Dear Editor,

We would like to thank the reviewers for their very helpful comments on our manuscript.

We have incorporated the majority of suggestions in a revised version of the manuscript. Our detailed responses to reviewer comments are shown in italics below, directly following the reviewer comments.

We believe that the manuscript has been substantially improved by the review process and we hope that it is now acceptable for publication in *SOIL*.

Sincerely,

Marie-Anne de Graaff

On behalf of all the co-authors

Anonymous Referee #1

General Comments:

This meta-analysis of the effects of soil biodiversity on carbon cycling pools and processes is very topical and interesting. As the authors also state, compared to our knowledge about the relationship between plant diversity and ecosystem functioning, our understanding of the impact of soil biodiversity on ecosystem functioning is still very limited. In the light of the ongoing global loss of biodiversity, including soil biodiversity, at unprecedented rates, quantitative reviews such as this one are of critical importance to improve our ability to predict the consequences of this diversity loss for the functioning of ecosystems.
I commend the authors for the well-written manuscript. The introduction and discussion are very in-depth with ample citations to the relevant literature and I have very little to add to them.

Thank you for these positive comments.

A short statement at the end of the conclusions paragraph of the discussion about the importance of elucidating links between soil biodiversity and C cycling and its broader implications would be nice (cf. page 909, line 10 and further). Now this paragraph is mostly focused on methodological challenges and knowledge gaps.

Thank you for this suggestion. We have added some text at the end of the conclusions paragraph that indicates the importance of the soil community to global C cycling and the importance of understanding the role of soil biodiversity in understanding how biogeochemical cycles may shift under climate change: "Given the importance of the soil community in regulating the direction and magnitude of C fluxes between the atmosphere and terrestrial ecosystems, advancing our understanding of soil biodiversity impacts on biogeochemical cycles may enhance the efficacy of climate change mitigation efforts. " L523-526

Most of my specific comments below are fairly minor. I do, however, have a few main concerns. First, the mixed use of terms such as "organismal groups" and "trophic groups" is often confusing.
We appreciate this concern and have worked to make the terminology less confusing. We no longer use the term "organismal groups" and we define all grouping terms clearly (L197-207):" Soil biodiversity impacts on C respiration and decomposition were assessed by manipulating biodiversity either within a single body size group (i.e. microbes [including bacteria and fungi], micro-, or meso-, or macrofauna) or across multiple body size groups (e.g., micro-, meso-, macrofauna; e.g. Bradford et al. 2002). We treated the within-body size and across-body size groupings as two separate categories for the analysis. For plant biomass, however, there were not enough studies to run meta-analyses for individual categories. We also categorized the studies by soil microorganisms or soil fauna (micro-, meso- and macro fauna grouped together due to inadequate numbers of studies to split these up). Categorizing studies in this manner allowed us to assess whether species diversity within or across body size groups affected C cycling differently, while also enabling us to compare the relative impacts of diversity within the soil microbial community versus soil biodiversity within the soil faunal community." See additional comments regarding this point below.

Second, I do not understand the explanation about the natural log of the response ratio, as the latter was defined as a value ranging from negative to positive.

We have reworked this section and now better explain how the natural log of the response ratio (which we now define more clearly as 'lnR') was calculated (lines 228-236).

"The response ratio (R) was calculated as the value of a particular response variable at low diversity divided by the value at high diversity. The natural log of the response ratio R (lnR) was used as a metric for all of the response variables (de Graaff et al., 2006; van Groenigen et al., 2006). To ease interptretation of figures, the results for the analyses on lnR were back-transformed to response ratios and reported as percentage change under a reduction in diversity (that is, 100 x [R-1]). Thus, for response variables where there was no change between higher and lower diversity communities the change would equal 0. For cases with greater values for response variables in low diversity communities than high diversity communities the percent change would be would be positive, and lower values for response variables in low diversity communities than high diversity communities would yield negative values for the percent change."

Third, I wonder if the data points in the regressions using multiple levels of diversity reduction per study (if I understood this correctly) can be considered independent.

We agree that the results from the regression analyses need to be interpreted carefully, and we have outlined this in the manuscript. We do think that depicting the data in a regression in addition to the meta analysis provides the reader with an important alternative way of observing the results. Namely, because of the nature of the studies we *reported on, the absolute number of species manipulated typically varies by body size group. Thus, presenting changes in pools and processes as a function of relative changes in diversity provides an additional way to look at the data.*

*We have outlined our rationale for conducting our regressions in L250-266: "Further, we tested how a loss of belowground species diversity is linked to changes in C pools and processes by performing linear regressions with percent change in species diversity and the effect size (lnR) of each of the response variables. Percent change in diversity was calculated as (low diversity – high diversity/high diversity)*100. Since the absolute number of species typically manipulated for diversity gradient studies varies among species that differ in body size in absolute terms (i.e. many more species are usually present in studies of microbial diversity than in studies of faunal diversity), we calculated relative differences in species diversity for each treatment. Thus manipulation of microbial diversity might include a low diversity treatment of 100 versus a high diversity treatment of 1000 species, while manipulation of soil fauna might span from low diversity of 1 species to high diversity of 10 species. Calculated as relative differences in diversity, both examples would be the same (i.e., low diversity is 10% of the number of species present in high diversity). We performed two sets of regressions. The first included all soil biodiversity levels, and the second included the highest and lowest biodiversity levels only. We used linear regression (SPSS v. 20) to regress lnR against relative change in species diversity. We performed regressions in which we considered lnR (the effect size) between every diversity level, and also regressions in which we only considered lnR between the highest and lowest diversity levels, omitting intermediate diversity levels."*

The reviewer is correct in that the data points are not entirely independent but we did not want to decrease our sample size given the limited data available. We also recognize that some studies included more points along the gradient than others, which may lead to some studies having more weight in the analysis than others. For this reason, we also ran regression analyses only including the highest and the lowest value.

Fourth, some of the groups within the regressions seem to be represented by very few data values, and I have questions about the validity of some of the conclusions about them in the discussion.

We agree with the reviewer and we have clarified in the results section that we did not perform regressions on groups of organisms for which there was inadequate data available.

L293-304: "Regression analyses revealed a negative linear relationship between soil biodiversity and lnR for soil C respiration (Fig. 4). This relationship was significant when we regressed the percent change in soil biodiversity and lnR for C respiration based on all diversity treatments in the compiled studies (Fig. 4a) and also when we calculated lnR for the highest and lowest diversity treatments only (Fig. 4b). We further examined how a decline in diversity within body size groups (data available for microorganisms and macrofauna) and across body size groups (multiple body size *groups) was related to soil C respiration. Soil microbial diversity was the only body size group significantly related to soil C respiration, with a decline in soil microbial diversity reducing C respiration (Fig. 4a). The paucity of data available for the other body size groups prevented us from running any meaningful regression analyses. We have, however, highlighted the other body size groups in the regression figure to depict the dearth of studies on these organisms relative to microbes."*

In addition, we have ascertained that any conclusions in the discussion were supported not only by the regression analyses, but also by the meta analysis.

Specific Comments:
1. Page 908, line 15. Not clear what "overall" means here. I assume this refers to the analyses including both studies that manipulated diversity within and across groups, but I had to read the methods and results section to realize this. Please clarify so that the abstract is clear by itself.

We have reworked this sentence so that it is clear that we are referring to diversity manipulations within and across groups. Please see: L31-34: "When studies that manipulated both within- and across-body size group diversity were included in the meta-analysis, loss of diversity significantly reduced soil C respiration (-27.5%) and plant tissue decomposition (-18%) but did not affect above- or belowground plant biomass."

2. Page 909, line 5 and further. You mention land use change and fertilization, but I would think climate change qualifies as one of the main drivers of (future) biodiversity reduction as well.

We agree, thank you for the suggestion. We now include mention of climate change. Please see: L51-54: "Reductions in biodiversity have been linked with anthropogenic global change drivers such as climatic change, land cover change, reduction and fragmentation of natural areas, and human dependence on synthetic fertilizers (Vitousek and Mooney, 1997; Sanderson et al., 2002; Stevens, 2004; Phoenix et al., 2006; Fischer and Lindenmayer, 2007; Clark and Tilman, 2008)."

3. Page 912, line 19 and further. "Further, we tested the hypothesis that biodiversity manipulations across multiple organismal groups more strongly affect C cycling processes than manipulations within organismal groups, due to a higher degree of functional redundancy within than across organismal groups (Andrén and Balandreau,1999; Setälä, 2002)." From the abstract and the figures, it seems that these so-called "organismal groups" are just trophic groups. If so, I would prefer "trophic group" as "organismal group" is very vague. See also comment #6.

We understand the confusion resulting from the terminology. We had used the term organismal group in this manuscript to avoid assumptions of our groupings (necessarily) reflecting trophic groups, taxonomic groups, or functional groups. Rather, the groupings reflect organismal body size groups (i.e. microbes, vs, micro-, meso- and macrofauna), which generally provide useful functional information. We have clarified the terminology

(L197-207) and do not use the term 'organismal groups' anymore: " Soil biodiversity impacts on C respiration and decomposition were assessed by manipulating biodiversity either within a single body size group (i.e. microbes [including bacteria and fungi], micro-, or meso-, or macrofauna) or across multiple body size groups (e.g., micro-, meso-, macrofauna; e.g. Bradford et al. 2002). We treated the within-body size and across-body size groupings as two separate categories for the analysis. For plant biomass, however, there were not enough studies to run meta-analyses for individual categories. We also categorized the studies by soil microorganisms or soil fauna (micro-, meso- and macro fauna grouped together due to inadequate numbers of studies to split these up). Categorizing studies in this manner allowed us to assess whether species diversity within or across body size groups affected C cycling differently, while also enabling us to compare the relative impacts of diversity within the soil microbial community versus soil biodiversity within the soil faunal community."

