Dear Dr Alonso,

Please find our response to your and the reviewer's comments on the first version of our manuscript "The hidden side of the Allee effect: correlated demographic traits and extinction risk in experimental populations". We are deeply grateful for the time and effort you all put into improving our manuscript, for all the constructive comments and the excellent suggestions you made.
We have reworked on the manuscript accordingly, and we believe that it has been significantly improved. We detail our replies to all comments below, and we truly hope that we managed to correct all shortcomings that were found in the first version of the manuscript, so that it will now meet the high-quality standard required for a recommendation from *PCI Ecology.*

Sincerely,
Elodie Vercken, on behalf of the authors

Comments from Recommender David Alonso

- *Although it is true that you find positive density-dependence in 3 (out of 20) populations, the statistical methods to come to your main conclusion need to be very much improved. Please follow the recommendations of van Dooren, who reviewed very thoroughly your statistical methods and did a great job at pointing to the main weaknesses in your analysis.*

We modified three main points in our analysis, following the excellent recommendations from Dr Van Dooren : (i) we included all 30 populations that were in the initial dataset as they were sampled from either different sites or different host plants, and included "species" as a random effect in our statistical model ; (ii) we modelled population size at generation (t+1) as a Poisson variable, with log (population size at generation (t)) as an offset and a smooth term depending on population size at generation (t) that represents the density-dependence in per capita growth rate ; (iii) we tested for the difference between Allee and non-Allee populations in demographic parameters with a likelihood-ratio test. Our initial conclusions stand to this new, undeniably better analysis.

- *Notice that central figure 2 is not very conclusive. You need to add confidence bands to your plots as stated by referees 1 and 2.*

Done.

- *Also, recall that figure 3 is based on the grouping sorting out presence and non-presence of Allee effects in your populations, but, if you are left only with one population (out of 20) showing significant Allee effects, then the statement "the presence of positive density-dependence and impaired demographic performance" (Fig 3) is clearly shaky.*

Including all populations, we have now 8 Allee populations compared to 21 non-Allee populations, and the differences we observed in demographic parameters are confirmed by the new analysis.

- *My feeling is that you introduce with elegance the topic, but then you don't take advantage of your theoretical models in your statistical analyses. As a suggestion, you could use a time-discrete version of the modified logistic model of Lewis and Kareiva 1993, and then, in the light of the data you gathered, analyze the significance of the Allee effect parameters.*

We now explain in more details in the intro (L.100-116) why we chose not to go with a model-based approach, as we feel that it puts unnecessary constraints for the detection of Allee effects.

- *The discussion should be also rewritten in the light of referee recommendations, particularly, explaining (or speculating about) the mechanisms underlying the Allee effects seemingly found in your experimental populations. For instance, within the same species (cac), why do you find different results?*

We did expanded our discussion to include a more thorough reflection on the potential mechanisms underlying Allee effects in our populations (L. 290-330)

- *You could be able to interpret your results differently, as referee 1 points out, in terms of stochasticity at low numbers.*

We did a good amount of thinking and re-thinking on this point, went back to the original works on stochastic Allee-like effects, and we finally concluded that this was unlikely to be the main process here, as we observed positive density-dependence directly on the per capita growth rate and not on extinction probability. The dispersion of data at low density also did not seem to be in support of the hypothesis of a reduced mean performance because of high variance. We nevertheless discuss this point in the manuscript (L. 317-330).

Comments from Anonymous Reviewer

- *Fig. 2. Non-linear fits show clear evidence of Allee effect in three populations. However, there is a population (cac8) for which per-capita growth rate data seem to show an increase for small populations, but the presented fit does not seem to account for that fact (other populations like sem4 clearly account for that initial increase). Please, explain why and add a bit of discussion about this.*

We changed our analysis, according to another reviewer's suggestions, and the visual pattern of positive density-dependence in the cac_8 population is now detected by the GAM.

- *2. Given that experimental conditions are controlled and remain the same across populations, I find intriguing why all the cacoeciae populations do not exhibit Allee effects at all except for one population (cac_8). Do the authors have any idea of why this population is singular compared with the remaining cacoeciae? Please discuss this point a bit in the manuscript.*

With the new analysis on the complete dataset of 30 populations, we now find 5 populations with Allee effects in the species T. cacoeciae. We discuss some potential mechanisms (L. 290-315), but at this point we do not have further insight on the emergence of differences across populations of the same species.

