

9th of September 2016

Dear Editor,

we are very grateful to you and the 3 reviewers for such helpful and constructive comments. We have addressed most suggestions and rewritten the sentences that were not clear enough. We hope these changes make the manuscript easier to follow and the results more patent and understandable.

In relation to the major concerns addressed, we have paid special attention to those about the statistical analyses (rev #1), and have thoroughly answered to all the concerns. We have additionally reanalyzed the data of relative abundances inside the cupules as well as those on total abundances in different ways as to be more confident that our approach is not flawed. For instance, we have run the two main models (the binomial for micro-habitat selection and the Poisson for facilitation effects) using a Bayesian approach, which works particularly efficiently for small sample sizes by resampling from the posterior distribution, and found qualitatively similar conclusions. We can show these results upon your request, if necessary. We have also provided references to support our statistical approach. Hence, although we had a fairly low number of replicates (main plots), we are now confident that our statistical analyses are correct. Furthermore, in order to take care of the repeated measures and the right nested temporal design shown in Fig. 1, we have now included 'Time block' nested within 'Plot' for all of the analyses. Second, we have dealt with the critical comments about some of the addressed concepts. Reviewer 2 thought that the theoretical background of our study was weak. We have answer to this reviewer to support our conclusions and explain our interpretation more clearly. Finally, we have addressed all the conceptual and presentation concerns addressed by Reviewer 3.

We think that our manuscript is now ready for publication in *PeerJ*.

Yours sincerely,

Nereida Melguizo-Ruiz

## **Editor's Comments**

### **MAJOR REVISIONS**

You'll see that there are a number of small points and a few big points. In particular, pay close attention to Reviewer 1's comments about your analysis. If you cannot deal with his/her comments, I think it will be tough to consider this paper further. In addition - addressing the comments by all 3 reviewers will dramatically improve the paper.

### **Reviewer 1** (Anonymous)

#### Basic reporting

This is a very interesting paper and the introduction does a good job of providing sufficient background on facilitation and keystone structures and highlighting the research gaps that will be addressed.

The figures are relevant, but it would be more informative to see the raw data and SEs in the figures, rather than the predicted values. I think that presenting the data this way obscures some of the variation (the SEs are extremely low for an N of 2 (table in appendix 3)) and also does not allow the paper to be readily used in meta-analyses. - We agree, and therefore we have included the raw data in a table (now Appendix 3, Table S1) with the mean abundances and sd of each group. Now, the predicted values (statistical results of the GLMMs) are in Appendix 3 (Table S2).

The writing is clear but some sentences could be shortened/simplified (e.g. line 93-96; line 113 – start this sentence with “low relative...”). Try to restructure the sentences (e.g. divide into two sentences) on line 78 and line 86 to remove the sections in parentheses. - Done

Some word choices should be changed:

line 77 – lapse does not seem like the best word to use here - Removed (sentence restructured)

Line 105, the use of the word ‘first’ seems unnecessary since there is no second - Removed

Line 117 – change loss to lose - Done

Line 194 – would be clearer to say None (i.e., no cupules) - Done

Line 212 being = been - Done

Line 232 – should be nonexistent not inexistent - Done

Line 499 – “we showed” instead of we actually proved - Done

The hypotheses could be reorganized so that both of the moisture related hypotheses are together (1 and 3). - Done

Line 414/415 – could delete the last sentence in this paragraph - Done

#### Experimental design

The research question is clearly identified and methods are generally well described.

-How far apart were the plots (line 169)? - The plots were ca. 1.5 meter apart from each other, so the 4 plots covered an area of 12-13 m<sup>2</sup>. Taking into account the plastic roofs, the entire experiment extended across only around 25 m<sup>2</sup>.

-Why was commercial mineral water used? How does this compare to rain water? - Since we did not have access to rain water, we used commercial water instead of tap

water because we believe that this mineral water may be more similar to rain water. Tap water is systematically treated, and contains chlorine and other chemical elements, which are, in addition, difficult to know. Commercial water is labelled, so one can know the mineral composition. We thus considered this water more reliable as we could be aware of its contents. Even though this water has some extra-minerals relative to rain water, we do not think that this inorganic addition could have an effect in such short-term experiment. Besides, providing the water mineral composition in the Methods section allows an exact replication of our experiment.