4. Page 912, line 23 and further. "In addition, we tested whether diversity of the type of group, soil microbes vs. soil fauna (including micro-, meso- and macrofauna), impacts C cycling differently. Finally, since "biodiversity" is a metric that differs greatly in absolute numbers for different soil organismal groups, we evaluated how the relative loss of diversity (in percent) within organismal groups (i.e., microbes, soil fauna) affects soil C cycling." This use of the phrases "type of group" and "organismal group" is confusing. Why not just write something like: " In addition, we tested whether diversity of soil microbes vs. soil fauna (including micro-, meso- and macrofauna) impacts C cycling differently. Finally, since "biodiversity" is a metric that differs greatly in absolute numbers for soil microbes and soil fauna, we evaluated how the relative loss of diversity (in percent) within these two groups affects soil C cycling."

Thank you for the suggestion. We have changed it in accordance with our new terminology for the different groups of organisms: "In addition, we tested whether diversity of soil microbes versus soil fauna (including micro-, meso- and macrofauna) impacts C cycling differently. Finally, since 'biodiversity' is a metric that differs greatly in absolute numbers for soil organisms that differ in body size, we evaluated how the relative loss of diversity (in percent) within body size groups (i.e., microbes, soil fauna) affects soil C cycling." (L147-151)

5. Page 914, line 1 and further. Why not add that there were 3 studies investigating effects on soil C pools? Then this would flow logically into "All soil C pool data...".

Thanks for this suggestion. We have changed the text in this section: "In total we analyzed 45 published studies, of which 8 examined the effects of soil biodiversity on total plant biomass, 10 examined effects on aboveground plant biomass, 9 examined effects on root biomass, 13 examined effects on C respiration, 25 examined effects on decomposition, and 3 used laboratory microcosms to examine effects on soil C pools (Table 1)." L177-180

6. Page 914, line 23 and further. "Soil biodiversity impacts on C respiration and decomposition were assessed by manipulating biodiversity either within a single organismal group or across multiple organismal groups; we treated these two categories separately in

the analysis. For plant biomass, however, there were not enough studies to run meta-analyses for individual categories. For studies that manipulated diversity across multiple organismal groups, soil biodiversity was altered by manipulating either (1) the number of organismal size class groups (e.g., micro-, meso-, macrofauna; e.g. Bradford et al., 2002) or (2) the number of functional or taxonomic groups within an organismal size class group (e.g., mycorrhizal fungi, saprophytic fungi and bacteria, root herbivores; e.g. Ladygina et al., 2010)." Are "organismal groups" just trophic groups? You explain that studies conducted across such groups either manipulated the number of size classes, or the number of functional or taxonomic groups within a size class. I can understand this. But does this mean that "within group" studies manipulated the numbers of species/taxa within a distinct trophic group? Please clarify these terms throughout the manuscript. See also comment #3. See also comment #13 about changing size classes and diversity.

We have changed the terminology used for describing groups as described in response to comment 3.

7. Page 916, line 3 and further. Explain to me how you would take a natural log of r, when r becomes negative? Usually one just divides the response value of the experimental treatment by the response value of the control treatment. This ratio is always positive if measured response variables do not contain negative values, and is thus bounded at the lower end by zero. Taking the log linearizes and normalizes the raw ratios, which has several desirable properties. Or did you just use the response ratio r, as defined by the formula in Line 5, without taking the natural log? The figure captions stating "percent response" seem to indicate so. Please clarify.

We thank the reviewer for pointing out this lack of clarity. Below follows a description of how we calculated the response variable and then how we presented this as a percent change in our figures.

To calculate the r (response ratio), we used: r =response at high diversity / response at low diversity. Then, we used the natural log of that number (similar to what the reviewer suggests above). This is the number that is used in Metawin and from which an effect size is calculated, we anti-log transform this effect size prior to calculating a percent change (lines 228-237).

"The response ratio (R) was calculated as the value of a particular response variable at low diversity divided by the value at high diversity. The natural log of the response ratio R (lnR) was used as a metric for all of the response variables (de Graaff et al., 2006; van Groenigen et al., 2006). To ease interptretation of figures, the results for the analyses on lnR were back-transformed to response ratios and reported as percentage change under a reduction in diversity (that is, 100 x [R-1]). Thus, for response variables where there was no change between higher and lower diversity communities the change would equal 0. For cases with greater values for response variables in low diversity communities than high diversity communities the percent change would be would be positive, and lower values for response variables in low diversity

communities than high diversity communities would yield negative values for the percent change."

8. Page 917, line 9. "We performed two sets of regressions. The first included all soil biodiversity levels, and the second included the highest and lowest biodiversity levels only." Would this be all biodiversity levels within a given study vs. the highest and lowest diversity levels within a given study? Does this mean that in the regressions including all diversity levels several observations from a same study were used? If so, these data are not truly independent, and I wonder if the authors could have corrected for this source of data dependence, i.e. grouping of data points per study, in some way, e.g. by the use of a random effect.

Yes, the reviewer is correct. The first set of regressions included all biodiversity levels and the second included the highest and lowest levels only. The reviewer is correct in that the data points are not entirely independent but we did not want to decrease our sample size given the limited data available. We also recognize that some studies included more points along the gradient than others, which may lead to some studies put more weight into the analysis than others. For this reason, we also ran regression analyses only including the highest and the lowest value. We agree that the results from the regression analyses need to be interpreted carefully, and we have outlined this in the manuscript. We do think that depicting the data in a regression in addition to the meta analysis provides the reader with an important alternative way of observing the results (please see our earlier response for more details). We have ascertained that any conclusions in the discussion were supported not only by the regression analyses, but also by the Meta analysis.

9. Page 918, line 21. "We further examined how a decline in diversity within organismal groups (microorganisms, microfauna, mesofauna, or macrofauna) was related to soil C respiration." Your summation seems to imply that four different groups of organisms were tested, whereas Fig. 4 distinguishes between "Microbes", "Macrofauna" and "Multiple Organismal Groups", so three groups. Please explain.

We have fewer body size groups in the figure (microbes and macrofauna) than the possible number of groups as there were no studies that manipulated only microfauna or only mesofauna (although these body size groups were included in some of the studies that manipulated multiple body size groups). We have clarified this in the text (L293-301) and in the figure legend (L980-988).

L293-301: "Regression analyses revealed a negative linear relationship between soil biodiversity and lnR for soil C respiration (Fig. 4). This relationship was significant when we regressed the percent change in soil biodiversity and lnR for C respiration based on all diversity treatments in the compiled studies (Fig. 4a) and also when we calculated lnR for the highest and lowest diversity treatments only (Fig. 4b). We further examined how a decline in diversity within body size groups (data available for microorganisms and macrofauna) and across body size groups (multiple body size groups) was related to soil C respiration. Soil microbial diversity was the only body *size group significantly related to soil C respiration, with a decline in soil microbial diversity reducing C respiration (Fig. 4a).”*

*L966-974: “Figs. 4a and b Regressions between a percent change in the soil microbial, soil macrofaunal or soil microbial and soil faunal communities (i.e. multiple organismal groups) and the natural log of the response ratio of soil C respiration (lnR; calculated as the natural log of the response ratio, R, which was the value of the response variable at low diversity divided by the value at high diversity). No studies in our literature compilation of soil C respitation included manipualation of only soil microfauna or mesofauna, so these body size groups are not included in the figure. Percent change in diveristy was calculated as (low diversity – high diversity/high diversity)*100. Figure 4a includes all possible comparisons across diversity gradients in studies, whereas 4b includes the comparisons between the lowest and highest diversity levels only.”*

10. Page 918, line 23. "Soil microbial diversity was the only organismal group significantly related to soil C respiration, with a decline in soil microbial diversity reducing C respiration (Fig. 4a)." As change in macrofauna diversity is only represented by a single value, how does a regression for this group make sense? Or was this group not tested? In panel b, there are only two values for the change in diversity of multiple organism groups, so I wonder how useful a regression is in this case as well. Consequently, it is not so surprising that a significant relationship was only found for soil microbial diversity. See also comment #11.

We have clarified how we conducted our regression in the text, and we added a sentence indicating that a shortage of data in soil organism groups other than soil microbes prevented us from conducting any meaningful regressions (L293-304): “Regression analyses revealed a negative linear relationship between soil biodiversity and lnR for soil C respiration (Fig. 4). This relationship was significant when we regressed the percent change in soil biodiversity and lnR for C respiration based on all diversity treatments in the compiled studies (Fig. 4a) and also when we calculated lnR for the highest and lowest diversity treatments only (Fig. 4b). We further examined how a decline in diversity within body size groups (data available for microorganisms and macrofauna) and across body size groups (multiple body size groups) was related to soil C respiration. Soil microbial diversity was the only body size group significantly related to soil C respiration, with a decline in soil microbial diversity reducing C respiration (Fig. 4a). The paucity of data available for the other body size groups prevented us from running any meaningful regression analyses. We have, however, highlighted the other body size groups in the regression figure to depict the dearth of studies on these organisms relative to microbes.”

11. Page 922, line 14. "In addition, the regression analysis revealed that a loss in soil biodiversity was significantly related to a loss in soil C respiration only when soil microbial diversity was included in the analysis." Again, I wonder how much this has to do with the lack of levels of diversity manipulation for groups of soil organisms other than microbes. See also comment #10.

Please refer to our response to comment 10 and the following statement in the text (L301-304): "The paucity of data available for the other body size groups prevented us from running any meaningful regression analyses. We have, however, highlighted the other body size groups in the regression figure to depict the dearth of studies on these organisms relative to microbes."

12. Page 924, line 14. "Our analysis, however, suggests that diversity across multiple organismal groups has similar impacts on soil C cycling to diversity within organismal groups." This was true for the effects on plant tissue decomposition. For soil C respiration, the effect of reduced diversity within groups was even stronger than that of altered diversity across groups. Maybe include this information here.

