Dear Editor

Please find enclosed the manuscript entitled "Live and let reproduce: Crown defoliation decreases reproduction and wood growth in a marginal European beech population". This is the revision of the manuscript which received a "Minor revision" decision after review by three editors of PCIEcology on the 24th of January.

First we are sorry that the revision process took such a long time. Besides the many other commitments of the authors, this delay is due to our will to account as properly as possible for the suggestions of the reviewers, in particular those related to the use of path analyses (see below). We provide here a thoroughly revised version of our manuscript taking into account most of these suggestions (changes are highlighted in blue in the main text), with a particular focus on the three main points raised by the reviewers and the editor (in green below):

- "The main concern that has been pointed out by the three referees is related to the interpretation of tree defoliation as a proxy of drought stress." We agree that we do not present in the manuscript sufficient evidence to claim this causal relationship. We are still pretty confident that drought stress is a main driver of beech defoliation in the study site, and this conviction is based in particular on a companion study by Petit-Cailleux et al., which we recently finalized and submitted to PCIEcology (https://doi.org/10.1101/645747). This companion study investigates the relationship between defoliation and mortality (which was found positive) and uses physiological process-based model to investigate the underlying factors triggering mortality in the studied population (which were found to be a combination of drought and late frost). The contribution of this companion study to the knowledge on stress drivers is better highlighted in the discussion (L439-448). Moreover, in the manuscript considered here, the causes of crown defoliation, whether they include drought or other factors, do not necessarily affect our reasoning nor our results. Therefore, as suggested by the editor, the focus on tree defoliation as an indicator of drought stress has been tempered down throughout the manuscript, in particular in the introduction and discussion. Crown defoliation is now presented as an "indicator that the tree has experienced a stress" (L138-139) (due to drought or other factors). The diversity of stresses and decline symptoms is better acknowledged (L50-61) and the various stresses potentially causing crown defoliation in rear-edge of species distribution are better introduced (L62-75) and discussed (L463-465).
- "Both referee 2 and 3 have questioned the series of the linear regressions that are used to analyze the complex interaction between BAI, DEF and Fecundity (male or female) and proposed path analysis as a more elegant solution for the analysis". This was a very interesting suggestion, considering the potential of path analyses to account for the hierarchical relationship between the variables of the study. Although none of the author was completely familiar with this approach, we thoroughly investigated this issue, based on Bill Shipley's book (2016) and R documentation (see the paragraph "On the use of path analyses", pages 3-7 of this letter). This led us to the conclusion that path analyses were not well adapted to our data set, and we incorporated part of this reasoning in the discussion of the revised manuscript (L512-529). Moreover, we added a new figure 1 to better introduce the complex hierarchical relationships among the studied variables.
- "One referee also raised concern about the use of linear relationship for several variables rather than non-linear functions" We agree with reviewer 3 that we should not have neglected such non-linear relationship between predictor and response variable as well known for DBH and growth. This is now corrected in the revised version of the manuscript, where we systematically used a quadratic function of DBH (DBH, DBH^2) in model 3. This improved only the model for BAI and DEF; in particular, while none of the most parsimonious models for female fecundity included quadratic DBH terms. We also added supplementary materials showing scatter plots between each predictor

variable and each response variable (new Figure S4), which generally support the choice of linear relationship. Finally, we also provide the linear regression diagnostic plots (new Figure S7).

In addition, we join below a detailed answer to all reviewers' comments (From Page 8 of this letter).We thank the reviewers and the editor for their positive comments on our manuscript, as well as for their numerous suggestions which helped us a lot during the revision process. The revised manuscript is ~ 7200 words long, excluding the 57 references, and it includes 5 figures and two tables, as wee as supplementary materials. All authors have read and approved the material being submitted. This article is not being considered for publication elsewhere.

With kind regards,

Sylvie Oddou-Muratorio

On the use of path analyses

Among the sophisticated statistical tools adapted to complex natural systems, Structural Equation Models (SEMs) have gained a significant notoriety in the last decades, due to their potential ability to resolve complex multivariate relationships among a suite of interrelated variables. We considered carefully the possibility to use this tool in our case. The hypotheses we want to test are summarized on figure A, and in its legend.

Figure A: Hypothetical relationships among the studied tree-level variables, with black arrow showing causal relationships (with their hypothetical sign). Rounded-corner rectangles represent the variables for which we have observations (the circles including variable names). The straight-edge rectangle represents the latent variable "resource" for which we have no observation, but which is likely to be influenced (i) by the plant resource status, a combination of size (measured through DBH) and vigor (here we measure the loss of vigor through defoliation) and (ii) the quality of the environment (measured here only through competition indexes and density, although resource availability may vary according to other feature, eg soil depth). Growth (measured by BAI) and reproduction (measured by male and female fecundities) are supposed to be influenced indirectly by competition, plant size and defoliation through their effect on resource. Under our hypothesis H1 (coordinated fecundity and growth decline), defoliation only affects reproduction through this indirect path. Under our hypothesis H2, defoliation may act as a signal stimulating investment in reproduction at the expense of a reduced growth, ie there may be a direct path from defoliation to reproduction (dashed red arrows represent the trade-off between growth and reproduction).
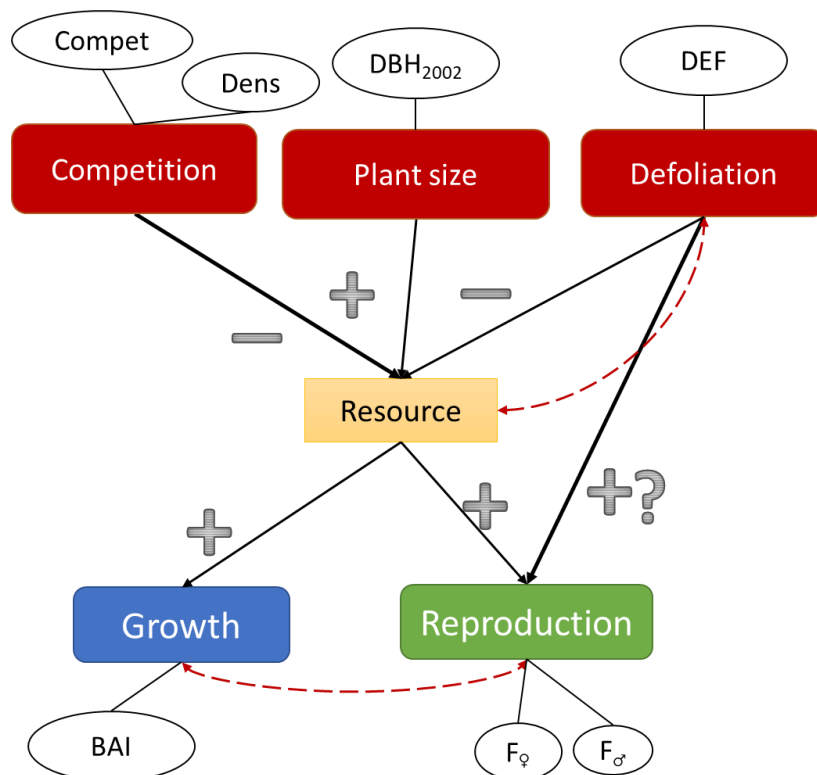