-When were the different temporal blocks sampled (i.e., what was the timing of the sampling?) It looks like they were a couple of weeks apart according to the raw data? Each temporal block was sampled one week apart: the first one the 12th of May, the second one the 19th, the third one the 26th and finally the fourth the 2nd of June. Thus, the entire experiment lasted for 4 weeks. We have included this information (now lines 235-236).

-On line 251, was it 122 321 invertebrates? (I assume the decimal point should not be there) - Corrected. 12.232 invertebrates were counted, measured and classified.

#### Validity of the findings

The level of replication does not seem adequate (2 dry and 2 wet plots) to obtain a very reliable estimate of variance, especially with two fixed effects, an interaction, and three random effects in some of the models. I do not think the article meets PeerJ's standards in that respect. For random effects, there is some argument that there should be enough levels of the factor in the data that an estimate of the variance of the population of effects can be based on them which I don't think is the case here. - We are aware about the controversy on including factors with a low number of levels as random factors, as the estimates of variance may be inaccurate and this may in turn affect both the estimates of standard errors and the number of degrees of freedom for the fixed effects. However, we would like to stress that our results are unlikely affected by the above. First, our approach does not affect the number of degrees of freedom, as we present the results of GLMM models with binomial or Poisson distributions, and type-III Wald tests for the fixed effects, in which the degrees of freedom (1 for continuous variables,  $k$ =number of levels, for categorical variables) are not affected by the inclusion of random effects. Second, here we follow the recommendations of Gelman and Hill (2007) which state that there is absolutely no problem on parameter estimation by including a smaller number of groups in random effects in hierarchical models. To end this controversy, we believe that simulations to estimate type-I errors in fixed effects when including a low number of groups in random factors are badly needed. However, our results are also conservative as most are based on fairly small p-values, which means they are significant for very low alpha levels. Therefore, even if we were having slightly higher type-I errors for a nominal alpha of 0.05, our conclusions would not change and would be likely correct. In addition, and for insurance, we ran the two main models (the binomial for micro-habitat selection including taxonomic group and the Poisson for facilitation effects but with overall numbers, adding up the abundances of all groups for each subplot – see below) using a Bayesian approach, which works particularly efficiently for small sample sizes by allowing re-sampling from the posterior distributions (package MCMCglmm), and the conclusions were qualitatively the same. Thus, although we understand the concern of the reviewer, with all of the

above arguments we are confident that our statistical approach is valid despite the logistically unavoidably low replication number for the main plots.

I'm not sure about the use of taxonomic group as a random effect either – can some further explanation of this be added? - Including taxonomic group as a random factor served a very important and relevant purpose: allowing to control for differences across groups in the response to the treatments, and thus be confident that the pattern found was independent on the group included. The only two alternatives that we know of would be 1) MANOVA-like approach with all the taxonomic groups in a matrix as response variables, which was unfeasible given the distribution of our data (presence-absence and counts) and the complexity of the design, or 2) Pooling up all the groups in each subplot and summarizing them as a single response. This last approach, however, is highly inadvisable as it is a potential source of pseudoreplication (e.g., a single abundant group responding to the treatment could inflate the added numbers driving the conclusion that the entire community is responding). In any case, in response to your concern we did such approach and found that the distribution of the errors was normal and could run a GLMM with normally distributed errors. We only found a major qualitative difference in which a former p-value of 0.042 for the water\*cupule interaction in the total abundance of fauna became non-significant (0.176). Given that we are claiming that our tests are conservative and robust to type-I errors (see above), we considered this interaction to be non-significant (see lines 379-384). In addition, we took advantage of this data and ran a MCMCglmm analysis with these pooled data to answer your above concern on the inclusion of plot as a random factor, given the low number of groups. We found no qualitative differences with the additive model including taxon as random factor. However, for simplicity we are not showing these last results. The hypothesis behind using taxonomic group as a random factor is that any site in which we perform an experiment can include a random sample of taxa (from the regional pool), which has not been fixed by the researcher. Also, we were not interested to test for differences in response across groups (which would be a justification to include this as a random factor but would unnecessarily sacrificed a large amount of degrees of freedom that we did not have anyway – see Zuur et al. 2009). We were however interested in knowing which groups responded and this is why we then performed separate analysis for the more abundant groups. Furthermore, it is not the first time that this approach is used, see for instance Ehnes et al. 2011. We believe that the above explanation is too long for the ms and we have merely included the following: “In order to control for differences across taxonomic groups in the response, we included 'Taxonomic group' as a random factor (e.g. Ehnes et al. 2011).”