Thank you, we have added these suggested sentences. L456-458.

13. Page 925, line 21. "inoculating sterilized soils with soil communities derived through a series of different sized filters". Although this technique has its merits and is interesting, I would think that body size and diversity are confounded by such an approach. As one filters out larger organisms, one will not only lower the diversity of the soil community, but also the average body size, and with that the functional composition of the community. If one then observes a change in e.g. an ecosystem function, is this due to the functional differences between large and small soil organisms, or because of the lower diversity? This approach can demonstrate what happens when one changes the body size classes, which correlate to some degree with functional groups, and the taxonomic richness simultaneously. It does not, however, enable one to assess the effects of altered biodiversity per se.

The reviewer makes a great point here. We had intended to highlight the uniqueness of the Wagg et al study for doing any sort of biodiversity manipulation. We agree with the reviewer, however, that there are a lot of drawbacks and limitations to the methods of Wagg et al. Unfortunately there is no 'magic bullet' method to address these questions, and we now clarify in the text some of the limitations of sorting by filters (L 479-488).:

"A recent study by Wagg et al. (2014) used a method for manipulating a broad size range of soil organisms by inoculating sterilized soils with soil communities derived through a series of different sized filters. This method allowed the researchers to successfully obtain a broad soil biodiversity gradient within and across groups of soil organism that span a gradient in body sizes in their grassland microcosms, and showed that soil biodiversity loss and simplification of soil community composition impairs multiple ecosystem functions, including litter decomposition and soil C sequestration. However, filtering groups of organisms based on body size does not allow separating between effects of functional dissimilarity from effects of biodiversity (species richness) per se. This underscores the pervasive challenge to truly measuring biodiversity effects on ecosystem processes."

14. Page 944, fig. 4. Here I read in the y-axis label "ln-R". Is this R the response ratio as defined in line 5 of page 916, or just the ratio of the high diversity response and the low

diversity response? If it is the ratio as per the formula on page 916, again, I don't understand how you can take the natural log of a negative number. Please explain.

Please see our response to Comment 7, above. We now use lnR throughout and clarify how the calculations were made. We have also added clarification in the figure legend.

15. Page 945, fig. 5: The caption mentions three groupings of organisms, while the figure displays four groups. I suggest replacing "faunal" in the caption by "mesofaunal" and "macrofaunal" for consistency.

We have clarified the body size groupings in the figure legend (L976-984) and the figure.

*"Figs. 5a and b Regressions between a percent change in the soil microbial, mesofaunal, macrofaunal, or soil microbial and soil faunal communities (i.e. multiple organismal groups) and the natural log of the response ratio of litter decomposition (lnR; calculated as the natural log of the response ratio, R, which was the value of the response variable at low diversity divided by the value at high diversity). No studies in our literature compilation of litter decomposition included manipualation only of soil microfauna, so this body size group is not included in the figure. Percent change in diveristy was calculated as (low diversity – high diversity/high diversity)*100. Figure 5a includes all possible comparisons across diversity gradients in studies, whereas 5b includes the comparisons between the lowest and highest diversity levels only."*

Technical Comments:
16. Page 908, line 14. Change "amd" to "and". 17. Page 912, line 18. Change "processes rates" to "process rates". 18. Page 919, line 1. Change "biodiversityim-pacteddecomposition" to "biodiversity impacted decomposition". 19. Page 920, line 24. Change "promotes" to "promote". 20. Page 923, line 17: I suggest changing "mediated through earthworm-mediated changes" to "mediated through changes". 21. Page 923, line 27 and further. I suggest changing "and manipulation of soil faunal biodiversity on plant tissue decomposition was significant" to "and the effect of manipulation of soil faunal biodiversity on plant tissue decomposition was significant". 22. Page 924, line 26. Change "(e.g., Ingham et al., 1985, resulting" to "(e.g., Ingham et al., 1985), resulting". 23. Page 925, line 4. I suggest changing "diversity of any organisms" to "diversity of any group of organisms" and "manipulation of soil organisms" to "manipulation of soil organism diversity". 24. Page 925, line 28. Change "functionstudies" to "function studies". 25. Page 937, line 2. Change "multifunctionalityl" to "multifunctionality".

We thank the reviewer for catching these errors. We have corrected all of the typos and suggested wording changes. The run-on words appear to be an error in typesetting our Word document into the online version. We will carefully check the typeset final version for similar errors.

Anonymous Referee #2

I have read this paper with great interest. As its authors point out, works on effects of soil biodiversity on soil functioning are scarce and often yield conflicting results. In this sense, I really appreciate the effort made in this meta-analysis to collect and put in order the available knowledge to produce a comprehensive and quantitative evaluation of potential effects of soil biodiversity loss on some soil processes and environmental services.
The paper is correctly written and, in general terms, allows a fluid reading. The two general hypotheses formulated in the introduction (a: soil biodiversity positively influences soil C pools and process rates, and b: biodiversity manipulations across multiple organismal groups more strongly affect soil C processes than manipulations within organismal groups) are correctly tested based on correct data selection and treatment.

We appreciate these encouraging remarks.

There are, however, some exceptions to the general clarity of the presentation:
(1) First of all, I'm afraid that the term "organismal groups" is confusing. I presume that it refers to diverse organisms belonging to different taxonomic levels but sharing some kind of common traits. If this were the case, I'd like to know which kind of traits (morphological, physiological, trophic.... traits?) we are talking about.

As discussed in response to comments from Reviewer 1, we have taken to heart that our use of the term "organismal groups" was confusing. We have clarified the meaning of these groupings by instead using the term "body size groups". These groups do indeed differ in taxonomic levels but body size is a good proxy for functional trait groupings. We now clarify the definition and functional relevance of body size groups in the text (L197-207).

" Soil biodiversity impacts on C respiration and decomposition were assessed by manipulating biodiversity either within a single body size group (i.e. microbes [including bacteria and fungi], micro-, or meso-, or macrofauna) or across multiple body size groups (e.g., micro-, meso-, macrofauna; e.g. Bradford et al. 2002). We treated the within-body size and across-body size groupings as two separate categories for the analysis. For plant biomass, however, there were not enough studies to run meta-analyses for individual categories. We also categorized the studies by soil microorganisms or soil fauna (micro-, meso- and macro fauna grouped together due to inadequate numbers of studies to split these up). Categorizing studies in this manner allowed us to assess whether species diversity within or across body size groups affected C cycling differently, while also enabling us to compare the relative impacts of diversity within the soil microbial community versus soil biodiversity within the soil faunal community."

(2) Another terminological difficulty arises from the use of species richness (here called "number of species") as a synonym of "biodiversity". Although, as the authors state in pg 913 (lines 10-15), this is becoming a common practice in works on plant science, it can

easily lead to confusion.

We agree with the reviewer on this point and look forward to the time when soil organism identification techniques advance to the point where biodiversity can truly be assessed. To minimize confusion on this point, we now reiterate the difference between species richness and biodiversity in the Discussion (L493-500).

"Finally, we caution that measuring soil biodiversity is exceedingly difficult, and in many cases treatments were assumed to affect biodiversity for the duration of the experiment, but this was often not measured. It is also possible that a change in the relative abundance of organisms is an important component of biodiversity and studies in our compilation typically equated species richness with diversity, whereas biodiversity sensu stricto includes both species richness and abundance (Magurran, 2005). To fully comprehend how biodiversity impacts ecosystem function, an attempt should be made at manipulating and maintaining different levels of soil community diversity, in the strict sense of the definition."

(3) Pg 911, lines 26-28, "functional redundancy .... is manipulated". Please, clarify this sentence.

Thank you for pointing out this sentence, we made an error. The words "greater than" have been replaced with 'reduced', which should improve the clarity of the sentence (121-126).

"Although different taxa within soil microbial (Cox et al., 2001; Hanson et al., 2008; Orwin et al., 2006) or faunal (Bignell and Eggleton, 2000; Milcu et al., 2008; Heemsbergen et al., 2004) groups can have unique impacts on the C cycle, functional redundancy among taxa would be expected to be reduced when a more complex food web of organisms is manipulated (e.g., across different size classes or feeding guilds) (Setälä, 2002)."

(4) Pg 912, lines 25-27. This paragraph should be moved to Methods

We feel that these few sentences that broadly describe the study help focus the reader on what to expect next in this manuscript. They are not describing the specific methods, but rather providing an overview of the general approach. For clarity, we would prefer to keep these sentences in place.

(5) Page 918, lines 21-24. The groups mentioned in the text do not match the groups that appear in figure 4.

Please see our response to Reviewer 1's comment 9, above. We have clarified this apparent mismatch.

(6) Pg 920, line 20. What do you mean with "more complex food webs consisting on

multiple organismal groups"? May I suggest "several trophic levels of the soil food web"?

As with the rest of the text, we now use the term "body size groups" in the sentence in question. We hope that it is now clearer. (L347-349): "…or more complex foodwebs consisting of multiple groups of different body sizes (Sulvaka et al., 2001; Laakso and Setälä, 1999; Ladygina et al., 2010; Eissenhauer et al., 2010; Eissenhauer and Schadler, 2011)."

(7) Pg 944 and 945, figs 4 and 5. I find the axes very confusing: How should I interpret a -100% change in diversity? Zero diversity?; What does a negative value mean for a natural logarithm?

We have included an explanation of percent change in biodiversity, as well as an explanation of lnR in the figure headings. Please see our response to Reviewer 1's comment 7.

I would also like to mention some methodological issues:
(8) Pg 913, lines 18-20: C pools were measured as total soil C, but also as dissolved organic carbon and as microbial biomass. I agree that microbial biomass is a sub-pool of the total soil C pool, but I'm not that sure about DOC that could be considered a flux and a vector for C loss from soil.