Comments from Dr Tom Van Dooren

I enjoyed reading the preprint but have doubts concerning the conclusions and would appreciate that the Allee-like effects discussed by e.g. Lande (1998) are treated from the introduction and more seriously considered. I would personally prefer reserving the term "Allee effects" for growth rate effects due to lack of social interactions at low densities. That does happen in the discussion but insufficiently so in general. In the introduction Allee effects are equated with positive density-dependence, which is a good choice as well, but then all potential mechanisms have to be introduced immediately. The abstract should define Allee effects as positive density dependence in that case as well. What you call "Allee-like" effects are there because of stochastic variability, interactions of means and variances. If you can attribute your results to them, please do so clearly. Lande (1998) calls them a type of Allee effect, so why not categorize different causes which can make one conclude from a time series analysis that there is positive density dependence and call all of them Allee effects?

- We are grateful for this insight on our misguided interpretation of Allee-like effects. After careful reflexion, and re-reading of many references citing the Lande et al. (1998), we have come to the conclusion that the positive relationship we observe in some populations between population size and per capita growth rate is not caused by demographic stochasticity. First, the dispersion of data at low population size in what we refer to as “Allee populations” does not include both high and low values for the per capita growth rate. Then, as stated in Boukal and Berec (2002), the transformed scale in Lande’s approach is not easy to interpret biologically, and Stephens (1999) makes a distinction between this Allee-like effect related to demographic stochasticity and “real” Allee effects determined by positive density-dependence in individual fitness. In our case, we do analyze per capita growth rate and not extinction probability, as is classically done in other studies aiming at detecting Allee effects. So there is no reason that our conclusions on the presence of a “true” Allee effect in some of our experimental populations are any less valid than those of, for instance, Johnson et al. 2006.

We re-wrote the discussion to better argue this point on the mechanisms underlying the Allee effects we observe in some of our Trichogramma populations (L. 317-330).

I am unconvinced by the way Allee effects are detected: that happens just in the predicted time series, as if these predictions are perfect and without any uncertainty. You should consider the confidence bands for the predictions and detect an Allee effect from them.

- We did add the 95% confidence bands to the GAM predictions, and we confirmed the presence of an Allee effect only in cases where only positive slopes were included in the band at low densities.

Introduction: Plead add a citation to the first paper where the Allee effect was introduced.

- Done

The papers added as references for the modified logistic model in fact refer to several different modified models, so there are "modified versions" of the logistic model.

- We partly disagree with this comment:

Lewis and Kareiva (1993) f(u)=ku(1-u)(u-a)

Amarasekare (1998): dN/dt=rN(1 - N/K)(N/K – A/K)

Boukal et Berec (2002): dN/dt=Ng(N) where g(N) can be of different forms, one of which, model (4), is r(1 – N/K) (N/K – A/K)

The last two models are exactly the same, while the first one is dimensionless as regards to K but the structure is the same. So its seems to us that we can consider that the three listed references do refer to the same model. If this remains a major point for the reviewer, we will propose a different formulation.

The terminology of Boukal and Berec is more precise than "weak" and "strong" Allee effects so please introduce it and use it.

- Boukal and Berec (2002) refer to weak/strong Allee effects by the equilibrium states of the populations, i.e. respectively “unconditional survival (US)” and “extinction-survival (ES)”. However, most of the empirically-based relevant literature uses the terms “weak/strong” or synonyms like “severity” or “strength” of the Allee effect (e.g., Gascoigne 2003, Petrovskii et al. 2005, Courchamp et al. 2008, Saha et al. 2013, Hart and Aviles 2014), so it may sound more familiar to most empirical ecologists. We propose to keep the weak/strong distinction throughout the manuscript, but to explain the difference in more details in the introduction (L.36-40).

Maximum per capita growth rates are smaller with an Allee effect: does -A have to be smaller than K for this, please be more precise.

We apologize if this part was unclear: we mean that the per capita growth rate (i.e., 1/X dx/dt) observed in the Allee-effect model is always smaller, for all x values, than the maximum per capita growth rate in the logistic model (r). We stated this more clearly in the text (L. 57-59). We also specified the range of values for A for which the model makes sense biologically (L. 51-52).