What is the ‘case’ variable that was used as an additional random factor? -

As stated in the original submission, “case” was used to control for overdispersion. We have now cited a reference for this (Elston et al. 2001, see lines 296-298). We used a function (`overdisp_fun` at <http://glmm.wikidot.com/faq>) to test for overdispersion and indeed all models that showed significant overdispersion before fitting case, became well fitted to the corrected Poisson model afterwards. In addition, we also fitted negative binomial models (this time through the library `glmmADMB`) and found qualitatively identical results (not shown).

In addition, the subplots were sampled at different time periods but this does not appear to have been accounted for in the models. Or is the case variable actually for different

time periods? – We had formerly included the ‘Time block’ in our original models but because the results did not change we decided to remove it for simplification. However, we agree that it is better to include it as to take care of the repeated measures and the correct nested temporal design we depict in Fig. 1 (i.e. fewer animals are expected to be collected in the first temporal block – when less water had been accumulated from our treatment than in the last temporal block, when all the accumulated watering effect was at play). Therefore, for all of the analyses we have now included ‘Temporal block’ nested within ‘Plot’ and removed the nesting of ‘Water treatment’ from ‘Plot’ as this one nesting effect was rather negligible in all the models. We make this point clearer now on lines 278-280 and 302.

What distance metric was used for the NMDS and how many iterations were run? - Bray-Curtis dissimilarity distances (now explained in line 359). 200 iterations were run by default in the vegan package.

Is it possible that abundance of fauna was lower in dry plots due to reduced survival, rather than immigration to deeper layers? – As stated in the original submission, our drought conditions fell well within the natural rainfall patterns. Simulating an 18 day drought is not imposing a very strong level of stress upon these forests. Thus, we do not think that such partial (not severe) droughts were causing actual mortality as soil organisms have all sorts of mechanisms to cope with drops in water availability, the main one being migration to wetter spots (e.g. deeper in the soil). Furthermore, relative humidity did not likely drop to dramatic levels as the plot neighbourhood was under normal rainfall patterns. We have witnessed far worse droughts in these forests and no sign of mortality after water resumed (i.e. densities recover to former numbers). After rainfall returns fauna returns everywhere in a question of a couple of days. We have even experimental data (not published) that shows this. A more severe drought would be needed to provoke the death of soil invertebrates; for instance, a drought that will cause an extreme dryness in the deeper soil layers, which was not the case here (deeper layers were wet enough in the dry plots).

## **Reviewer 2** (Anonymous)

### Basic reporting

I found this manuscript to be interesting and nicely written. I do not have much to say about its basics. The language is good and clear. The length of the different sections is adequate. I like it very much you have an experiment. The database is superb (the amount of work you should have done sorting and counting all those litter critters is chilling). The stats are appropriate, clear, and accompanied by nice figures. The discussion is well framed (but see my comments below).

### Experimental design

Excellent! But see my comments below.

### Validity of the findings

See my comments below.

### Comments for the Author

Like I said before, I liked it very much to read your manuscript. However, there are some major issues that I would like you to review.