We agree with the reviewer that DOC can, in some cases and in some ecosystems, move and thus could under some conditions lead to a flux of C. However, in many cases DOC does not move rapidly (or at all). In the one study where DOC was measured in our literature compilation there was a static DOC pool (mesocosms). We feel it is best considered a sub-pool of the total soil C pool.

(9) As mentioned in several points of the text (and is also shown in figs 4 and 5), the number of studies on macro and mesofauna is very low (1 and 3 works on soil fauna in the meta-analysis). Is this enough to build up regressions and to sustain your discussion on effects of biodiversity manipulation at these levels of the soil trophic web?
We have fewer body size groups in the figure (microbes and macrofauna) than the possible number of groups as there were no studies that manipulated only microfauna or only mesofauna (although these body size groups were included in some of the studies that manipulated multiple body size groups). We have clarified this in the text (L293-301) and in the figure legend (L980-988).

L293-301: "Regression analyses revealed a negative linear relationship between soil biodiversity and lnR for soil C respiration (Fig. 4). This relationship was significant when we regressed the percent change in soil biodiversity and lnR for C respiration based on all diversity treatments in the compiled studies (Fig. 4a) and also when we calculated lnR for the highest and lowest diversity treatments only (Fig. 4b). We further examined how a decline in diversity within body size groups (data available for microorganisms and macrofauna) and across body size groups (multiple body size *groups) was related to soil C respiration. Soil microbial diversity was the only body size group significantly related to soil C respiration, with a decline in soil microbial diversity reducing C respiration (Fig. 4a)."*

*L966-974: "Figs. 4a and b Regressions between a percent change in the soil microbial, soil macrofaunal or soil microbial and soil faunal communities (i.e. multiple organismal groups) and the natural log of the response ratio of soil C respiration (lnR; calculated as the natural log of the response ratio, R, which was the value of the response variable at low diversity divided by the value at high diversity). No studies in our literature compilation of soil C respitation included manipualation of only soil microfauna or mesofauna, so these body size groups are not included in the figure. Percent change in diveristy was calculated as (low diversity – high diversity/high diversity)*100. Figure 4a includes all possible comparisons across diversity gradients in studies, whereas 4b includes the comparisons between the lowest and highest diversity levels only."*

(9) Also for conclusions and just as a suggestion: when working on soil biodiversity, could we talk about "key functional traits" more than about key species?

This is a good suggestion - we have worked this idea in to the text.

Please, also review the whole text for some minor errors such as: "process" instead of "processes" - pg 92 line19-; separate words in pg 919, line 1, etc.
We have carefully reviewed the manuscript for typographical errors.

Finally, I want to congratulate the authors for the election of the references. You probably want to include two very interesting papers based on field experiments and covering a wide geographical scale that have been published from 2013 to now: de Vries et al. 2013 (PNAS 110, 14296-14301) worked on diverse soil food web structures caused by differences in soil use, and Handa et al. 2014 (Nature 509, 218-221) manipulated biodiversity in litter.

We appreciate the suggestion of these references. De Vries published an important piece of work that relates soil food web structure to ecosystem functions. We have now included this reference in our article (L94-98):"This complex soil community plays an important role in determining the magnitude and direction of C fluxes between the atmosphere and terrestrial ecosystems, controlling soil C mineralization and promoting plant growth by regulating soil nutrient availability (e.g., De Deyn & Van der Putten, 2005; Fitter et al., 2005; Wall et al., 2010; de Vries et al., 2013)." Data from this paper were not included in the analysis, as the study did not manipulate soil biodiversity, which was a requirement for studies included in our analysis. The Handa paper unfortunately is too recent to be picked up by out literature search. Although at this point we do not include this paper in the analysis, we do cite it in our article (L440-442): "This notion is supported by a recent article showing that a reduction in the diversity of detrivores (both microorganisms and invertabrates) slows the rate at which litter is decomposed, regardless of the location of the experiment (Handa et al., 2014).

A meta-analysis of soil biodiversity impacts on the carbon cycle

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Abstract

Loss of biodiversity impacts ecosystem functions, such as carbon (C) cycling. Soils are the largest terrestrial C reservoir, containing more C globally than the biotic and atmospheric pools together. As such, soil C cycling, and the processes controlling it, have the potential to affect atmospheric CO_2 concentrations and subsequent climate change. Despite the growing evidence of links between plant diversity and soil C cycling, there is a dearth of information on whether similar relationships exist between soil biodiversity and C cycling. This knowledge gap occurs even though there has been increased recognition that soil communities display high levels of both taxonomic and functional diversity and are key drivers of fluxes of C between the atmosphere and terrestrial ecosystems. Here, we used meta-analysis and regression analysis to quantitatively assess how soil biodiversity affects soil C cycling pools and processes (i.e., soil C respiration, litter decomposition, and plant biomass). We compared the response of process variables to changes in diversity both within and across groups of soil organisms that differed in body size, a grouping that typically correlates with ecological function. When studies that manipulated both within- and across-body size group diversity were included in the meta-analysis, loss of diversity significantly reduced soil C respiration (-27.5%) and plant tissue decomposition (-18%) but did not affect above- or belowground plant biomass. The loss of within-group diversity significantly reduced soil C respiration, while loss of across-group diversity did not. Decomposition was negatively affected both by loss of within-group and across-group diversity. Furthermore, loss of microbial diversity strongly reduced soil C respiration (-41%). In contrast, plant tissue decomposition was negatively affected by loss of soil faunal diversity, but was unaffected by loss of microbial diversity. Taken together, our findings show that loss of soil biodiversity strongly impacts on soil C cycling processes, and highlight the importance of diversity across groups of organims (e.g., primary consumers and secondary decomposers) for maintaining full functionality of C cycle processes. However, our understanding of the complex relationships between soil biodiversity and C cycling processes is currently limited by the sheer number of methodological concerns associated with these studies, which can greatly overestimate or underestimate the impact of soil biodiversity on soil C cycling, challenging extrapolation to natural field settings. Future studies should attempt to further

elucidate the relative importance of taxonomic diversity (species numbers) *versus* functional diversity.

1 Introduction

Reductions in biodiversity have been linked with anthropogenic global change drivers such as climatic change, land cover change, reduction and fragmentation of natural areas, and human dependence on synthetic fertilizers (Vitousek and Mooney, 1997; Sanderson et al., 2002; Stevens, 2004; Phoenix et al., 2006; Fischer and Lindenmayer, 2007; Clark and Tilman, 2008). Over the past few hundred years, human activities have driven the species extinction rate to ca. 1,000 times the typical background extinction rate (MEA, 2006). This global decline in biodiversity impacts important ecosystem functions, such as net primary production (NPP) and biogeochemical cycles of carbon (C) and nutrients, threatening the services that ecosystems provide to the human population (Wardle et al., 2011; Cardinale et al., 2012).

The C cycle is a particularly important ecosystem service because the dynamic balance between C stored in ecosystems and in the atmosphere plays a key regulatory role in the global climate. Although vegetation stores a significant amount of C, soils are the largest terrestrial C reservoir, containing more C globally than the biotic and atmospheric pools combined (Lal, 2004). As such, soil C dynamics, and the processes that influence them, have the potential to impact atmospheric carbon dioxide (CO_2) concentrations and subsequent global change. Perturbations in terrestrial ecosystems that influence soil C dynamics could help mitigate the current rise in atmospheric CO_2 and associated climate change by promoting soil C storage (e.g., Cramer et al., 2001; Johnson and Curtis, 2001). Alternatively, they could exacerbate climate change by causing increased soil CO_2 efflux rates through increased decomposition rates of soil organic C (SOC) (e.g., Mack et al., 2004; Bardgett et al., 2008).

Loss of biodiversity has the potential to influence climate change if it alters SOC pools by reducing ecosystem C uptake or by increasing CO_2 outputs from terrestrial ecosystems to the atmosphere (Jastrow et al., 2007). Greater plant species diversity can increase C uptake by promoting biomass production (Tilman et al., 2006; Cardinale et al., 2012), which can enhance SOC storage (Fornara & Tilman, 2008; Steinbeiss et al., 2008; Cong et al., 2014). Conversely, declines in plant species diversity can reduce SOC storage (Hooper et al., 2012). Despite the growing body of evidence suggesting strong links between plant species diversity and soil C cycling, there is a dearth of information on whether similar relationships exist between biodiversity of soil organisms (hereafter ‘soil biodiversity’) and C cycling (Nielsen et al. 2011).

With ongoing losses in diversity belowground (Hooper et al., 2000), understanding relationships between soil biodiversity and C cycling is critical for projecting how loss of diversity under continued human alteration of the environment will impact global C cycling processes.

Soil communities typically have high levels of both taxonomic and functional diversity (e.g., De Deyn and Van der Putten, 2005). High taxonomic diversity, small sizes of organisms, and large population sizes make characterization of soil communities much less straight forward than that of plant communities. As such, characterization of soil organisms is often based on body size (e.g., Bradford et al., 2002), grouping organisms into macrofauna (>2 mm) such as earthworms, mesofauna (100 μm-2 mm) such as mites and springtails, microfauna (<100 μm) such as nematodes and protozoa, and soil microorganisms including bacteria and saprophytic and mycorrhizal fungi. These body size classes typically are useful functional groupings as they correlate with metrics such as metabolic rate, generation time, and food size (Peters, 1983). Estimates suggest that 1 g of soil can harbor tens of thousands of bacterial taxa, up to 200 m of fungal hyphae, and a wide range of micro-, meso-, and macrofauna (Roesch et al., 2007; Bardgett, 2005). This complex soil community plays an important role in determining the magnitude and direction of C fluxes between the atmosphere and terrestrial ecosystems, controlling soil C mineralization and promoting plant growth by regulating soil nutrient availability (e.g., De Deyn & Van der Putten, 2005; Fitter et al., 2005; Wall et al., 2010; de Vries et al., 2013). Despite a general consensus that the soil community is integral to the global C cycle, the impact of soil community diversity on ecosystem function is still little understood (Nielsen et al., 2011; Briones, 2014).