Please state in the introduction how an Allee effect is detected in an actual population dynamical time series, so how its presence can be determined. Explain whether this then automatically implies that other statistics of the population dynamics will correlate with the strength of an Allee effect estimated from a time series or not. The introduction now gives us a feeling for what Allee effects do in models, but not how they emerge from time series analysis. I would already interpret a conclusion potentially differently here: did a time series with an extinction increase the likelihood of detecting an Allee effect of the kind Lande 1998 studied?

- We added a part in the introduction to explain how Allee effects are classically investigated in time series, and to justify the approach we chose (L.97-116). We reckon that extinctions occurring more frequently at low density should tend to increase the likelihood of detecting positive density-dependence in the per capita growth rate. Yet if these extinctions are purely stochastic while the deterministic growth rate remains positive, then the dispersion of data should encompass both high (many) and null (few) values for per capita growth rate, resulting on an average slope that is positive.

Methods: I don't agree with removing some of the time series from the analysis. You removed your true replicates. A mixed model analysis can deal with it easily: you did fit random line effects.

- Done

There seemingly is an error in one of the sentences: one T. cordubensis population was removed for which there were several replicates? In the list the number (3) only goes down to (2). The text has to be written more clearly and state much earlier that replicates were initiated with different densities.

- There is no error: as seen on Fig S1 and Fig 2, all eight replicates from the population “cor_2” went extinct at the first generation (i.e., the individuals introduced initially did not leave any offspring). We have modified the text to make the protocol clearer regarding the replicates (L. 172-174).

You could drop the correlation tests on small population sizes, it's not treated in the results.

- Done

The statistical analysis of per capita growth rate: Please use a Poisson model with an exponential link function. Your data are counts. Figure 2 suggest that your analysis might be too optimistic and underestimate expected demographic noise. I also don't see the need for the transformation in Eqn. 1. Use the density of the previous time step t as an offset. Then the model fits ln(lambda): in "R" a simple model version reads: glm(Nt+1 ~ 1 + offset(ln(Nt)), family = poisson). The intercept is ln(lambda).

- Thanks a lot for this excellent suggestion. We did exactly that.

Fixing the spline parameter at k = 8 in the presentation: first of all, which method was used to fit the models, and second, the figure doesn't give the impression k was fixed. Was it allowed to be simplified automatically? Figure two needs to show confidence bands of the predictions.

- We specified in the text that we use penalized regression splines, i.e. the optimal number of degrees of freedom for the smoothing term is determined by the procedure for each model, within a given range (here, with a maximum of 7 degrees of freedom, L. 181-184). We added 95% confidence bands to Fig 2.

Glmm analysis: there are three response variables. Three population sizes are converted into a maximum value and a mean, which is hardly any data reduction. The expected variability of the mean will depend on the length of the time series, so this should be accounted for. Since the response is multivariate, a multivariate model should be fitted with each replicate as unit of observation, and an overall anova test done of the Allee effect on these responses.

- Our time series include between 1 and 3 generations, so it seems that the effect of time series length on the variability of the mean should be minimal in our case. The response is actually not multivariate, as we analyze the response variables independently.

In a way, however, this test is a bit strange, because the presence of an Allee effect is derived from grouped growth rates i.e. population density data (is this circular or not?) and as if the Allee effect is a lineage property which is perfectly known. However, you probably don't and you need to keep this in mind for the discussion.

- The presence of an Allee effect is indeed derived from the relative values of growth rates (inferred from density data) at different density levels within each group, but this is independent from quantitative differences in demographic parameters (also inferred from density data) across groups. We agree that the Allee/non-Allee distinction is not perfectly known : some populations show some signals of positive density-dependence (cac_3 eva_1, eva_2) at very low densities, but the confidence intervals include the possibility for a flat slope, so they were not retained. Yet, we also know that the presence and intensity of Allee effects vary in nature are context-dependent, so what our results show is that the populations that show positive density-dependence in per capita growth rate under our experimental conditions also tend to have a lower maximum growth rate, lower population size, and higher extinction probability.

AIC are not good for hypothesis testing, because they tend to select models which are too rich in parameters (That's why they are very efficient at predicting). So simply use an anova applicable to your mixed models, which will probably be a parametric bootstrap for example. Interpreting the p-value of the fixed effect estimate is strange, because you already went through a frequentist procedure (the way you apply AIC) before looking at these.