First, I think that the theoretical background is weak. It seems you framed your manuscripts using so many \*important\* concepts, i.e. facilitation, ecosystem engineers, niche construction and keystone structures, that it gave me the feeling that you tried way too much to "hype" it. For example, I wonder if you really are dealing with a case of facilitation (by the way, not including any of the manuscripts by Maestre et al. --the group with most recent and important research in the topic-- is weird). It is my understanding that, and I can easily see how, a plant facilitates the living of other plant in an almost permanent way, by reducing stress in some of its forms. But in your case, I have many problems considering beech cupules as something different to resource provisioning. My main point is that beech cupules are a \*dead\* substrate. And soil food webs rely, by definition, in dead substrates. Beech cupules are not serving soil critters in a different way (and maybe less so) than dead wood is serving sacroxylic fauna! Right? I may be loosing something, but I really find it difficult to frame your manuscript as a case of facilitation. I find similar issues with the other concepts you invoke. Are (all) plant species that get rid of dead plant tissues ecosystem engineers? If they are building niches, beech cupules need to have species specialized (in some form) to them. I am not sure you are able to test this idea with your dataset. I find it difficult for any taxa to specialize in something dead. - We disagree with this reviewer in the interpretation of our results. We believe that our conclusions follow from the data and that we are only suggesting in the Discussion that beech cupules are "keystone structures" and beech trees "ecosystem engineers" and that "facilitation" is taking place. Our interpretation is not contradicting most of the literature and we believe that this reviewer may embrace a rather narrow meaning of these concepts, which is not the case for us, not for most of the literature. Thus, we are quite surprised that upon what we believe is a fair interpretation of the literature this reviewer is recommending rejection. We offer a more detailed answer to the reviewer below.

In a previous version of this ms we cited several works by Maestre, Callaway and several other authors, but these studies focus on plant-plant interactions, and therefore we thought they did not really fit the topic for plant-animal interactions. Here, we stressed the facilitative effect exerted by beech trees (and likely other deciduous trees) on soil fauna maintenance in dry conditions. The concept of facilitation is mostly used in plant ecology, while its application on animal ecology is currently very scarce, especially in the context of soil communities. This is why we would like to make a different point here. However, for the sake of fairness to other works we have cited some plant papers (i.e. Callaway 1995; Callaway et al. 2002; Brooker et al. 2008). We do not understand your concern distinguishing dead vs alive tissue. Season after season the "facilitator" (the beech tree) is alive, no matter what is the status of the facilitating structure. In addition, and most importantly, such facilitation could actually affect its own nutrient availability in the years to follow, which means that it could even be adaptive. We have only briefly mentioned this in the ms, but would like to stress our point here that the interaction is of the type alive-alive and not dead-alive. It is very different that the one occurring when a tree dies. Thus, we strongly believe that this is a case of facilitation which fits perfectly in the definition.

On the other hand, we do not quite follow why we need cupule specialists to support the fact that facilitation is taking place. We can talk about plants regarding this issue. Most facilitation in plants occur among plants that are generalists (if not all), and can therefore live with our without being facilitated by other plants, they just perform better when facilitated (e.g. by cushion plants). This is especially obvious in the work of the

team by Dr. Francisco Pugnaire, for instance, which we have been witnessing in our Institute for almost two decades now.

Moreover, we understand your concerns about the broader application of the 'ecosystem engineering' concept, which has actually been subject to intense debate in ecology (see Wright & Jones 2006). While some authors argue that the widespread use of this concept can weaken its meaning (e.g. Reichman and Seabloom 2002), equating ubiquity with nonutility, others stress that the ubiquity of ecosystem engineering highlights its importance and interest in ecology (Wilby 2002; Wright & Jones 2006). We concur with the later view, and think that in our study beech trees affect soil characteristics and notably influence the distribution and abundance of soil animals (for instance those responsible for leaf litter decomposition and nutrient cycling), and can therefore be considered ecosystem engineers.

