and budburst variation, extracting the genetic component of the selection gradient is not expected to yield significantly different results. However, it is possible that our estimation may be biased by the family structure of the data, which results in non-independent observations (seedlings from the same or different families). Therefore, it may be beneficial to use bivariate analysis to estimate the genetic covariance between phenology and growth at the family level. However, due to the limited number of families per population (only 20), we may not have sufficient power to accurately estimate these covariances.

Line 351. A piece of the sentence is repeated.

SOM et al. R5) This is corrected in the revised version

Line 411. "as the best one"

SOM et al. R6) This is corrected in the revised version L415

Finally, I advise to tone down the end of the Discussion, as even a higher-than-average selection gradient may not translate in a significant response to selection (for which both the phenotypic variance and the heritability of the trait are important), in particular if the selection gradient proved not to be consistent across years.

SOM et al. R7) We concur with the editor's assessment that the discussion's tone was overly optimistic. We have now moderated it L657-666.

Reviewed by anonymous reviewer, 06 Jul 2023 00:41

Dear Editor,

The manuscript submitted by Oddou-Muratorio and colleagues present novel and interesting data on the functional value of flowering phenology in a well known beech species. The study estimated viability, fecundity and sexual selection combining field and common garden data with paternity analyses. These provides a unique combination of data to better understand the selection regime on flowering phenology. The study was performed using two populations that characterized an altitudinal gradient. The main result was that sexual selection through assortative mating acted on flowering time conditioning (stabilizing selection) on male fitness, while fecundity selection favored early flowering on female fitness. During the reading, the result section was one of the most difficult to follow, maybe because in my opinion it is not clear enough the value of using two populations and the description of what was found in one or the other distract from the relevant points. Overall the manuscript is clearly written and the analyses are sound but still I found some points for further clarification. In particular I am not complete sure that the analytical approximation can really address the main goal. Please found below more specific comments and suggestions.

1) Line 3: Two populations are not enough to characterize a gradient. I would focus the tittle on the contribution of the study.

SOM et al. R1.1) We have removed the term altitudinal gradient from the title.

2) Lines 17-19: Why is this relevant?

SOM et al. R1.2) We concur with Reviewer 1 that the initial sentence of the abstract was not easily comprehensible. Therefore, we changed it for: "Plant phenological traits such as the timing of budburst or flowering can evolve on ecological timescales through response to fecundity and viability selection".

3) Lines 22-23: To address the main goal it doesn't seem you need populations at different elevations. What justify this selection of populations?

SOM et al. R1.3) we have added the sentence L155-155 and the new Table 1 to justify why it is interesting to compare selection gradients at the two plots. See also the main answer.

4) Lines 28-34: I would try to follow the same order as in background section, first viability, then fecundity and then assortative mating.

SOM et al. R1.4) We agree with Reviewer 1 that the same order would be better used in the Abstract, Material and methods and Result sections, but we have rather used the following order: first fecundity then assortative mating, then viability

5) Line 57: It is not clear why an altitudinal gradient is necessary.

SOM et al. R1.5) See response R1.3 above

6) Lines 79-83: These four explanations are not easy to visualize. If you are not going to provide more details, please check whether it would be better to relocate these lines.

SOM et al. R1.6) we agree with reviewer 1 and we have removed these lines from the introduction

7) Lines 114-128: I am not sure a multiple regression analysis is the best approximation since viability, mating and fecundity are expressed sequentially during development and one can condition the other. Since you have a nice hypothesis about the interconnection among the three components of selection why you did not try with a path analysis. In other words, please justify a bit more how the Lande and Arnold approach can help in this case more than other analytical approximations. If you find differences between selection differentials and selection gradients then indirect selection may be relevant and you may loose this information using only multiple regressions. I can understand that multiple regression allowed you to estimate non-linear selection gradients, but at the same time it can only test the more simplified hypotheses which in your case is not very realistic.