- We did as suggested an anova test for each of the response variables (L. 207-208).

In the equation for RI, what is "C_8"? If extinction occurs, isn't replicability automatically lower? Is it reasonable to use this measure, because when the difference is large after one generation, do you expect further large differences or again small ones? Do the densities at all time points contribute the same information? Maybe just t=1 is most informative?

- According to suggestion we analyzed the sum of squares between replicates at 1st generation as an alternative proxy of repeatability. We did not find any difference between Allee and non-Allee populations.

Results: Figure two: connect the three points per replicate by a line. Confidence bands please for the predicted curves. Describe how you derive that an Allee effect is present from inspecting these confidence bands. If k changes automatically due to the model fitting procedure, indicate that.

- We did not connect the replicate points (which are the same color already on the figure), as it would add a lot of confusion on the Figure. Replicate points are connected on Fig S1 though, as it does represent time series. We complied with the other requests (L. 181-184, L.188-191).

AIC: if you use AICc which is more pertinent, which values do you get? I find the p-values for the fixed effect parameters in two cases on the edge. What are the confidence intervals for these parameters? RI: what does a randomization test produce as p-value?

- These comments did not apply anymore once we modified our analyses.

The extinction probability of populations assigned to Allee is about 50%. Maybe you are just detecting population extinctions with your Allee effect. What happens to the splines when you re-run the same three lineages, but without the replicates which went extinct?

- We did the analysis that was suggested: the same populations were selected as Allee or non-Allee as with the complete dataset. We chose to retain the original analysis in the manuscript, as we do not believe that extinctions are a "false signal": actually if growth rate is decreased at low densities, then we should observe more extinctions at low density. Extinctions that contribute to the positive relationship between population size and per capita growth rate are actually informative. For instance, if the population had not gone fully extinct, but decreased to 1 individual, the biological meaning would be equivalent. This is what is actually represented on Fig 2, where extinction events translate into highly negative growth rates.

Discussion: I cite from Lande 1998 on the Allee-like effect: " . For example, if the infinitesimal mean is positive and the infinitesimal variance increases with population size, it may nevertheless be true that starting from a given size most population trajectories tend to decrease, but that a small proportion of population trajectories undergo relatively large increases so that the expected population size increases with time" Please try to come up with a manner to falsify this hypothesis in your data. I believe you should give more attention to variability in the amounts of stochasticity between lineages, not just by calculating the RI index. The discussion, second paragraph, already suggest that differences in the amounts of stochasticity determine what you observed. If they do, you actually did a study detecting stochastic aspects of population dynamics. Please make it very clear what the difference is between weak Allee effects and stochastics producing the same patterns as Allee-effects (here they seem to be defined as effects due to the lack of interactions again).

- We have re-written the discussion to account for this possibility (L. 317-330).

Comments from Dr Dani Oro

Finally, it would be nice to discuss about the mechanisms producing an Allee effect in some (but not all) populations. These effects may occur in solitary or territorial species, and can be greater for social species for which facilitation processes may be hindered. Even though authors mention this issue in the Discussion, some more specific mechanisms in the study species would be illustrative for an external reader working on different biological systems with other life histories. In fact, the study species has a particular evolutionary strategy that may influence (or deter) the occurrence of Allee effects, and this is something to discuss further in your paper.

- We have re-written the discussion to better highlight this point (L.290-330).

Some minor comments:

"...populations with an Allee... have lower maximum growth rate, both of which increase the extinction risk of populations" from an evolutionary point of view, I doubt this is a proper statement. It applies only to small populations, but many organisms have evolutionary stable strategies living at very low densities and having extremely low population growth rates.

We entirely agree with that remark for natural populations, nevertheless the sentence refers to theoretical analyses of population dynamics, in which both these factors decrease the persistence of populations.

Not sure the variables you consider (λ max, Nmax and the mean population size) are Gaussian. They should rather follow other distributions, but perhaps you checked with some normality tests before.

- A Normal distribution was indeed the best fit for these three variables in our data.

Last sentence in the Discussion: "importance for the prediction of the establishment success of introduced species", that could be generalized to any population that colonizes a patch, independently of its features, and is thus interesting for other ecological topics, such as colonization-extinction rates in metapopulation dynamics, or predator-prey Lot.

- We did acknowledge this larger range of possible topics at the end of the discussion (L. 365-367).