Second. I also feel uneasy with the concept of beech cupules as keystone structures. You did a superb work, showing with a great experiment that soil fauna benefit from beech cupules, specially so when it gets dry. I clearly understand the idea of separating the effects of one/two factor(s) experimentally (in your case beech cupules and water). But the litter is full of other structures and components that you did not include in your experiment. For example, likely, a lot of the soil fauna dig themselves deep in the soil during dry periods of time. Is the \*soil\* another keystone structure? More important, of the total soil fauna what % hide themselves in the beech cupules vs. hide in the soil? My point is that in your manuscript you clearly showed that the smaller soil fauna uses beech cupules as shelter, and they do more so in dry times, but you have not tested for fauna preferences on other substrates (not sure if you in Europe have acorns, for example) and how preference for beech cupules differs from preference to other substrates. I am neither suggesting that you need to do these other experiments nor saying that your work lacks value, I just want to see how other litter compartments affect litter critters before I say that beech cupules are a major part of soil biology. -

We think there is no conflict with the nature of these cupules, either dead or alive. Tews and col. were the first to propose the concept of "Keystone structure" in their literature survey (Tews et al. 2004). They define a keystone structure as "a distinct spatial structure providing resources, shelter or 'goods and services' crucial for other species", and stressed the importance to not confound this term with the concepts of 'keystone species' nor 'keystone habitat' (perhaps this latter fits better for your suggestion of soil?). We have shown that beech cupules are actually spatial structures that provide shelter to soil invertebrates, and we therefore hold the application of the concept in this context. The first example that Tews et al. provide in their study is precisely the dead wood in mixed beech-spruce forests, whose removal would reduce saproxylic insect diversity. In our experimental study, we aimed to investigate the role of beech cupules as moist shelters for soil animals. We did not consider them as trophic resources (although we mention they may also provide important resources for some animals). In addition, we did not test for fauna preferences on other substrates such as acorns, since in this pure beech forest there are no acorns at all. Beech cupules are the only fruit husks in the soil as these forests are monospecific. There are beech twigs, little and large fallen branches, cupules, and of course, dead leaves. As we understand it, given their abundance, beech cupules are the most relevant spatial structures (as empty cavities which may be used as shelter by the mesofauna) in the leaf litter of this type of forest.

That is all I have to say about your manuscript. Again, I suggest you to revise many of these underlying concepts and use them more conservatively across your manuscript. Because dealing with these suggestions (if you consider my comments appropriate) will likely change profoundly the theoretical framework of your work, which subsequently will affect all other parts of the manuscript, I suggest to the editor your manuscript to be rejected.

**Reviewer 3** (Jacob Heilmann-Clausen)

Basic reporting

No comments

Experimental design

No comments

Validity of the findings

See general comments for the author

Comments for the Author

This is a nice experimental study on the effect of beech cupules on soil fauna in Spain. The study combines a desiccation treatment, with an experimental gradient in beech cupule numbers and finds interesting responses in the soil fauna. The study is generally well presented and certainly valid for publication, but revision, especially on structural aspects are needed before publication.

Major points:

- 1) The order in which the hypotheses are posed could be improved. I suggest to start with the simpler hypotheses, on single factors, i.e. overall effects of number of beech cupules and water treatment on fauna, before going to the inside/outside use of beech capsules and the interactions between the two treatments. This restructuring should be repeated also for the Results section.

Following yours and suggestion by rev #1 we have now re-organized the hypotheses at the end of the Introduction.

- 2) The Material and Methods section is very wordy, especially in relation to statistical analysis. Try to condensate, and move results on beech capsule humidity (line 220-233) to the Results

Unfortunately we believe that the Statistical section needs all the details that are there to grant replication. In addition, we had to expand it a little to accommodate to the new results and analyses suggested by Rev #1.

We have removed the results on humidity to the Results section and now included a new section called "Effect of experimental watering in the soil and cupules" (now lines 365-375).

- 3) Please provide one or more tables to give summary results of the main model runs. The many statistics given in the main text makes part of the Results section very heavy to read

We have provided all the detailed tables in the Appendix. However, for the sake of accuracy, we prefer to give the statistical tests of the main findings in the main text. We understand that for some readers it is more difficult to follow. However, the actual pattern should be read combining the text with the graphs in the figures anyway, and this is how papers are usually read. Giving the results without providing actual

statistical support in the line gives more work to other readers who prefer seeing these right the way. Therefore, basically these are different writing styles and we prefer to stick to the one providing the main statistical results in the main text or the Results section.