SOM et al. R1.7) The relationships between the different traits (timing of bud burst, timing of flowering, and flowering synchrony) and the different components of fitness (survival, fecundity, mating success) shown in Figure 1 may indeed argue for the use of path analyses or structural equation models (SEMs). SEMs have gained considerable prominence in recent decades due to their potential ability to resolve complex multivariate relationships among a number of interrelated variables. In our case, however, we identified several difficulties that prevented the straightforward application of SEMs to our problem:

(1) Among the phenological traits (blue boxes in Fig 1), we only have observations on timing of budburst, TBB (and budburst synchrony), and our analyses rely on the hypothesis that TBB is a good proxy for the timing of flowering; this severely limits our ability to examine all the relationships described on this Figure 1.

(2) Some fitness components are observed in adult (e.g., fecundity) while others are observed in seedlings (e.g., growth as a proxy for survival), and thus not on the same individuals. This is a major problem in analyzing the joint relationships between phenology and multiple fitness components.

(3) The distribution of some variables shows a large deviation from a Gaussian distribution, especially the distribution of fecundities. Although deviations from a Gaussian distribution are not necessarily problematic for predictor variables in a linear model, they become problematic in SEMs, where the computation of the variance-covariance matrix assumes multivariate normal variables. Some extensions of variance-covariance-based methods have been proposed to account for special cases such as non-normality, but they would require additional effort.

These various arguments led us to reject path analysis for this study. We agree with reviewer 1 that the multiple regression analyses we used to fit selection gradients may also have some limitations. But this approach is also widely used by the community of quantitative genetics in the wild, at least in

forest trees (see for example Alexandre et al. 2020, Westergreen et al. 2023). Therefore, using this well-supported approach ensures that estimates of selection gradients across studies can be compared with a high degree of confidence.

8) Lines 120-128: I would eliminate these lines since they do not provide additional information to the reader. I would explain in more detail how you are going to distinguish between the different forms of selection on flowering phenology.

SOM et al. R1.8) We have removed these lines in the revised version. The end of the introduction has been modified to better explain how we distinguish between different forms of selection on flowering phenology.

9) Lines 145-146: At this point I am not sure why using two populations that describe an altitudinal gradient makes a difference. Why you need these two populations to understand the selection regime acting on flowering phenology? Please explain this point early in the Introduction.

SOM et al. R1.9) See response R1.3 above

10) Lines 150-152: This is a strong assumption! Is there any evidence that seedling growth is positively associated with viability under natural conditions?

SOM et al. R1.10) There is a broad consensus on the positive effect of fast growth rates and/or large size on fitness in plant species and in trees in particular (Lanner 2002; Petit and Hampe 2006). This is because taller trees generally have greater competitive ability by avoiding shading from neighbors (Landis and Peart 2005), have more resource for seed production (Klinkhamer et al. 1997), and are also more resilient to disturbances such as surface fire and ground-based herbivory. Unfortunately, forest inventories usually focus on life stages >1.30 m in height (especially in temperate forests), so the relationship between growth rates and survival within species and populations is better characterized at the adult stage than at the seedling stage.

European beech is a shade-tolerant species, which means that seedlings usually show slower growth in deep shade as compared to other species, and also a lower mortality rate, which allows beech regeneration to reach the canopy more often than its competitors in forests with low canopy turnover rate (Petrovska et al. 2022). However, these between-species patterns provide little information about within-species growth dynamics. It is likely that among neighboring beech seedlings, those with a higher growth rate when the canopy opens and favors recruitment have a higher probability of reaching the adult stage.

11) Line 180: How many branches were monitored per tree to obtain phenological data. How synchronized are phenological changes within individual trees? Does the variance within individual trees can have a consequence on their fitness success? Please justify your methodological approach and make explicit the assumptions.

SOM et al. R1.11) The developmental stages of budburst were determined assigning a specific score at the level of the whole tree crown. The crown of each individual was divided in two components, lower and upper. Phenological scores for each component were assessed from the ground using binoculars by two observers, each observing the tree at two different positions. For our analyses, we used the average score between the top and the upper part of the crown. The detailed protocol is described in a recently published study (Jean *et al.* 2023), which is now cited in the text. Regarding the effect of within-tree variance on individual fitness, we believe that the development of budburst in European beech is usually quite rapid, so that the within-tree variance of phenological stages at a single date is much lower than the between-date variance of phenological stages.