The positive impact of plant species diversity on soil C cycling processes can be mirrored in the soil community, with reported positive relationships between soil biodiversity and C cycling processes (e.g., Setälä, 2002; Heemsbergen et al., 2004). However, evidence suggests that this positive relationship is not universal, as other studies have found no significant impacts of soil biodiversity on C cycling (e.g., Griffiths et al., 2000). Understanding the relationship between soil biodiversity and C cycling is thus not so much a question of "does diversity matter?", but "under which circumstances does soil diversity affect C cycling?” One possibility for addressing this question is to consider the role of functional similarity among taxa, because relatively small or no responses of ecosystem processes to loss or gain of soil biodiversity would be expected in case of functional redundancy among soil organisms (Bengtsson, 1998; Andrén and Balandreau, 1999; Setälä et al., 2005).

To date, studies have assessed soil community diversity impacts on soil C cycling by manipulating diversity within or across multiple organismal groups (specifics of grouping criteria differ among studies, but are often taxonomic, functional, or body size groups). For example, studies have manipulated the diversity within groups of microorganisms [(e.g., bacteria, Bonkowski and Roy, 2005; Griffiths et al., 2000) and mycorrhizal fungi (van der Heijden et al., 1998; Maherali and Klironomos, 2007)], soil mesofauna (e.g., microarthropods, Liiri et al., 2002), and macrofauna (Heemsbergen et al., 2004; Zimmer et al., 2005). Other studies have manipulated the diversity across groups of soil organisms that differ in body size (i.e., microbes, and micro- meso- or macrofauna), or, alternatively, have manipulated diversity of trophic or functional groups (Hedlund and Ohrn, 2000; Ladygina et al., 2010). Although different taxa within soil microbial (Cox et al., 2001; Hanson et al., 2008; Orwin et al., 2006) or faunal (Bignell and Eggleton, 2000; Milcu et al., 2008; Heemsbergen et al., 2004) groups can have unique impacts on the C cycle, functional redundancy among taxa would be expected to be reduced when a more complex food web of organisms is manipulated (e.g., across different size classes or feeding guilds) (Setälä, 2002). Thus, studies assessing biodiversity impacts on ecosystem processes across multiple groups of soil organisms may yield very different answers than studies that probe for biodiversity impacts within single groups.

Although our knowledge of relationships between soil biodiversity and soil C cycling processes has increased with expanding research emphasis in this area, a comprehensive understanding to date is hampered by a lack of quantitative synthesis of existing studies. Nielsen et al. (2011) performed the most extensive synthesis on this topic to date, with a qualitative analysis. They found that diversity is often positively correlated with ecosystem function (e.g., soil respiration), although they cautioned that negative relationships between soil biodiversity and C cycling may be related to experimental limitations. In particular, Nielsen et al. (2011) found that strong relationships between soil biodiversity and C cycling were most common under unrealistically low levels of diversity. Further, their synthesis showed that the soil community composition, rather than species richness *per se*, had significant impacts on C cycling processes. This indicates high levels of functional redundancy among soil organisms and suggests that a loss of soil biodiversity may not necessarily impact the C cycle.

We aimed to quantitatively assess how soil biodiversity affects soil C cycling pools and processes using meta-analysis. We tested the general hypothesis that soil biodiversity positively impacts the soil C cycle, where reductions in diversity decrease soil C pools and process rates. Further, we tested the hypothesis that biodiversity manipulations across groups of organisms with different body sizes more strongly affect C cycling processes than manipulations within groups, due to a higher degree of functional redundancy within than across groups (Andrén and Balandreau, 1999; Setälä, 2002). In addition, we tested whether diversity of soil microbes *versus* soil fauna (including micro-, meso- and macrofauna) impacts C cycling differently. Finally, since 'biodiversity' is a metric that differs greatly in absolute numbers for soil organisms that differ in body size, we evaluated how the relative loss of diversity (in percent) within body size groups (i.e., microbes, soil fauna) affects soil C cycling.

2 Methods

2.1 Data compilation

We compiled published studies that explicitly manipulated soil biodiversity and measured responses of soil C cycling pools and/or processes. We systematically searched ISI Web of Science using all possible combinations of one soil C search term (plant biomass, soil C, decomposition, respiration, or NPP), one soil organism search term (microbes, bacteria, fungi, microorganism*, soil fauna, soil biota, soil organism*, microfauna, mesofauna, macrofauna, nematode*, collembola, acari, termite*, earthworm*), and the term "*diversity". We used "*" as a wildcard character such that papers using either singular or plural terms were returned. Additional relevant studies referenced in those returned by the search engines were also included in the literature compilation. While biodiversity *sensu stricto* includes both species richness and abundance (Magurran, 2005), we follow the recent nomenclature used in plant and soil studies and assume that the number of species present in a community represents the diversity of the community.

Each study included in our analysis presented data on one or more commonly measured biogeochemical C pool and/or process. Biogeochemical pool measurements were plant biomass and soil C pools [either total soil C, dissolved organic C (DOC), or microbial biomass]. Measured biogeochemical processes were soil C respiration and plant tissue decomposition. The duration of manipulative experiments included in this analysis ranged from 14 days to 3 years. More studies were conducted under controlled laboratory and greenhouse conditions than under field conditions (37 and 8 studies, respectively). When extracting data from these studies, we took values directly from published tables or the text whenever possible. If necessary, we estimated values from graphical data with image analysis software (ImageJ, National Institutes of Health, Bethesda, MD, USA).

In total we analyzed 45 published studies, of which 8 examined the effects of soil biodiversity on total plant biomass, 10 examined effects on aboveground plant biomass, 9 examined effects on root biomass, 13 examined effects on C respiration, 25 examined effects on decomposition, and 3 used laboratory microcosms to examine effects on soil C pools (Table 1). For soil C respiration, we included data that were obtained from either laboratory or *in situ* incubation studies in which the substrate was soil only or soil with organic amendments other than plant tissue (e.g., glucose). Laboratory studies typically estimated potential C mineralization rates, using temperature and moisture conditions assumed to be optimal for microbial activity. These measurements were made in closed microcosms with flux rates estimated from two or more repeated measurements of headspace gas concentrations. *In situ* studies used static or flow-through chambers to measure CO_2 flux rates from the soil surface, and thus would include both microbial heterotrophic and root (autotrophic) respiration (Holland et al., 1999). Plant tissue decomposition data were obtained from studies that measured either litter mass loss through time or C respiration from plant tissues decomposed under controlled laboratory conditions. Litter mass loss analyses used mesh litterbags and measured mass at two or more points in time (Harmon et al., 1999). For studies in which the source of decomposed material (i.e., soil or plant C) could be partitioned, data were separated and included in soil C respiration or plant tissue decomposition data groupings. For all biogeochemical pool and process studies in which data were available from multiple measurement times, we calculated the mean value for all measurement times and used only that value in the meta-analysis.

Soil biodiversity impacts on C respiration and decomposition were assessed by manipulating biodiversity either within a single body size group (i.e. microbes [including bacteria and fungi], micro-, or meso-, or macrofauna) or across multiple body size groups (e.g., micro-, meso-, macrofauna; e.g. Bradford et al. 2002). We treated the within-body size and across-body size groupings as two separate categories for the analysis. For plant biomass, however, there were not enough studies to run meta-analyses for individual categories. We also categorized the studies by soil microorganisms or soil fauna (micro-, meso- and macro fauna grouped together due to inadequate numbers of studies to split these up). Categorizing studies in this manner allowed us to assess whether species diversity within or across body size groups affected C cycling differently, while also enabling us to compare the relative impacts of diversity within the soil microbial community *versus* soil biodiversity within the soil faunal community.

Many of the studies we compiled assessed soil biodiversity impacts on C cycling by quantifying responses to a diversity gradient (e.g., > 2 diversity levels). Inherent to this design is the possibility for multiple comparisons among diversity treatments. For example, an analysis of how diversity of a three species community (species a, b, and c) affects ecosystem processes could yield a comparison of each single species community (a, b, or c) with the three-species community (a+b+c). This comparison yields three observations: (1) ‘a’ *versus* ‘a+b+c’, (2) ‘b’ *versus* ‘a+b+c’, and (3) ‘c’ *versus* ‘a+b+c’. In our meta-analysis we did not consider these three comparisons to be independent, but we calculated the mean of the three single species treatments and then calculated one response variable based on the comparison between that one single species mean and the three-species community. Intermediate levels of diversity were excluded from the meta-analysis to avoid any individual study from unduly weighting the analysis. This method prevented studies with a large species diversity gradient (i.e., a multitude of species included in the analysis) from dominating our meta-analysis.

2.2 Statistical analyses

To test how soil microbial and/or soil faunal diversity affects ecosystem C pools (plant biomass) and processes (C respiration and decomposition), and to test whether biodiversity manipulations across multiple body size groups affected C cycling differently from manipulations within groups, we analyzed the data set with meta-analysis (Curtis and Wang, 1998; Hungate et al., 2009), using the statistical software MetaWin 2.0 (Rosenberg et al., 2000). We were unable to use meta-analysis for soil C pools because the number of studies available (3) was inadequate for a meaningful analysis. The response ratio (R) was calculated as the value of a particular response variable at low diversity divided by the value at high diversity. The natural log of the response ratio R (lnR) was used as a metric for all of the response variables (de Graaff et al., 2006; van Groenigen et al., 2006). To ease interptretation of figures, the results for the analyses on lnR were back-transformed to response ratios and reported as percentage change under a reduction in diversity (that is, 100 x [R-1]). Thus, for response variables where there was no change between higher and lower diversity communities the change would equal 0. For cases with greater values for response variables in low diversity communities than high diversity communities the percent change would be would be positive, and lower values for response variables in low diversity communities than high diversity communities would yield negative values for the percent change.