Based on figure A, SEMs appear as an elegant solution to test hypotheses H1 (indirect effect of defoliation on growth and reproduction, inducing a coordinated response to stress) versus H2 (additional direct effect of defoliation on reproduction, potentially decoupling the responses to stress in terms of growth and reproduction from each other). The main advantage of SEMs would be to model the resource pool allocated to growth and reproduction as a latent variable itself governed by the plant

resource status (size and defoliation) and environment (competition), thereby hierarchizing the effects of the different studied variables of interest on each other. However, a well-known limitation of SEM is that they are unable to properly handle resource allocation between two compartments (here growth and reproduction). This is for instance detailed in chapter 2.12 in Shipley (2016), which explicitly states that "systems that contain imposed conservation laws cannot yet properly expressed using directed graphs and d-separation". This means that such a reciprocal relationship between Growth and Reproduction as depicted by the red double arrow on Figure A cannot be considered in SEM. More generally, reciprocal relationships are difficult to handle in SEM, and we would also be unable to account for the fact that defoliation can both reduce the resource, and increase in response to a reduction of resource (red double arrow between resource and defoliation on Figure A). Shipley (2016) proposed a solution to this problem which consists in accounting for the time dimension, but our dataset does not allow to implement it (as growth and reproduction were measured as averaged values over the period 2002-2012, and we cannot decompose them in temporal series).

To overcome this first limitation, we can still solve an SEM as described in Figure A by choosing one direction for the relationship between growth and reproduction, as we did in the linear model described by equation (4) in the main document. However, our data set present a second limitation for the use of SEMs, related to the distribution of the variable defoliation, which shows major deviation from a Gaussian distribution (Figure B). Although deviations from a Gaussian distribution are not necessarily problematic for predictor variables in a linear model, they become so 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 consider special cases such as non-normality (Lefcheck, 2016), but to our knowledge, they unfortunately do not currently allow to consider simultaneously a latent variable such as our Resource variable in Figure A.

Figure B: Distribution of DEF variable in the 432-trees data set. There were 95 trees with a DEF-value > 0 value, including 60 trees with DEF = 1, 18 trees with DEF = 2, 12 trees with DEF = 3, 3 trees with DEF = 4and one tree for DEF = 6/7
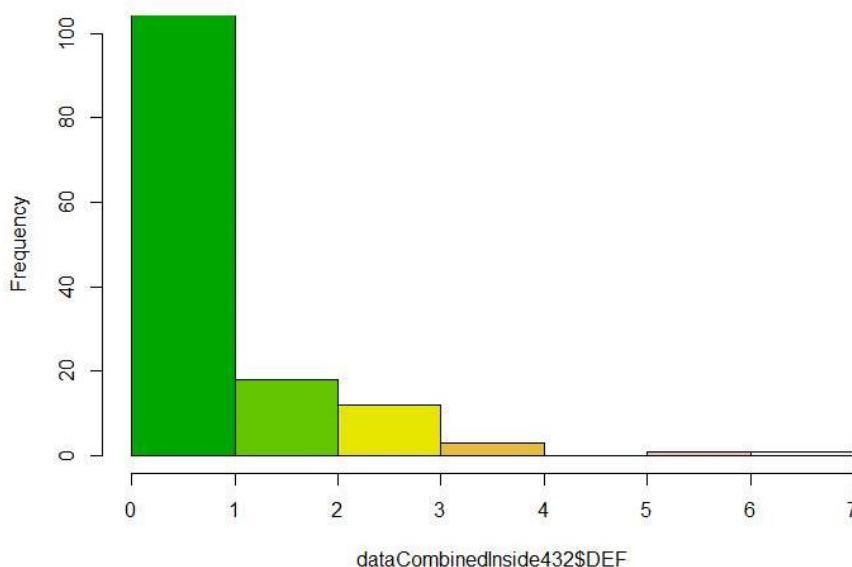
To address the two limitations, we investigated another solution to fit an SEM where defoliation was treated as a grouping binary variable (Figure C). We fitted this SEMM in order to test whether the paths between competition, plant size, resource, growth and reproduction differ among defoliated and non-defoliated individuals. We used the package lavaan, and outputs are shown in figure D. Firstly,

and most importantly the variance-covariance matrix generated under the model poorly fits the observed variance-covariance matrix (P-value =0). We tried to transform all the variables to improve the fit, without success (Fig.D legend) . Secondly, the estimated negative effect of density and competition on the latent variable resource were reassuring. Thirdly, both growth and female fecundity were found to increase with increasing resource. Also, the slope of the regression of female fecundity on growth was positive for non-defoliated and negative for defoliated trees, but not significant in both cases. Altogether, these result suggest that SEM were not well adapted to our data set.