12) Line 261: If there is a hypothesis behind the use of these two populations, then a more solid approach will be to demonstrate first that populations differed in their selection gradients. That is, by performing an ANOVA for the multiple regression including both populations. A significant Altitude x Population effect will be indicative of differential selection and this justify all the subsequent analyses that you did.

SOM et al. R1.12) see answer R1.13) below.

13) Lines 457-458: How can you know that selection gradients differ, without doing a statistical test. See comment above.

SOM et al. R1.13) we agree with reviewer 1 that in the case of selection gradients on fecundity, a more robust approach would be to fit them (one for male, one for female fecundity) in a single model for both plots together. This model should include an additional term "Plot", and an interaction term between Plot and TBB. This was the strategy used in our previous paper where we examined whether the selection gradient on tree size differed between plots (Oddou-Muratorio et al. 2018). The reason why we did not use this strategy in this study is that we were interested globally comparing the strength of fecundity selection on female fecundity, of fecundity selection on male fecundity, and of sexual selection on male fecundity. To our knowledge, there is no way to integrate these different components of selection and test whether their strengths differ among plots at different altitudes. Therefore, we computed standardized selection gradients, which are at least theoretically comparable, and chose to qualitatively compare the intensity of selection across elevations based on the "verbal" integration of the different standardized selection gradients.

During the revision of this manuscript, however, we followed the suggestion of reviewer 1 and tested whether each specific selection gradient differed among altitudes by fitting a single model that included both plots. The results were that (1) the interaction effect between plot and TBB on female fecundity was not significant, (2) the interaction effect between plot and TBB on male fecundity was significant. (3) the interaction effect between plot and TBB on male fecundity sexual selection was also not significant. These results are consistent with the large standard errors associated with the standardized selection gradients, that were already presented in the previous version of the manuscript (Table S5). In the revised version of the manuscript, we kept only these standardized selection gradients with their standard errors for the sake of simplicity, but we highlighted L494-494 which selection gradients did not differ among plots.

This led us to significantly change the discussion on this topic. Nevertheless, we believe that we have a convincing body of qualitative evidence suggesting that selection for earlier phenology is overall stronger at high than at low altitudes in the population studied. They are listed 634-645.

14) Line 479: Several lines in the Discussion section are good summaries of the results and can be used to make the point clearer in the Result section. This can allow you to release some space to focus the Discussion on the main conceptual and empirical advance of your results. For instance, what does this study added to what we already know from short lived-species studies? Which of the three forms of selection (viability, fecundity, sexual selection) dominate the selection regime on flowering phenology? Throughout the Discussion it was hard to extract a simple take-home message. At the end it seems that your main contribution is the finding of assortative mating in a tree species.

SOM et al. R1.14) We thoroughly reorganized the entire manuscript and tried to clarify the Results and Discussion sections. The new sentences L533-550 may be a good example of how we better emphasize what this study adds to what we already know from studies of short-lived species. We also explicitly mention L686-689 the problem of quantitatively estimating which form of selection (viability, fecundity, sexual selection) dominates the selection regime on flowering phenology. Hopefully, the take-home messages are now clearer.

Reviewed by anonymous reviewer, 25 Sep 2023 09:50

*This paper by Oddou-Muratorio et al. analyses the different selection components of phenology. In their conceptual framework, the authors explore fecundity and viability selection on phenological traits and their relationship with sexual selection by assortative mating, using two plots dominated by *Fagus sylvatica* (European beech) with 300 m of difference in altitude. Authors regressed fecundity vs. the phenological mismatch on the timing of bud burst (TBB) as a proxy of the sexual selection. The*

regression between fecundity and TBB was used as the proxy of fecundity selection. And the regression of TBB vs. seedlings growth (greenhouse experiment) was used as the proxy of viability selection.