Conventional meta-analyses weight each individual observation by the reciprocal of the mixed model variance (Curtis and Wang, 1998). However, such an analysis requires that the standard deviations of individual studies are known. These data were not available for a large proportion of the studies used in our analysis. Thus, we weighted individual values included in the analysis by experimental replication (Hedges and Olkin, 1985; Adams et al., 1997), assuming that better replicated experiments resulted in data with lower variance. We choose this metric because well-replicated studies provide more reliable estimates of the response of individual variables (e.g., Hungate et al., 1996; Hungate et al., 2009). We used bootstrapping to calculate confidence intervals on mean effect size estimates for the whole data set and for individual categories (Adams et al., 1997). We considered diversity effects significant if the 95% confidence intervals did not overlap with zero. In addition, we considered diversity effects for individual categories different from each other if they varied significantly at the $p \leq 0.05$ level.

Further, we tested how a loss of belowground species diversity is linked to changes in C pools and processes by performing linear regressions with percent change in species diversity and the effect size (lnR) of each of the response variables. Percent change in diversity was calculated as (low diversity – high diversity/high diversity)*100. Since the absolute number of species typically manipulated for diversity gradient studies varies among species that differ in body size in absolute terms (i.e. many more species are usually present in studies of microbial diversity than in studies of faunal diversity), we calculated relative differences in species diversity for each treatment. Thus manipulation of microbial diversity might include a low diversity treatment of 100 versus a high diversity treatment of 1000 species, while manipulation of soil fauna might span from low diversity of 1 species to high diversity of 10 species. Calculated as relative differences in diversity, both examples would be the same (i.e., low diversity is 10% of the number of species present in high diversity). We performed two sets of regressions. The first included all soil biodiversity levels, and the second included the highest and lowest biodiversity levels only. We used linear regression (SPSS v. 20) to regress lnR against relative change in species diversity. We performed regressions in which we considered lnR (the effect size) between every diversity level, and also regressions in which we only considered lnR between the highest and lowest diversity levels, omitting intermediate diversity levels.

3 Results

3.1 Impacts of soil biodiversity on ecosystem C pools and processes

Results from our meta-analyses indicate very different responses to changes in soil biodiversity among C pools (plant biomass; soil C pools not included because of inadequate number of studies) and processes (soil C respiration and plant tissue decomposition). Plant biomass did not respond to changes in diversity, either when analyzed as total biomass or partitioned into aboveground and belowground biomass (Fig. 1). In contrast to the lack of impact on plant C pools, decreased soil biodiversity (including studies that manipulated diversity within and across body size groups) corresponded to a mean 27.5% reduction in soil C respiration (Fig. 2) and a mean 18% reduction in decomposition (Fig. 3).

When soil C respiration responses were partitioned into studies that manipulated diversity within body size groups *versus* those that manipulated diversity across body size groups, we found a significant effect only for within group manipulations (Fig. 2). Due to a lack of studies that manipulated solely soil fauna (there was just one study; Scheu et al., 2002), we were unable to compare how a change in soil faunal biodiversity *versus* soil microbial biodiversity impacts soil C respiration. However, when we omitted studies manipulating soil faunal biodiversity from our analysis and assessed impacts of reductions in soil microbial biodiversity alone on soil C respiration, we found that soil C respiration was reduced by 41% (Fig. 2).

Plant tissue decomposition generally responded negatively to reductions in soil biodiversity (Fig. 3). Studies that manipulated diversity within soil organismal groups and those that manipulated diversity across organismal groups both led to similar reductions in decomposition (means of 23% and 15%, respectively; Fig. 3). Further, whereas reduced soil microbial diversity did not significantly reduce decomposition rates, reduced soil faunal diversity led to a 37% reduction in mean decomposition (Fig. 3).

3.2 Relationships between diversity loss and C cycling processes

Regression analyses revealed a negative linear relationship between soil biodiversity and lnR for soil C respiration (Fig. 4). This relationship was significant when we regressed the percent change in soil biodiversity and lnR for C respiration based on all diversity treatments in the compiled studies (Fig. 4a) and also when we calculated lnR for the highest and lowest diversity treatments only (Fig. 4b). We further examined how a decline in diversity within body size groups (data available for microorganisms and macrofauna) and across body size groups (multiple body size groups) was related to soil C respiration. Soil microbial diversity was the only body size group significantly related to soil C respiration, with a decline in soil microbial diversity reducing C respiration (Fig. 4a). The paucity of data available for the other body size groups prevented us from running any meaningful regression analyses. We have, however, highlighted the other body size groups in the regression figure to depict the dearth of studies on these organisms relative to microbes.

Regression analysis also revealed a significant response in decomposition to altered biodiversity when all studies were included (Fig. 5a), but not when only the highest and lowest diversity treatments were included (Fig. 5 b). Reductions in biodiversity did not significantly affect decomposition in studies that measured litter mass loss. Conversely, when decomposition was measured via CO_2 efflux, there was a significant relationship between decomposition and biodiversity change when all diversity treatments were included in the analysis (R^2=0.307, $p<0.001$; data not shown).

4 Discussion

Changes in biodiversity have been linked with changes in ecosystem functioning, but so far studies have largely focused on plant diversity (e.g., Isbell et al. 2011). Whether or not similar patterns exist for soil biodiversity remains largely unknown. Here, we provide the first quantitative synthesis of studies testing effects of soil biodiversity on C cycling. Using meta-analysis and regression analysis, we showed that loss of soil biodiversity can have negative consequences for the soil C cycle, but that relationships between C cycling processes with soil biodiversity vary across groups of soil organisms and are process-dependent. Below we explore how our findings contribute to our knowledge of how soil biodiversity drives ecosystem functions. We also discuss experimental short-comings, methodological challenges and suggest directions for future research.

4.1 Biodiversity impacts on C pools

Few studies have assessed the relationship between soil biodiversity and soil C pools. We found just three studies in our literature search, and these studies all used different indices of soil C pools: ergosterol, which is a measure of fungal biomass (Liebich et al., 2007); dissolved organic C (Cragg and Bardgett, 2001); and soil organic C concentration (Zimmer et al., 2005). All three studies were short lived (range = 42 to 70 days) and were conducted in microcosms in which diversity of the microbial community (Liebich et al., 2007), microfauna (collembola; Cragg and Bardgett, 2001), or macrofauna (earthworms and woodlice; Zimmer et al., 2005) was manipulated. Due to the small number of studies we were unable to conduct a quantitative analysis. However, none of the individual studies showed an impact of soil biodiversity on soil C pools. It is probably not surprising that very few studies attempted to relate soil community diversity to soil C pools, due to the difficulty of maintaining soil biodiversity manipulations in microcosms for long time periods. Bulk soil organic C pools are typically stable on the order of years to decades due the large pool sizes and the relatively slow rates of biological processes (Conen et al., 2003; Smith, 2004), so short-term effect of soil biodiversity on this pool would be expected to be low and undetectable. We expect that some metrics of the relatively labile fraction in the soil C pool (e.g., particulate organic matter, DOC) will be more temporally dynamic than the bulk pool (Six et al., 2002) and would be better target response variables for assessing biodiversity impacts. Even more likely to provide information on soil biodiversity impacts on soil C cycling are studies assessing diversity effects on short-term C fluxes.

Plant biomass, assessed as a whole or partitioned into root and shoot biomass, was not significantly affected by soil biodiversity. Our analysis included studies that manipulated diversity of mycorrhizal fungi (Baxter and Dighton, 2001), microarthropods (Liiri et al., 2002), meso- and macrofaunal decomposers (Eissenhauer and Schadler, 2011), or more complex foodwebs consisting of multiple groups of different body sizes (Sulvaka et al., 2001; Laakso and Setälä, 1999; Ladygina et al., 2010; Eissenhauer et al., 2010; Eissenhauer and Schadler, 2011). The lack of a response of plant biomass production to soil biodiversity results from the contradicting results generated across a number of studies, and indicates that soil biodiversity does not unequivocally promote plant production (reviewed in van der Heijden et al., 2008). With the exception of rhizosphere organisms such as mycorrhizal fungi, rhizobia, and root pathogens or herbivores, linkages between soil organisms and plant biomass are indirect, i.e., decomposer organisms break down organic compounds and make nutrients available for plant uptake (Wardle et al. 2004). This indirect link between plant growth and soil organisms may result in a rather weak relationship between soil biodiversity and plant production (Balvanera et al., 2006). In line with this, we did find a trend of decreased plant production with loss of soil biodiversity. However, the limited number of studies reduced our statistical power, restricting our ability to quantify soil biodiversity impacts on plant biomass production. Another complication in assessing biodiversity impacts on plant production is that to date studies have exclusively been conducted in laboratory and greenhouse settings. While laboratory manipulations can provide useful information about potential controls over ecological processes, these manipulations are by necessity short-term (range 35 days – 52 weeks for the studies we compiled) and may include only a subset of the complex food webs and biogeochemical processes that occur in natural field settings (Hol et al., 2010). Furthermore, diversity effects may become more apparent over time as functional redundancy declines (Reich et al 2012).