Figure C: Tentative SEM fitted on our data set. Defoliation was considered as a grouping binary variable (Defoliated versus non-defoliated individuals), and the variance-covariance matrix was estimated for each group.
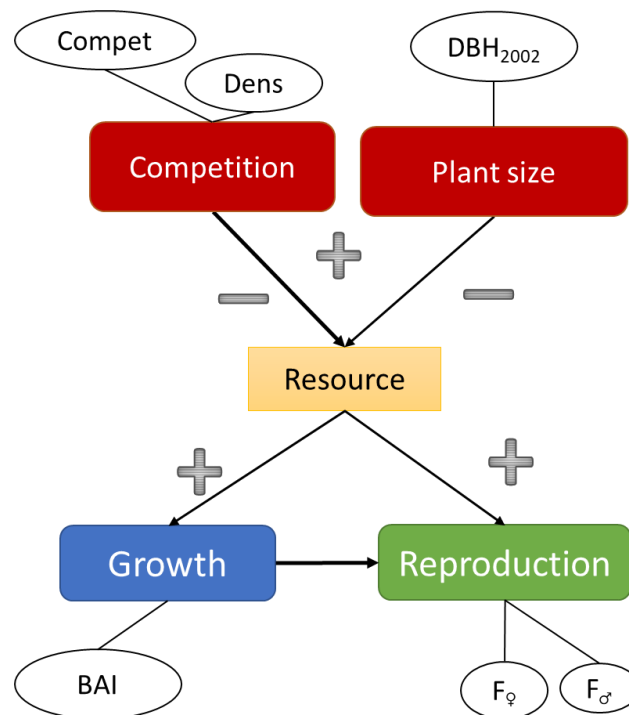