I find that this manuscript presents an interesting collection of field and greenhouse data. The authors combine genetic analyses from seeds and seedlings collected in the field for estimating paternity and parentage with seedling growing data from a greenhouse with a drought treatment. The paper is well written and the statistical analyses seem appropriate (although I do not understand why phenological mismatch has negative values in fig. 5 are negative, see my comments below).

My main concern is that results seem to be too specific of the study plots, female or male fertility, age of individuals and altitude, being difficult to generalize. Also, the combination of data needs more rationale behind. For instance, the spatial design of the study includes an elevational gradient, although with only two plots separated by only 300 m in altitude. This is not so much regarding the distribution range of beech in the area (from 750 to 1700 m a.s.l.). But above all, it is not clear how the altitudinal gradient is going to affect different selection types on the phenology. I am missing a more formal hypothesis regarding this.

SOM et al. R2.1) We agree with reviewer 2 that the previous version of our manuscript lacked more formal hypotheses regarding the effect of elevation on selection gradients. We have added the sentence L155-155 and the new Table 1 to present these hypotheses and to justify why it is interesting to compare selection gradients at the two plots.

Regarding the low number of plots, we can only agree with reviewer 2 that, in principle, any study in ecology would benefit from a high level of replication; however, note that the type of study we conducted involves very extensive monitoring of each plot, both for phenotyping (extensive phenological monitoring of adults over ~2 months) and for genotyping adults and regeneration. It was beyond the scope of this study to carry out such extensive monitoring in a large number of plots covering the distribution range of beech.

Similarly, the inclusion of a drought treatment for the seedling experiment in the greenhouse needs more justification and link with the main objective of the manuscript (i.e., detecting selection gradients). I have the impression that the manuscript collates data originally designed for other independent studies and the internal logic of the design is difficult to discern.

SOM et al. R2.2) The common garden was not specifically designed to address the question of this study. This experiment was used to quantify the level of genetic variance for quantitative traits within and between populations (results published in Gauzere et al. 2016, 2020) and the drought treatment was set up to quantify the role of plasticity on the phenotypic variance of traits. Nevertheless, common garden experiments are also relevant designs to study selection gradients at the seedling stage (see, for example, Alia et al. 2014). Here, the drought treatment provides an opportunity to study how selection gradients vary with environmental conditions.

In the discussion section, the authors explain assortative mating at the lowest elevation because phenology was more spread out. But this could be also being an effect of higher beech density. How can these two factors be separated?

SOM et al. R2.3) The density in plot N1 is ~32.3 trees/ha, compared to 59.3 trees/ha in plot N4 (Gauzere et al. 2013). In this previous study, we indeed showed that canopy density can be an important determinant of the mating system within a population, acting as a barrier to pollen flow, and we showed that mother trees with higher density of conspecific neighbors also had a weaker proportion of long-distance pollen flow and a higher proportion of selfing. It is therefore possible that higher canopy density in plots N4 may limit mating between trees with synchronized phenology. We now mention this possibility L607-608.

In short, I believe that the manuscript is a very valuable piece of science, although I consider that it should clarify a bit more the rationale for the combination of methods. Also, it has numerous tables that I believe that could be summarized or included in the supplementary material. A more organized description of the results according to the original framework (three selection types, three proxies of it) would clarify the message for the reader.

SOM et al. R2.4) we followed the advice of reviewer 2 and reorganized the different sections to follow the original framework.

Minor edits:

L22. Include the species name here.

SOM et al. R2.5) corrected

L23. Here and elsewhere, the authors use the term “low altitude” for referring to plot N1, which is 1,020 m a.s.l. I consider that this gives a fake impression of low altitude to the reader, whereas it corresponds to a relatively high altitude compared to other systems. I suggest to use another term throughout the text such as “mid altitude” or something equivalent.

SOM et al. R2.6) We agree with reviewer 2 that there is no absolute concept of altitude; in our case, the N1 plot is at the lower altitude where beech is present on Mont Ventoux, which is a good reason to call it a LOW ALTITUDE plot.

L49. Define microevolution.

SOM et al. R2.7) replaced by “evolution over a few generations”

L84. I suggest including here a reference that all the hypotheses are for “temperate ecosystems”.