Minor points:

53: members -> partners - Done

88-93: Rewrite to improve clarity. The cross-pollination aspect seems out of context - Done

103: Both “seed husk”, “fruit husk” and “cupule” are used throughout the MS. One of the two former expressions should be used throughout at least as a more general expression (across tree genera), whereas cupules can be used specifically for beech, as a special case Done

106: fungivorous - Done

107: Rewrite to improve clarity - Done

117: loss -> lose - Done

132-33: To me this hypothesis is illogical. I would expect higher use of a limiting resource under low resource availability in harsh conditions rather than the opposite. We agree that this point is controversial and we had indeed thought about it thoroughly. In order to understand this point one has to think about the potential alternative outputs. First, one could think that increasing the number of cupules, no differences would be found between low and high availability in the number of animals found inside relative to outside. Little could be said then about cupules being limiting resources as they would be used as any other item in the forest floor according to their availability. The second possibility would be that less, no more, animals are found inside relative to outside the cupules in the high availability treatment. In that case, the obvious conclusion would be that this structure would not be limiting, as animals do not seem to be restricted (e.g. waiting outside) to use this structure. It is only when one shows that animals that are outside are significantly less frequent than inside that one shows that the use is restricted and that increasing the availability there is more (differential) use of the resource. We have now expanded the text in the Introduction to make this point clearer as follows: “2) if these structures are limiting resources in the leaf litter, more invertebrates overall would be found inside relative to outside the cupules as cupule availability increases. That is, artificially increasing the availability of cupules would prompt those animals in the litter to be more likely found using the cupules than in the litter, demonstrating that cupules are limiting resources”.

134: posited -> hypothesized - Done

140-142: I don't think this hypothesis makes sense. You are studying a purely (?) deciduous forest ecosystem, and hence it is absurd to think that deciduous trees, as formers of the system, are not important for the processes going on in that system. The hypothesis would be valid if you studied e.g. the role of single intermixed beech trees in coniferous dominated systems, but this is not the case here. - Beech trees are obviously important and decisive in their system, although we think that our hypothesis goes further. Fruit husks have a protective role, shielding the nut from frugivores and other organisms potentially able to damage them. Beech cupules do some good at that, but are not supposed to facilitate soil invertebrates maintenance, are they?

151-152: Please provide more details on the study system, e.g. stand age, current/past management admixing tree species, dominant herbs, soil pH, humus type. The study

system is indicated to be primary forest, but is this really true considering common interpretations of this concept, e.g. [https://en.wikipedia.org/wiki/Old-growth\\_forest](https://en.wikipedia.org/wiki/Old-growth_forest) ? - We have now included soil pH and tree density of the area, as we do not have accurate information about stand age, management, dominant herbs or humus type. We stated the forest was primary because it included trees with greatly variable heights and diameters (very young beeches and older ones). Moreover, there was no specific or designed management in the area, so we considered this forest as an old-growth forest. We agree that this concept can be imprecise, as we actually do not have data to prove it, so we accept to remove "primary" from the text.

175-176: Clarify at what stage of the experiment this was done. Also clarify how deep down to the litter layer you searched for cupules (i.e. only in the litter layer?) - Done. Yes, we collected and manipulated the cupules present in the leaf litter layer, not in lower ones. Beech cupules of deeper soil layers are in the latest decomposition stages, practically disintegrated.

195-196: Better to start this part by "The experimental manipulations were initiated after the 18 days of rainfall..." - Done

202-209: Even if this can be easily recalculated to mm of rainfall, please provide the measures also on this scale to help the reader - Done. We decided to avoid providing the amount of rainfall in mm as the plots had an area of 1 m<sup>2</sup>, and therefore the liters per plot were the effective mm/ m<sup>2</sup>, but we agree that this can complicate the reading.

212: being -> been - Done

214-5: Unclear what "N" refers to - N refers to the number of plots/patches where beech cupule density was assessed.

215-6: Rewrite to clarify text. I guess you refer to the preceding year, rather than the actual study year, as a mast year? - Well, we referred to the preceding autumn (when beech cupules ripen and fall), 6 months before the experiment took place. We have now rewritten the sentence.