Figure D Lavaan output for SEM depicted on Figure C. Variables were transformed to meet the assumption of multivariate normal variables (square root transformation for Compet, Density and DBH, log transformation for BAI and FemaleFecundity)

```
lavaan 0.6-3 ended normally after 76 iterations

  Optimization method                           NLMINB
  Number of free parameters                         32

  Number of observations per group
  NonDef                                           337
  Defoliated                                        95

  Estimator                                         ML
  Model Fit Test Statistic                      55.768
  Degrees of freedom                                 8
  P-value (Chi-square)                           0.000

Chi-square for each group:
```

```
    NonDef                                          44.567
    Defoliated                                      11.201
Parameter Estimates:
    Information                                     Expected
    Information saturated (h1) model                Structured
    Standard Errors                                 Standard

Group 1 [NonDef]:
Latent Variables:
                    Estimate  Std.Err  z-value  P(>|z|)
    resource =~
      sqrtDBH         1.000
      sqrtCompet7    -0.402    0.023   -17.153   0.000
      sqrtDens14     -0.604    0.067    -8.945   0.000

Regressions:
                    Estimate  Std.Err  z-value  P(>|z|)
    logBAI ~
      resource        0.752    0.039    19.194   0.000
    logrelatFecFemale ~
      resource        0.179    0.083     2.152   0.031
      logBAI          0.002    0.089     0.024   0.980

Intercepts:
                    Estimate  Std.Err  z-value  P(>|z|)
    .sqrtDBH          4.501    0.093    48.365   0.000
    .sqrtCompet7      2.193    0.044    49.897   0.000
    .sqrtDens14       7.827    0.108    72.368   0.000
    .logBAI           3.411    0.075    45.327   0.000
    .logrelatFecFml  -0.875    0.308    -2.841   0.004
     resource         0.000

Variances:
                    Estimate  Std.Err  z-value  P(>|z|)
    .sqrtDBH          0.492    0.091     5.426   0.000
    .sqrtCompet7      0.259    0.024    10.624   0.000
    .sqrtDens14       3.058    0.243    12.572   0.000
    .logBAI           0.536    0.063     8.507   0.000
    .logrelatFecFml   1.000    0.078    12.830   0.000
     resource         2.427    0.237    10.261   0.000

Group 2 [Defoliated]:

Latent Variables:
                    Estimate  Std.Err  z-value  P(>|z|)
    resource =~
      sqrtDBH         1.000
      sqrtCompet7    -0.345    0.041    -8.460   0.000
      sqrtDens14     -0.294    0.128    -2.291   0.022

Regressions:
                    Estimate  Std.Err  z-value  P(>|z|)
    logBAI ~
      resource        0.606    0.075     8.054   0.000
    logrelatFecFemale ~
      resource        0.348    0.123     2.830   0.005
      logBAI         -0.044    0.140    -0.311   0.755

Intercepts:
                    Estimate  Std.Err  z-value  P(>|z|)
    .sqrtDBH          5.636    0.174    32.451   0.000
    .sqrtCompet7      1.844    0.068    26.976   0.000
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.sqrtDens14        7.971    0.186   42.881    0.000
.logBAI            3.905    0.124   31.552    0.000
.logrelatFecFml   -0.734    0.558   -1.317    0.188
 resource          0.000

Variances:
                  Estimate  Std.Err  z-value  P(>|z|)
.sqrtDBH           0.560    0.202    2.767    0.006
.sqrtCompet7       0.169    0.033    5.097    0.000
.sqrtDens14        3.084    0.451    6.833    0.000
.logBAI            0.608    0.115    5.288    0.000
.logrelatFecFml    0.806    0.124    6.477    0.000
 resource          2.306    0.448    5.149    0.000
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Detailed answer to reviewers' comments (which appear in green below)

Decision

by Georges Kunstler, 2019-01-24 10:42
Manuscript: https://doi.org/10.1101/474874
Minor revision

First, I'm sorry that the review process has taken longer than usual (this is because of the Christmas vacation), but the three reviewers have provided very thoughtful reviews (the referee are listed by date in the email generated by PCI website as follows referee 1: 2019-01-02, referee 2: 2019-01-21, referee 3: 2019-01-23).
This preprint investigates how crown defoliation affects both tree female and male fecundity and basal area growth in a population at the dry edge of beech distribution. The question explored in this preprint is whether defoliated beech trees have different relative investment in reproduction vs. growth in comparison with non-defoliated trees. To do this, the authors use an innovative method to estimate individual tree effective fecundity based on marker-based parentage analysis of seedling. They have already published a paper describing the methods and using it to test size and competition effect on fecundity (Oddou-Muratorio et al. 2018 Mol Ecol). In this new preprint they connect their fecundity analysis method to broader evolutionary and ecological questions to test the coordination between fecundity and growth and its response to a defoliation stress. This is clearly a very interesting and solid study that will be of wide interest to forest ecologist as shown by the comments of the three referees. The three referees have, however, pointed out several general concerns that need to be solved before a final recommendation can be published.

- The main concern that has been pointed out by the three referees is related to the interpretation of tree defoliation as a proxy of drought stress. Tree defoliation can be induced by drought but also by numerous other processes. Thus, if there are no other solid evidences to demonstrate that in your study tree defoliation can be used as a proxy of drought, I think it would be more cautious to focus on tree defoliation per see (an indicator that the tree has experienced a stress but not necessarily a drought stress). In my view this can be solved by substantially down playing the focus on drought in the introduction and the discussion (the analysis are not affected by this issue). The referee 1, 2 and 3 also provide important comments about the binary annual defoliation variable that could be included in the discussion.
- Both referee 2 and 3 have questioned the series of the linear regressions that are used to analyze the complex interaction between BAI, DEF and Fecundity (make or female) and proposed path analysis as a more elegant solution for the analysis. I think you should at least clarify the connection between these different regressions and discuss the limitation of your approach compared to path analysis (or structural equation models).
- The referee 1 also raised concern about the use of linear relationship for several variables rather than non-linear functions. This can be easily checked based on models residuals.

The three referees provide numerous additional comments that might help to improve the preprint. I have also listed some minor comments below.
Sincerely, Georges Kunstler

Editor's minor comments:

line 42: "in response to water stress". There is no clear evidence in the MS that water stress is the proximal cause of defoliation.
SOM et al.: The focus on water stress has been tempered throughout the manuscript, and the term "Water stress" was overall changed into "stress".

Line 70: Reference "Wiley, Casper & Helliker 2017" is missing in the references list.
SOM et al.: Added

Line 111: Reference "Camarero et al. 2015" is missing.

8

SOM et al.: Added

Lines 118-119: "assuming that crown defoliation is a proxy for drought vulnerability" this is a big assumption because defoliation can result from numerous other processes (insect attacks, wind disturbance, …). In my view to claim this you need solid evidence to demonstrate that in your study tree defoliation can be used as a proxy of drought. This is not presented in this version of the preprint. A large part of the introduction and discussion build on this interpretation of defoliation as a proxy of drought. If there are no additional evidences to support this hypothesis I would recommend to rather build the introduction and discussion around defoliation rather than drought stress. (same comment for lines 144-145 on water stress).