Although soil biodiversity did not conclusively impact soil C pools or affect plant biomass production, biodiversity as a whole appears to play an important role in maintaining and enhancing plant biomass production and soil C pools. For example, plant diversity can promote plant biomass production and soil C storage (Tilman et al., 2006; Cardinale et al., 2012; Fornara

& Tilman, 2008; Steinbeiss et al., 2008), and these benefits of aboveground biodiversity on ecosystem functions are often attributed to increases in plant nutrient uptake resulting from belowground spatial and temporal differentiation in resource use (e.g., McKane et al., 1990; Tilman et al., 1996; Casper and Jackson, 1997; Schenk et al., 1999; van Ruijven and Berendse, 2005; van der Heijden et al., 2003). As such, a single limiting resource (e.g., soil N) may be spatially partitioned among co-occurring plant species, which reduces inter-specific competition and thereby facilitates coexistence (McKane et al., 1990). It is reasonable to expect that similar mechanisms occur for soil organisms (Prosser and Nicol, 2012; Sechi et al., 2014), and effects of plant and soil organism diversity on ecosystem functions may not be independent of each other, as increased plant diversity may be accompanied by increased soil biodiversity (Scherber et al. 2010, Eisenhauer et al. 2011). If this is the case, soil biodiversity could explain, at least in part, the observed positive relationship between plant diversity and ecosystem C pools and processes. It is noteworthy here to mention that soil fungal pathogens have been found an important driver of observed positive relationships between plant diversity and productivity (Maron et al., 2011).

4.2 Soil biodiversity impacts on soil C processes

Results from our meta-analysis show that loss of soil biodiversity significantly reduces soil C respiration (-27.5%). This is a strong reduction in soil C mineralization that could have important ecosystem level consequences for the soil C cycle. However, some caution is warranted in interpreting these results as the experimental design of many of the studies included in the analyses may have inadvertently over- or underestimated soil biodiversity impacts on processes important to the soil C cycle (Nielsen et al., 2011). The response of C respiration to a loss in soil biodiversity was overwhelmingly driven by studies manipulating soil microbial diversity, and when we categorized the analysis by studies that manipulated the soil microbial community only, the average response to a reduction in biodiversity was even greater (-41%). In addition, the regression analysis revealed that a loss in soil biodiversity was significantly related to a loss in soil C respiration only when soil microbial diversity was included in the analysis. This suggests that these studies contributed in large part to the strong response of soil C respiration to a reduction in soil biodiversity. Many of these studies used a relatively low number of microbial species when compared to soil microbial diversity in natural ecosystems. For example, Setälä and

McLean (2004) used 43 taxa of saprophytic fungi, a large number relative to most manipulative experiments, but a small number relative to the estimated number of fungi in natural soils. In addition, the majority of the studies were conducted under highly controlled and short-term laboratory conditions. Some studies used fumigation or dilution methods to alter soil microbial diversity (Griffiths et al., 2000; 2001; 2004; Wertz et al., 2006), and although it appears that microbial diversity decreases with increased dilution or fumigation, the main impacts of these treatments may be on the community structure by favoring taxa that physiologically withstand the pressures of dilution or fumigation. Studies using this technique showed that with increasing species number, the response of C respiration to an increase in biodiversity leveled off (Bell et al., 2005), and that responses to these treatments are often idiosyncratic, which suggests that they are driven by the soil microbial community structure, rather than by diversity. Thus, although our synthesis indicates that the response of soil C respiration to a reduction in soil biodiversity can be significant, we contend that the response may be an overestimation of what would happen in soils with natural communities.

Although many studies have assessed the impact of soil microbial diversity on soil C respiration, only one study evaluated effects of soil faunal diversity (earthworms) on C respiration (Scheu et al., 2002). This study indicated that soil faunal richness impacts soil microbial community functioning, which may in-turn alter soil C respiration. Soil fauna can strongly affect microbial processes and community composition by enhancing the availability of resources to the microbial community (Edwards, 2000; Heal et al., 1997; Petersen and Luxton, 1982). For example, invasive earthworms in North America have been associated with changes in soil respiration, although these effects may be mediated through changes in the abundance of other organisms, such as microbes (Szlavecz et al. 2011) or availability of soil and litter resources (Huang et al. 2010). Thus, a change in the diversity of soil fauna is expected to alter soil C respiration, but more studies that manipulate soil fauna are required to confirm this hypothesis.

Results from the meta-analysis and the regression analysis show that loss of soil biodiversity significantly reduces plant tissue decomposition (-18%). Unlike the other response variables, soil biodiversity impacts on plant tissue decomposition were not dominated by studies that manipulated the soil microbial community. Rather, ca. 84% of decomposition studies in our compilation manipulated soil fauna or multiple groups of soil organisms; soil faunal biodiversity effects on plant tissue decomposition were significant (-37%). The significant impact of soil faunal manipulations on litter decomposition may be due to the strong direct effect of soil fauna on litter decomposition, particularly in the early stages of decomposition (Heemsbergen et al., 2004; Berg & Laskowski, 2006; Milcu & Manning, 2011). By contrast, soil microbial diversity reductions alone did not significantly suppress decomposition rates. This finding is despite individual observations that the diversity of litter-associated microbes increases as decomposition proceeds (e.g., Dilly et al. 2004). Nonetheless, based on our observation that soil faunal diversity has a strong impact on plant tissue decomposition, we propose that diversity of the soil community, and particularly soil faunal diversity, is an important factor driving rates of litter decomposition. This notion is supported by a recent article showing that a reduction in the diversity of detrivores (both microorganisms and invertabrates) slows the rate at which litter is decomposed, regardless of the location of the experiment (Handa et al., 2014).

We hypothesized that diversity across multiple organismal groups composed of different body sizes would impact soil C cycling processes to a greater extent than diversity within groups of organisms with a single body size, with the assumption that within-group diversity would be accompanied by a greater degree of functional redundancy (Laakso and Setälä, 1999; Wardle, 1999; Cragg and Bardgett, 2001). For example, a higher diversity of feeding guilds has been linked to more effective substrate use (Setälä & Huhta, 1991). Our analysis, however, suggests that for plant tissue decomposition diversity across multiple body size groups has similar impacts on soil C cycling to diversity within body size groups. For soil C respiration, the effect of reduced diversity within groups was even stronger than that of smaller diversity across groups. This may result from the approaches taken to assess community impacts on soil C cycling. First, there is a lack of consistency in approaches taken to study effects of soil biodiversity on C cycling, both for the within- and the across- body size group approach. As such, the level of functional diversity between 'high' diversity and 'low' diversity treatments may have varied across studies, and it is unclear whether shifts in functional diversity were greater for across-group manipulations than for within-group manipulations. Except for Heemsbergen et al. (2004), no studies explicitly tested for the functional dissimilarity among the species manipulated. Second, populations of soil organisms at lower trophic levels may show compensatory growth responses to loss of biomass predation by organisms of higher trophic levels (e.g., Ingham et al., 1985), resulting in no net effect of manipulation of trophic diversity on the processes regulated by lower-trophic level soil organisms. Third, effects of functional or trophic groups of organisms may have opposing effects on the C cycling pools and process rates. For example, Ladygina et al. (2010) showed that arbuscular mycorrhizal fungi and decomposer (enchytraeids and collembolan) cancelled each other out in affecting plant community biomass.

4.3 Methodological concerns

While manipulating diversity of any group of organisms is fraught with challenges, manipulation of soil organism diversity is particularly challenging. A more comprehensive assessment of soil diversity impacts on C cycling will require that some of these challenges are addressed. Nielsen et al. (2011) found that the response to a reduction in diversity was greater if diversity levels were low (i.e. < 10 species included in the analysis) and conducted under more controlled experimental conditions, rather than under high diversity (i.e. >10 species included in the analysis) and more natural experimental conditions. Our analysis set out to quantify how the design of the study affected soil C cycling processes, by comparing studies that manipulated soil biodiversity within a single body size group with studies that manipulated biodiversity across multiple groups. Across body size group manipulations approach the natural complexity of soil food webs to a much greater degree than within-group manipulations. However, even the most complex manipulations accounted only for a fraction of the diversity likely under natural field conditions. As such, to further enhance our understanding of soil community diversity impacts on soil C cycling, studies should incorporate more natural conditions in their design and manipulate more complete soil communities. A recent study by Wagg et al. (2014) used a method for manipulating a broad size range of soil organisms by inoculating sterilized soils with soil communities derived through a series of different sized filters. This method allowed the researchers to successfully obtain a broad soil biodiversity gradient within and across groups of soil organism that span a gradient in body sizes in their grassland microcosms, and showed that soil biodiversity loss and simplification of soil community composition impairs multiple ecosystem functions, including litter decomposition and soil C sequestration. However, filtering groups of organisms based on body size does not allow separating between effects of functional dissimilarity from effects of biodiversity (species richness) *per se*. This underscores the pervasive challenge to truly measuring biodiversity effects on ecosystem processes. A parallel concern is that soil biodiversity typically cuts across multiple trophic groups (e.g., manipulation of nematodes would potentially alter both herbivores and predators in the soil). Aboveground diversity-ecosystem function studies have typically been limited to the primary producer trophic level, but results may yield very different relationships if consumer trophic levels are included in diversity manipulations (Borer et al., 2014). Finally, we caution that measuring soil biodiversity is exceedingly difficult, and in many cases treatments were assumed to affect biodiversity for the duration of the experiment, but this was often not measured. It is also possible that a change in the relative abundance of organisms is an important component of biodiversity and studies in our compilation typically equated species richness with diversity, whereas biodiversity *sensu stricto* includes both species richness and abundance (Magurran, 2005). To fully comprehend how biodiversity impacts ecosystem function, an attempt should be made at manipulating and maintaining different levels of soil community diversity, in the strict sense of the definition.