SOM et al. R2.8) we agree with reviewer 2 and added these words

L93. I believe that this sentence is incomplete. Please, rewrite it.

SOM et al. R2.9) the sentence was rewritten

L147-150. These two sentences read very repetitive, try to improve the writing of them.

SOM et al. R2.10) We have tried to reformulate the paragraph, but basically the three selection analyses rely on regressing different traits on fitness components, so some repetition is inevitable here.

Figure 1. Try to improve the aesthetics of this figure. For instance, I cannot understand why you use a flag for assortative mating, the same for the circle with the cross. The right sided arrows are supposed to indicate delays in timing, but this is not intuitive.

SOM et al. R2.11) we redrawn the figure and changed the legend to account for reviewer 2 ‘s comment.

L163. Remove hyphen for Mont Ventoux.

SOM et al. R2.12) corrected

L166. I suggest changing the name of the plots for more informative ones. Plots N1 and N4 seem to me as names used for field work, but they are not intuitive for readers not working at Mont Ventoux (the majority). For instance, why they are not included plots N2 and N3 in the analyses? I recommend to change these names to “mid-altitude” and “high-altitude” plots. In fact, the authors have done so in figure 5, entitling the sites as “low altitude” and “high altitude”. However, I consider that 1000 m a.s.l. (N1) is not exactly low altitude, so a better term should be used. In addition, when reading results, it is difficult to remember which plot was high and which one was low with the current names. I believe that is better to include a name for the plots that gives information on the elevation gradient instead of the field design.

SOM et al. R2.13) We take this opportunity to answer the questions of reviewer 2 regarding the altitude range of the present study. We agree that 1000 m a.s.l. (N1) is not exactly a low altitude, but it is the lowest altitude where one can find beech populations with natural regeneration on the north face of Mont Ventoux, and thus it is the lower limit of the altitude range for beech on Mont Ventoux. Similarly,

plot N4 corresponds to one of the highest altitudes where beech populations regenerate mainly by sexual selection (some stands can be found at higher altitudes, but they produce very little seed and are likely to regenerate mainly by vegetative reproduction). We have added a sentence to detail this information L175-177.

Regarding the name of the plot, we would prefer to keep the full names N1 and N4 because these are the names of the plots in these long-term studied populations (thus ensuring continuity between studies). However, we have added -low and -high after these names all over the text to make them easier to remember for readers unfamiliar with Mont Ventoux.

L190. As the number of visiting dates was different per plot, should not the phenological score sum (PSS) be divided by the total number of visits?

SOM et al. R2.14) this would be required if we were analyzing data from plots N1low and N4high together; but PSS data are mostly used only to draw Figure 2 (separately for the two plots).

L237. Reference for the MEMM software is missing.

SOM et al. R2.15) There is no publication associated with this software. But it can be obtained at <https://gitlab.paca.inrae.fr/jfrey/MEMMseedlings>.

L331. This is not a clear reference, try to include the entire URL to the supplementary file instead.

SOM et al. R2.16) corrected

L351. Italics for lmer and lme4. Citation of the package needs to be included.

SOM et al. R2.17) corrected

L356. Instead of the mean, it is more informative to include the median or even the peak for phenological information on days (because it is a discrete variable).

SOM et al. R2.18) we agree, but as the whole distribution is provided as Figure S3, we did not add the median.

L375. Put space always after and before =

SOM et al. R2.19) This was corrected everywhere.

Table 2, heading. The name of the function used should not be included in the results, but in the description of methods. Also, include the reference of the package where this function comes from.

SOM et al. R2.20) This was corrected everywhere.

Figure 5. Why do you have negative value for the absolute mismatch (while the formula indicates the absolute value)?

SOM et al. R2.21) This is because these are the centered, reduced variables

L454. Put the exact reference of the appendix (including URL) here.

SOM et al. R2.22) This was an error and we removed this reference from the manuscript.

Fig. 8s. If you find that this figure is critical, include it in the main text

SOM et al. R2.22) we preferred to keep it as supplementary material (as there are already many figures in the manuscript)

References

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