SOM et al.: see answer to main comment on the first page of this letter.

Line 161: Change "one of the of the French beech" to "one of the French beech".
SOM et al.: Corrected

Line 202 Equation 1: Something went wrong with subscript (the sum should be from $\sum{j = 1}^{n{d_{max}}}$, no?)
SOM et al.: We thank the editor for detecting this problem in equation (1), it is now corrected.

Figure 1 page 7: It could be useful to add the circular plots on the panel A.
SOM et al.: done on figure 2.

Line 203: Again some problem with the subscript in dbh_i.
SOM et al.: corrected

Lines 215-216: I don't know if you have this information but it would be useful to say which years were masting year in the region between 2001 and 2012.
SOM et al.: we added that masting occurred in years 2002, 2004, 2006 and 2009 (L230-231)

Line 244: You probably need to give more details about the dispersal kernel (even if this is fully explained in your previous paper presenting the method). What are the parameters and their estimate and how do they differ from your previous estimates?
SOM et al.: We have added a new Appendix A1, with all estimates from MEMMseedlings.

Line 255: "our hypothesis IN that biases" should be "our hypothesis is that biases"?
SOM et al.: corrected

Line 291: What do you mean by "FULL linear model"?
SOM et al.: "full" removed

Line 325: should it be "correlations may be due TO variation in size"?
SOM et al.: corrected

Line 365 – 366: The fact that "Comp10" has a negative effect whereas "Dens10" has a positive effect could be discussed in more details. This seems quite important given that in your previous publication (Oddou-Muratorio et al. 2018 Mol Ecol) it was not the same.
SOM et al.: The opposite Type III effects of competition and density are probably driven by the facts that (1) only trees with low competition indexes showed a high female fecundity and that (2) only trees with low density in the neighborhood showed a very weak female fecundity. This can be seen on the scatter plots now presented as Supplementary Figure S4. Moreover, the positive correlation between compet10 and Dens10 may also contribute to these effects (cor=0.10, pval=.02). We chose not to detail this interpretation in the main manuscript because it is difficult to teas apart the role of real ecological processes from that of statistical effects, but we add some sentences on Figure S4.

Lines 372-374: Sentence unclear.
SOM et al.: the sentence was reformulated L383-386.

Page 14 Table 1: As pointed out by referee 1 you compute VIFs but doesn't seem to use them to check for multicollinearity. You call add a sentence such as "For all fitted models variance inflation factors were all below 10, ruling out any serious multicollinearity.".
SOM et al.: A new sentence was added on L380-381 to acknowledge that multicollinearity was not a problem in our case.

Lines 458 – 459: "However, the mitigating effect of increasing tree size on decreasing female fecundity for defoliated tree" sentence unclear.
SOM et al.: This paragraph was removed from the revised version.

Line 505: "Long-term consequences for population adaptive response to drought stress" again the lack of clear argument for the connection between defoliation and drought stress makes this subtitle problematic.
SOM et al.: removed from the revised version, and replaced by "Long-term consequences for population adaptive response to stress"

Line 521: Reference "Bontemps et al. 2017" is missing.
SOM et al.: reference added

Line 535: The reference "Hamanishi & Campbell, 2011" is missing.
SOM et al.: reference added

Line 543: Reference "Gerzabek et al. 2017" is missing.
SOM et al.: this reference was removed in the manucripy.

Review 1

Reviewed by anonymous reviewer, 2019-01-23 15:11
In this manuscript, the authors analyze the relationship between crown defoliation, basal area growth, and estimates of male and female fecundity in a population of European beech at its south-western distribution margin. Increasing crown defoliation was found to correlate with reduced basal area growth and reduced female fecundity. Growth reductions with increasing defoliation were relatively larger than reductions in female fecundity. Finally, a negative interaction term between basal area growth and defoliation level in the model of female fecundity is interpreted as a trade-off between growth and fecundity: while for non-defoliated trees female fecundity increases with growth, female fecundity decreases with growth for defoliated trees.
I found the topic relevant and timely, and the manuscript overall well-written. My main suggestions relate to the interpretation of results and a potential alternative for data analysis.
While drought is a plausible cause of crown defoliation, it is not the only one. Thus, results should be presented and discussed more carefully with respect to alternative causes of crown defoliation.
It may be useful to formulate the relationships between measured variables in a more explicit hierarchical fashion, which would then lend itself to be analyzed by structural equation models: e.g. competition might affect defoliation and competition and defoliation then affect growth, and all three affect fecundity.
SOM et al.: We thank the reviewer for his/her positive comments. The focus on defoliation as an indicator of drought has been tempered all along the manuscript, and we now better acknowledge the other possible stresses leading to defoliation (see answers to main comment on page 1 of this letter).
The possibility to use of SEM has been thoroughly investigated (see the paragraph "On the use of path analyses", pages 3-7 of this letter)

Detailed comments l.

Equation for basal area lacks division by 4 l. 179 "relative" increment – I suggest removing "relative" because this seems to be simply the increment, rather than "relative basal area increment", which would be the BAI divided by the initial BA l.

SOM et al.: We thank reviewer 2 for detecting the missing 4 term (now corrected L206). Also, we agree with reviewer 2 that our BAI is not relative. This is a residual error due to a bad actualization of a previous version of the paper, where we analyzed individual relative BAI, defined as $BAI_i/meanBAI_{pop}$ (to make it comparable with the relative fecundity estimated from MEMM). However, as pointed out by reviewer 1 and 2, such relative BAI would have been confusing because relative BAI is rather defined as the BAI divided by the initial BA. As we interested in none of these two possible definitions of relative BAI, we used BAI throughout the analyses (but omitted to remove the term "relative").

242 Please state how the estimation of FFj was made identifiable; I assume this was done by enforcing that the mean of FFj was equal to one. l.

SOM et al.: This is now detailed L263-265.

255 This hypothesis would benefit from further explanations

SOM et al.: Detailing this hypothesis would have result in a long paragraph of text in the main version of this manuscript, therefore we developed it in the new Appendix A1.

l. 402 The SSQ values in Table 2 do not seem to correspond to the P-values reported in the table. Please check. l.

SOM et al.: Thank you for detecting this error, we replaced the values by correct Type III sum of squares. (VIF values were also wrong).

570 This sentence seems out of context.

SOM et al.: Corrected

Appendix S3 B (Table on sampling size): Add units for fecundity and defoliation variables

SOM et al.: Being relative, fecundity values have no unit. Defoliation scores also have no values. This is now explicitly said in the footnote.

Review 2

Reviewed by anonymous reviewer, 2019-01-21 18:13