216-7: Better: "To mimic natural variability in cupule density, and to promote..." - Done

218-9. Please provide these densities also as cupules/m<sup>2</sup> - Done

220-233. Give more details on 1) when sampling was done, 2) how many subsamples were taken, 3) and for how many days the sampling continued. In addition give the results on the measured differences in water content etc. in the Results section (see also major point 2). - Done, and restructured.

240: delete "so as" - Done

252. delete "then" - Done

302-3: Clarify text in the parenthesis - Done

341-3: It seems a bit confusing that the results start out with some of the more complex results, especially since they are not really clear. See also my major point 1. - We agree that the beginning of the Results section was too abrupt. We have included now different sections as to make the Results section read better.

350-79: A lot of test results are given, with full details, making the text hard to read. Please provide main results in a table, and focus the text to guide the reader to understand these tables correctly. E.g. all groups, except XXX showed a positive response to XXX (Table YY)- As commented above, we accept that this way can be quite harder to read, but still propose to provide the main statistical results in the Results section. Giving the results without statistical support in the main text can complicate the understanding and interpretation of the study to some readers.

391-3: I guess these results stems from the Permanova? If yes indicate this in the text. Otherwise remember to provide the Permanova results - **Done**.

400-1: The sentence “probably because water stimulated the activity and immigration differently for different taxa” can be deleted. - **Done**

406-7: The opening of the discussion should be more specific, and explicitly mention the two treatments - **Done**

420. Delete “likely” - **Done**

423-6: This sound like a repetition of the Introduction. But now you have data to validate this expectation (wrongly presented in the Material and methods section, lines 227-230). Rewrite your text to reflect this. - **Done**. **Note that beech cupule and leaf litter humidities have been moved to the Results section.**

442-3: be more specific on “water-limited ecosystems”. Your results clearly indicate that deciduous forests, in some aspects, can be considered water-limited. - **Done?**

445-5. Don’t generalize too much here. You only studied beech cupules. - **Done**

447: delete “in addition” - **Done**

447-56: Again, I wouldn’t expect this result (cf. my comments to lines 132-33). I am no expert in this field, but please check how your results match similar studies on habitat use under variable stress/habitat abundance regimes. Your results at least indicate that even the high cupule treatment is below the limit where the number of cupules stops to be limiting. Was this what you intended and how does this compare to natural variation in this habitat? - **Please, see the response to this point above. We agree that it is difficult to interpret, but have thought it thoroughly and still believe the expectation and the result is consistent with cupules as limiting resources.**

463-5. Please rewrite - **Done**

484: “springtails, were” - **Done**

497-501: Please rewrite - **Done**

514: in which case trees would -> and hence - **Rewritten**

520-9: I have sympathy with this interesting and bold interpretation, but it need to be given in a shorter way, as a hypothesis for further testing, and without repeating the definition of mutualism. It is quite likely that these short term desiccation effects have no effect on the overall year-round soil processes, provided that sufficient water is present in long enough periods. There is even evidence that microclimatic fluctuations may in fact enhance soil biodiversity and decomposer processes, e.g: <http://www.sciencedirect.com/science/article/pii/S0031405604701080> and <http://link.springer.com/article/10.1007/s00442-006-0406-3> - **Done, we have shortened a little bit this paragraph. Moreover, we accept that environmental variability can enhance soil biodiversity, but we consider that this does not contradict the existence of reciprocal positive effects between trees and soil fauna. Beech cupules do not appear to change microclimatic conditions, but provide wetter conditions to those animals which may be more sensitive to desiccation. Indeed, primary and secondary decomposers such as mites, springtails and enchytraeids tend to avoid drier micro-patches and prefer moister ones, and they play an important role in decomposition processes.**

Fig. 1 and perhaps even fig. 2 could be easily moved to the appendix without losing clarity. - **Figure 1 is a schematic representation of the experimental design, so, even if one can understand it without this figure, we think that it greatly helps the reader. Figure 2 shows the different taxonomic groups investigated in the study, and was included to improve the understanding, specially to those readers that are not familiar or used to work with soil organisms. We think that both figures are useful and therefore suggest to let them in the main text.**

## References

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