The authors addressed the influence of drought on tree reproduction and forest regeneration in a relict population of European beech located at low elevation in Mediterranean France. They measured defoliation and wood growth, and used both a spatially explicit mating model and parentage analyses to assess female and male fecundities. Female fecundity was less sensitive than growth to defoliation, and decreased more slowly in large individuals. A tradeoff between growth and female defoliation suggested that large individuals could invest less in growth to maintain female fecundity. The authors conclude on some potential evolutionary implications and on the related vulnerability of the relict beech population to climate change.

The manuscript is well-written and easy to follow. The protocol and statistical analyses have been thoroughly designed and performed, although the complex set of linear models could be replaced with a (more appropriate?) Path Analysis or Structural Equation Model (see comments below). A relatively major revision should allow recommendation and publication of this work.

My main comments concern:
- The focus on the (long-term?) evolution of drought-resistance traits, which seems to be somewhat speculative on the basis of the present results. The scope should be rather focused on the ecological consequences of drought on growth and fecundity.

SOM et al.: We agree with reviewer 2 that the present manuscript does unfortunately not allow to fully investigate the alternative hypotheses related to evolution of stress-resistance traits as they were

presented in the previous introduction. However, trait evolution can be quite rapid (less than 5 generations), and may not only be seen as a long-term response even in long-lived trees.

In the revised version of the manuscript, we focused the introduction on the ecological consequences of the change in the relationship between growth and reproduction in response to stress (L131-146), and kept the evolutionary implications for the discussion section only (L531-540).

- The defoliation scores aggregate annual defoliation scores over 9 years. What about the between-year variation in climatic conditions and drought stress? For instance, the 2003 year had a very hot summer that could be much detrimental. Is there a specific signature of extreme drought stress experimented during this specific year? In addition, it would be interesting to analyze how the number of defoliated trees per year, or the binary defoliation state of individuals per year, depends to the variation of drought stress over years.

SOM et al.: We agree with reviewer 2 that yearly impact of defoliation would be interesting to investigate. However, as the reproductive investment could only be estimated in this study as an average over the period from 2001 to 2012, we preferred to focus also on the cumulative defoliation index presented here.

Yearly patterns of defoliation and mortality were analyzed more specifically in the companion paper by Petit-Cailleux et al., also submitted to PCIEcology, where 4327 trees where surveyed for defoliation, growth, and mortality. This study suggests that drought was particularly strong in year 2006, with a signature on mortality. Moreover, this study also showed that defoliation is associated to an increase risk of mortality. This is now better highlighted L439-448 of the present manuscript.

- The inference of female/male fecundities is highly parameterized (one fecundity value for each tree). Although I understand the overall logic of SEMM analyses and a priori trust its ability to provide proper inferences, it would be useful to include some further results of cross-validation and credible intervals of the estimated parameters in an Appendix.

SOM et al.: this in now done in the new Appendix A1, which details the material and method and results from the SEMM analyses.

- the rationale of equation (3') (L316) is quite confusing: here DEF is a function of predictors that are also included in equation (3) where DEF is also a predictor. The same issue also applies for eq. (4), as BAI becomes a predictor while it was an explained variable in eq. (3). In order to disentangle direct and indirect effects of predictors on BAI and fecundity variables, shouldn't some Path Analysis be more appropriate?

SOM et al.: see the paragraph "On the use of path analyses", pages 3-7 of this letter

- It is quite confusing that BAI is not actually a measure of relative increment. It should be divided by BA in 2002 to do so. Because it is still an absolute measure, a few big trees can have large BAI values.

SOM et al.: we agree with reviewer 2 and we call now BAI Basal Area Increment, and not relative BAI (see also response to reviewer 1). We agree that it is an absolute measure, and the effect of size is captured by the linear model described by equation 3.

Further detailed comments:

L37-39: based on previous and next sentences, is the trade-off specific to larger individuals?

SOM et al.: the trade-off between female fecundity and growth (BAI) holds for all individuals whatever their size (DBH), as shown on Figure 4 (so we did not change the text). Moreover, the detailed analysis of the interaction between DBH, DEF and BAI on female fecundity shows that those defoliated individuals maintaining a significant female fecundity at the expense of reduced growth were the largest ones, while the female fecundity of small individuals generally strongly decreased in response to defoliation. This is now better formulated L37-40.

L42-43: "compromise the evolution of drought-resistance traits" is debatable based on the present results.

SOM et al.: this is why we used the term "could", which make sense in the light of the discussion.

L49-97: there is much focus in the first paragraphs on the influence of drought and deaf defoliation on reproduction, although the central objective of the paper is to address a joint influence of drought on growth and reproduction through defoliation. I would suggest better emphasizing the hypotheses on both growth and reproduction from the beginning, to better introduce the general scope. Only from L92 the topic of growth is briefly introduced.
SOM: we hope that the revised version of the introduction is better focused, even though the investigation of stress impact on reproduction is also a central objective of the paper (now clearly acknowledged at the end of the introduction (L166-169)

L89: what "water ability" means?
SOM et al.: Corrected for water availability

L98: "evidence"
SOM et al.: Corrected

L99: "tree orchards"
SOM et al.: Corrected

L117: the focus on evolutionary dynamics sounds marginal here, although it is one of the key points in conclusion of the Abstract. In general, the Introduction does not emphasize well the motivation and objective of working on evolutionary dynamics.
SOM et al.: we finally choose to keep the focus on evolutionary consequences for the discussion only (see also answer to the first main comment of reviewer 1)

L166: "Acer monspessulanum"
SOM et al.: Corrected

L167: what "intensively" means here?
SOM et al.: we removed the term as it was not useful here. The trees within the fence are considered as highly monitored as compared to trees outside the fence since they are surveyed for defoliation and mortality twice a year.

L176: indicate here the number of individuals in the subset.
SOM et al.: Completed

L178-179: unclear what a "quadratic measure of size" really means.
SOM et al.: Removed

L179: the formula should be BA=Pi*(DBH/2)^2.
SOM et al.: Corrected

L179-L180: the formula here does not represent a "relative increment", it is rather an absolute increment.
SOM et al.: Corrected

L184: it is unclear how the aggregate defoliation score can represent both the recurrence of defoliation and the ability to recover from defoliation. More specific indexes should probably be designed to identify these specific components (see also my general comment on the aggregate measure of defoliation).
SOM et al.: actually this formulation rather aimed to warn that this aggregate defoliation score cannot tease apart the two components cited (recurrence of defoliation and ability to recover). Indeed, when a tree is observed as defoliated for several years, it is difficult to tell if this is due to a high sensitivity to stress, or to a weak ability to recover from stress from one year to the other (memory effect).

L202: to avoid confusion, "max" should be a subscript here. In addition, it is not clear why dmax appears in the equation: shouldn't it be instead ndmax? It is unclear how the individuals j are summed in a given radius dmax. The equation may be rewritten to clarify that.

SOM et al.: Corrected

L255: "is that biases".

SOM et al.: Corrected

L265: "SEMM-based"?

SOM et al.: Corrected

L300-302: it seems that the approach performing separate models with Densdmax and Competdmax, for different dmax and without interactions, does not allow selecting dmax values without bias if interactions actually play. Potential issues should be at least discussed.

SOM et al.: Actually, we searched for the dmax value leading to the highest R^2 for model including both Densdmax and Competdmax, although without their interactions.

L323: not sure to get what "individual correlation" means here.

SOM et al.: the term "Individual" was removed; this was to stress out that correlation is computed between individual data of female fecundity and growth

Fig. 2B: isn't it a bit surprising that there is not a better correspondence between BAI and radial growth?

SOM et al.: The weak correlation between BAI and radial growth (Pearson rho = 0.58) is not surprising considering the high heterogeneity of tree size (DBH) within the stand. A high radial growth (e.g. 20 mm) converts into a much larger BAI for a large tree (for DBH_{2002}=70 cm, BAI=452.4 cm²) as compared to a small tree (for DBH_{2002}=20 cm, BAI=138.2 cm²). This is why we estimated growth through BAI rather than radial growth, because when the focus is on investment in growth, it makes more sense to consider the total biomass a tree invest in wood.

L349: not sure that the precision on more or less "L-shaped" pattern is really useful.

SOM et al.: The more or less L-shaped distribution implies more or less important inter-individual variance in the focal performance trait.

L368-369: this result has already been mentioned just before.

SOM et al.: we are not sure to see the repetition.

L389: provide Figure number.

SOM et al.: Completed

Figure 3: it is not completely clear for me how the confidence intervals represent the estimation of interaction terms in the panels. Maybe provide some more information on what the interaction plots precisely represent here?

SOM et al.: the significance of the interaction terms is tested by the linear model, as reported in Table 1 & 2. Only significant interaction are plotted, and the graphs allow to visualize them.

Figure 4: it seems that a few large defoliated trees have still large BAI and greatly contribute to the overall variation here.

SOM et al: We are thankful to reviewer 2 because his/her comment allowed us to realize that we had forgotten to mention an important detail in the legend of Figure 4 (although it was in the main text): this plot depicts the relation between RAW BAI and RAW fecundity. So, the confounding effect of competition for instance should be removed to analyze the tradeoff between growth and reproduction.

L417: remove "significant".

SOM et al.: Corrected

: it seems that this paragraph should be better connected with, or ever merged, with the next section on the trade-off between growth and reproduction.

L509: "that" instead of "which".
SOM et al.: Corrected

L505-544: this final section sounds a bit speculative and quite outside the basically ecological scope of the paper (see also main comments above). Some more specific points:
SOM et al.: This section was thoroughly revised.

Globally, it is unclear how the relative quantity of pollen and seeds produced by large and small trees can affect the dynamics of allele related to drought stress resistance. There is much variance and the plausible evolutionary changes should be addressed specifically.
SOM et al.: This is now reformulated L 551-554

L506-507: the way a contribution of large defoliated trees to regeneration through female function can affect adaptation should be discussed relatively to the contribution of smaller trees to next generation. The global outcome is not trivial.
SOM et al.: rather than the contribution of smaller trees, it is the contribution of non-defoliated trees which matters in this case, because our results indicate that reproduction could be favoured relative to growth in response to stress (as better reformulated now L 531-540)

L515-517: it seems that the two strategies are not strictly exclusive. Multiple traits and substantial plasticity can underlie these strategies, and the genetic determinism may not be obvious.
It seems that some adaptation to defoliation could be a change in leaf phenology, i.e., with leaf shedding due to drought stress rather than to winter cold. If both summer becomes more dry and winter becomes cooler, a phenological shift could evolve. This kind of phenology is common in tropical dry deciduous vegetation.
SOM et al.: We agree with reviewer 2 that the two strategies are not strictly exclusive, and actually, we cite Bontemps et al. (2017) who found that these two strategies could co-exist within population. We also agree that phenological shift could come into play.

The possible role of density dependence sounds even more speculative in the context of the present study.
SOM et al.: this sentences were removed

Review 3

Reviewed by anonymous reviewer, 2019-01-02 11:50
General comments:
Sylvie Oddou-Muratorio and colleagues investigated associations between crown defoliation, radial tree growth, tree size, competition and female/male fecundity in a drought-prone beech population in Southern France. Reproductive beech trees were analyzed to estimate female/male fecundity. Increases in crown defoliation, competition and tree size resulted in decreases in both female fecundity and tree growth.
In general, I liked the approach that was used in this study. Allocation trade-offs between various tree compartments is an important research topic in tree ecology. However, several issues arose when reading the paper, which I want to briefly summarize:
Because the beech trees belonged to a drought-prone tree population, the findings were interpreted and presented in the context of drought effects (e.g. in the Summary L20-25, L42-43; most of the Introduction; a large part of the Discussion). However, the study does not explicitly consider any observed variability of drought conditions neither in space (e.g. different beech populations along a drought gradient) nor along time (e.g. year-to-year changes of drought conditions). Thus, there is no control, which would allow to assess the effects of drought on the findings. While there are some

information about beech and its susceptibility to drought (L128-L140), the same analyses as conducted in this study should have been conducted at other sites as well.

SOM et al.: We agree with reviewer 3 that drought variations may generally be more important among than within sites, as well as among years. However, drought and stress conditions in general also vary among individuals within population, due to different factors, related to (i) variation in resource availability, (ii) variation in plant resource status and/or (iii) variation in stress itself (see new figure 1 of the manuscript). Moreover, our hypothesis is that the susceptibility to stress (for instance, the susceptibility to defoliation) may be in part genetically controlled. Thus, this study takes advantage of all these source of among-individual variation to investigate the combined impact of stress on growth and reproductive performances, and their potential consequences on the population dynamics. Note that the population scale is particularly pertinent when addressing eco-evolutionary dynamics, since this is the scale at which those interactions occur. This is now reformulated L 136-146, and in the discussion (L531-570).

The variable "annual defoliation scores" was derived from observations over 9 years, whether dead branches and leaves were present. Dead branches and dead leaves should have been assessed separately, and rather than using just presence or absence, a percentage (or number, if applicable) of dead branches and leaves, respectively, should have been used. I guess that even under rather moist conditions, there are always a few dead branches or leaves. Dead branches are often a result of the natural tree development, which are not necessarily related to drought.

SOM et al.: We agree that defoliation may not be necessarily related to drought, and this is now better acknowledged in the revised manuscript. Regarding the qualitative survey of defoliation, we also agree that it may not be fully adequate; the main advantage of this defoliation survey is to be simple and easy to perform on a large number of individuals and every year. This advantage better appears in the companion study by Petit-Cailleux et al (submitted), where 4327 trees where surveyed for defoliation, growth, and mortality.

BAI is a non-linear function of age or tree size, i.e. BAI is increasing up to some culmination point and then decreases. A linear relationship is found for younger/smaller trees, but not for older trees. The DBH distribution in Fig. 4 tells us that the observed trees are rather big, i.e. increasing BAI is expected to be followed by decreasing BAI within the same tree. Thus a linear relationship with DBH does not allow to model the change in BAI (equation 3). A simple solution to that problem is to use a quadratic function of DBH (DBH, DBH^2) or to use a spline function. Also for the other variables in the same equation, it is not obvious whether linear relationships are useful. This needs to be checked visually using scatter plots between each predictor variable and each response variable. The fitted models should be checked using diagnostic plots.

SOM et al.: see answer to main comment on page 1 of this letter.

Specific comments:

L19: After reading the summary, it is not clear whether the paper is about individual severe droughts or about long-term drought conditions. It is further unclear, whether the effects of drought on the investigated processes have been really tested.

SOM et al. : The focus on drought has been tempered throughout the manuscript. The reference to Petit-Cailleux et al., which more specifically investigate the effect of drought using ecophysiological morels is better put forward in the discussion.

L26: It should be specified what is meant with wood growth (e.g. ring width, BAI).
SOM et al.: Corrected

L35: The term "twice less strong" needs to be rephrased.
SOM et al.: Corrected

L68: Omit "induced".
SOM et al.: Corrected

L87: Omit "a coniferous species".
SOM et al.: Corrected

L89: Do you mean "availability" rather than "ability"?
SOM et al.: Corrected

L101: "Hot, dry summers" do not fit into this context, since they are neither considered an experiment nor a cultural practice.
SOM et al.: We agree with reviewer 3 that climate is not controlled in seed orchard; however, this literature is one of the first to have documented the effect of climate on seed production in trees.
L119-123: The problem with testing these hypotheses is that there is no control, e.g. no comparison of drought and non-drought years or periods is made.
As detailed above, this study takes advantage of all these source of among-individual variation in the susceptibility to stress to investigate the combined impact of stress on growth and reproductive performances, and their potential consequences on the population dynamics. We do not have control, but we have a gradient of individuals more or less susceptible to stress.

L132: Write "altitudinally".
SOM et al.: Corrected

L161: Omit the second "of the".
SOM et al.: Corrected

L179: Correct is "BA = pi * (DBH / 2)^2"
SOM et al.: Corrected

L181-182: I wonder whether this measure is useful, see my general comments. A tree with only few dead branches or leaves is classified in the same way as a tree with many dead branches or leaves.
Only the presence of big dead branches or massive leaf fall was recorded as 1.

L203: Only "i" (dbhi) and "j" (dbhj) should be written in subscript.
SOM et al.: Corrected
L204: ndmax does not occur in the equation.
SOM et al.: Corrected

L276: Write "and combined the".
SOM et al.: Corrected

L281-282: Write "After sanding, cores...".
SOM et al.: Corrected

L292-293: See my general comments.
see answer to main comment on page 1 of this letter.

L306: Software like SAS uses procedures, R uses functions.
SOM et al.: Corrected

L324: I'm not sure whether this is a useful approach, and this is related to one of my general comments. Defoliation ranges between 0 and 100%, i.e. the values are part of a continuum. With the suggested arbitrary classification into two groups, a tree with 0% defoliation is assigned to one group, whereas a tree with 1% defoliation is assigned to the other group.
SOM et al.: Defoliation is not a percentage, it varies by 9 units at maximum. I practice, it varies from 0 to 7 in the sampled trees (see Table S2 and new figure S4 A).

L329-330: Here too, whether the relationships are linear first needs to be checked visually (particularly for BAI).
SOM et al.: This was done in the revised version of the manuscript (new figure S4).

L331-332: Does this mean that the expected BAI and DEF, respectively, are used (i.e. the predicted values)?
SOM et al.: no, we did not used the predicted values but the observed values.

L396: Rather than excluding BAI=0 values and log-transform the remaining raw BAI, it is possible to fit a GLM model with normally distributed errors and a log-link function for the expected BAI values.
SOM et al.: we thank reviewer 3 for this suggestion, which we did not follow here for practical reasons.

L397-403: Although the VIFs were calculated, it does not get clear, what was done with this information. VIFs > 4 tell us that the variable is correlated with other predictors, which need to be checked. VIFs > 10 indicate serious multicollinearity.
SOM et al.: we added a sentence L380-382 on this issue.

L404 (Fig. 3): None of these figures here nor in the Supplement allows to asses, how well the models are fitted to the data. I suggest to add the observations to the plots.
SOM et al.: Observations were added to the graphs (Figure 3 + S8)

L408: Why are 80% confidence intervals shown? Standard is a 95% CI.
SOM et al.: the significance of the interaction terms is tested by the linear model, as reported in Table 1 & 2. These graphs simply aiming at visualizing the interactions, we plotted the 80% CI (which overlap indeed less than the 95% CI).

L417: However, because the control is missing, we don't really know how the trees respond to water stress (see my general comments).
SOM et al.: see our response to reviewer 3 general comment.

L423-424: The described processes are generally plausible, however, there are no observations for the study site.
SOM et al.: In the revised version, we have added complementary information based on a companion study by Petit-Cailleux et al. on the same site (L439-448)

L469: Write "was shown".
SOM et al.: Corrected

L475: To test this hypothesis, observations at a dry site (such as the one in this study) and a moister site should have been taken, or even better observations along a drought gradient.
SOM et al.: see our response to reviewer 3 general comment.

L505: The response to drought stress was not explicitly measured, thus the conclusions in this chapter are rather speculations.
SOM et al.: This section was thoroughly revised.

L509-510: This is not shown in this paper
SOM: we agree with reviewer 1, this is an hypotheses based on our results (hence the "may")