5 Conclusions

If we are to fully understand how anthropogenic-induced changes in biodiversity affect the terrestrial C cycle, we must dig deeper and embrace the challenges associated with studying the belowground world. Understanding the complex relationships between soil biodiversity and C cycling processes is currently limited by the sheer number of methodological concerns associated with these studies, which can greatly overestimate or underestimate the impact of soil biodiversity on soil C cycling, challenging extrapolation to natural field conditions. Nonetheless, our data point towards a definite importance of soil community diversity on key C cycling processes. Our quantitative analysis revealed significant negative effects of loss of soil biodiversity on rates of soil respiration and litter decomposition. If this is the case, declines in soil biodiversity could significantly affect the rates and dynamics of C cycling. However, biodiversity effects were not always consistent across groups of organisms. Differential responses of groups of organisms could be related to their functional role in the respective processes. It is however important to emphasize that we are still lacking full understanding of the underlying changes in soil community functioning (or the lack of) with shifts in soil biodiversity (Nielsen et al. 2011; Briones, 2014). Future studies should therefore attempt to further elucidate the relative importance of taxonomic diversity (species numbers) *versus* functional diversity. Effects of loss of soil biodiversity on ecosystem C cycling should depend on the degree of functional dissimilarity of the organisms involved (Heemsbergen et al. 2004). Hence, unraveling the level of variation in functional traits among soil organisms, both within and across feeding groups, should be a future research priority. Such studies would improve predictions on the global C cycling in the face of future environmental changes. Given the importance of the soil community in regulating the direction and magnitude of C fluxes between the atmosphere and terrestrial ecosystems, advancing our understanding of soil biodiversity impacts on biogeochemical cycles may enhance the efficacy of climate change mitigation efforts.

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Figure legends

Fig. 1 The percent response of total plant biomass, shoot biomass and root biomass to a change in soil community diversity (i.e., 'high' vs 'low' diversity). Studies included in the analysis manipulated diversity of the soil microbial community, the soil micro-, meso, or macrofaunal community or a combination of these trophic groups. Data represent means with 95% confidence intervals; numbers in brackets represent the total number of data points included in the analysis.

Fig. 2 The percent response of soil C respiration to a change in soil community diversity (i.e., 'high' vs 'low' diversity). Studies included in the analysis manipulated diversity of the soil microbial community, the soil micro-, meso, or macrofaunal community or a combination of these body size groups ('all studies'). Further studies are categorized by studies that manipulated species diversity within or across body size groups, and by studies that manipulated the soil microbial community (including fungi and bacteria) or the soil faunal community (including micro-, meso- and macrofauna). Data represent means with 95% confidence intervals; numbers in brackets represent the total number of data points included in the analysis.

Fig. 3 The percent response of decomposition to a change in soil community diversity (i.e., 'high' vs 'low' diversity). Studies included in the analysis manipulated diversity of the soil microbial community, the soil micro-, meso, or macrofaunal community or a combination of these trophic groups ('all studies'). Further studies are categorized by studies that manipulated species diversity within or across body size groups, and by studies that manipulated the soil microbial community (including fungi and bacteria) or the soil faunal community (including micro-, meso- and macrofauna). Data represent means with 95% confidence intervals; numbers in brackets represent the total number of data points included in the analysis.

Figs. 4a and b Regressions between a percent change in the soil microbial, soil macrofaunal or soil microbial and soil faunal communities (i.e. multiple organismal groups) and the natural log of the response ratio of soil C respiration (lnR; calculated as the natural log of the response ratio, R, which was the value of the response variable at low diversity divided by the value at high diversity). No studies in our literature compilation of soil C respitation included manipualation of only soil microfauna or mesofauna, so these body size groups are not included in the figure. Percent change in diveristy was calculated as (low diversity – high diversity/high diversity)*100. Figure 4a includes all possible comparisons across diversity gradients in studies, whereas 4b includes the comparisons between the lowest and highest diversity levels only.

Figs. 5a and b Regressions between a percent change in the soil microbial, mesofaunal, macrofaunal, or soil microbial and soil faunal communities (i.e. multiple organismal groups) and the natural log of the response ratio of litter decomposition (lnR; calculated as the natural log of the response ratio, R, which was the value of the response variable at low diversity divided by the value at high diversity). No studies in our literature compilation of litter decomposition included manipualation only of soil microfauna, so this body size group is not included in the figure. Percent change in diveristy was calculated as (low diversity – high diversity/high diversity)*100. Figure 5a includes all possible comparisons across diversity gradients in studies, whereas 5b includes the comparisons between the lowest and highest diversity levels only.

Table 1. Overview of studies used in the analyses.

Response variable	Body size group	Size class	Taxonomic group	Number of studies	Reference
Total plant biomass	Microbes	< 5µm	Ectomycorrhizal fungi	1	Baxter and Dighton (2001)
	Mesofauna	100µm - 2mm	Microarthropods	2	Liiri et al (2002), Eisenhauer and Schädler (2011)
	Microbes + Microfauna	< 5µm - 100µm	Microflora, Nematodes	1	Bezemer et al (2005)
	Microbes + Macrofauna	< 5µm, > 2mm	Fungi, Earthworms	2	Eisenhauer et al (2010), Eisenhauer and Schädler (2011)
	Mesofauna + Macrofauna	100µm - > 2mm	Collembola, Enchytraeids, Earthworms	1	Eisenhauer and Schädler (2011)
	Microbes + Microfauna + Mesofauna	< 5µm - 2mm	Bacteria, Fungi, Protozoa, Nematodes, Microarthropods,	1	Sulkava et al (2001)

			Enchytraeids		
Shoot biomass	Microbes	< 5µm	Ectomycorrhizal fungi	1	Baxter and Dighton (2001)
	Mesofauna	100µm - 2mm	Microarthropods	3	Liiri et al (2002), Cole et al (2004), Eisenhauer and Schädler (2011)
	Microbes + Macrofauna	< 5µm, > 2mm	Fungi, Earthworms	2	Eisenhauer et al (2010), Eisenhauer and Schädler (2011)
	Mesofauna + Macrofauna	100µm - > 2mm	Collembola, Enchytraeids, Earthworms	1	Eisenhauer and Schädler (2011)
	Microbes + Microfauna + Mesofauna	< 5µm - 2mm	Bacteria, Fungi, Protozoa, Nematodes, Microarthropods, Enchytraeids	1	Sulkava et al (2001)
	Microbes + Microfauna + Mesofauna	< 5µm - 2mm	Bacteria, Fungi, Protozoa, Microarthropods,	1	Laakso and Setälä (1999)

			Enchytraeids		
	Microbes + Microfauna + Mesofauna + Macrofauna	5µm - > 2mm	Fungi, Nematodes, Enchytraeids, Microarthropods, Wireworms	1	Ladygina et al (2010)
Root biomass	Microbes	< 5µm	Ectomycorrhizal fungi	1	Baxter and Dighton (2001)
	Mesofauna	100µm - 2mm	Microarthropods	3	Liiri et al (2002), Eisenhauer et al (2011), Eisenhauer and Schädler (2011)
	Microbes + Macrofauna	< 5µm, > 2mm	Fungi, Earthworms	2	Eisenhauer et al (2010), Eisenhauer and Schädler (2011)
	Mesofauna + Macrofauna	100µm - > 2mm	Collembola, Enchytraeids, Earthworms	1	Eisenhauer and Schädler (2011)
	Microbes + Microfauna + Mesofauna	< 5µm - 2mm	Bacteria, Fungi, Protozoa, Nematodes, Microarthropods, Enchytraeids	1	Sulkava et al (2001)
	Microbes +	5µm - > 2mm	Fungi, Nematodes,	1	Ladygina et al (2010)

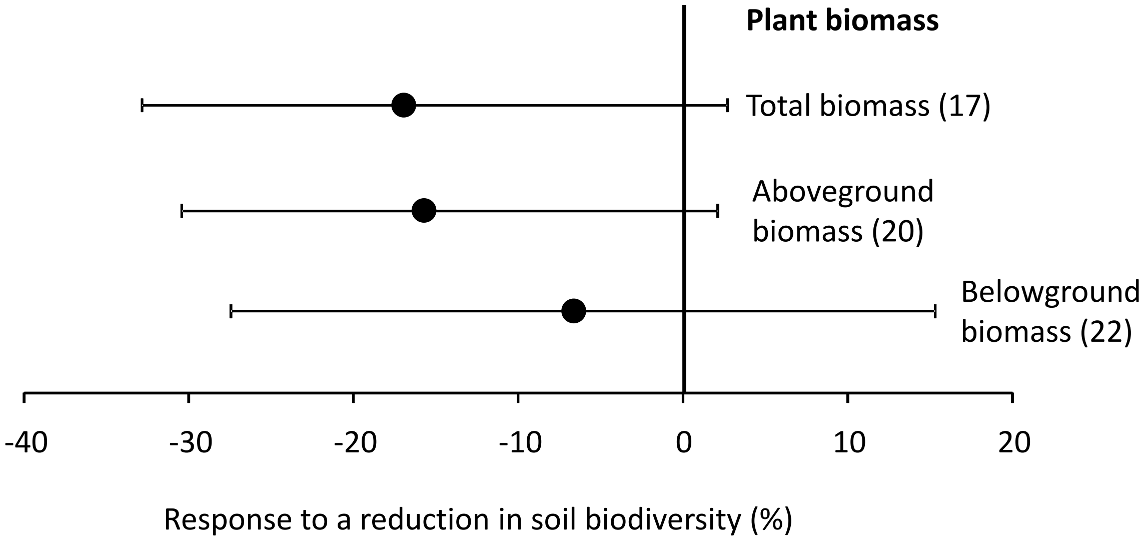
	Microfauna + Mesofauna + Macrofauna		Enchytraeids, Microarthropods, Wireworms		
Respiration	Microbes	< 5µm	Bacteria	1	Wertz et al (2006)
	Microbes	< 5µm	Bacteria, Fungi	3	Griffiths et al (2000, 2001 and 2004)
	Microbes	< 5µm	Fungi	5	Wilkinson et al (2010, 2011 and 2012), Tiunov and Scheu (2005), Setala and McLean (2004)
	Macrofauna	>2mm	Earthworms	1	Scheu et al (2002)
	Microbes + Mesofauna	< 5µm, 100µm - 2mm	Microflora, Enchytraeids, Microarthropods	1	Edsberg (2000)
	Mesofauna + Macrofauna	100µm - > 2mm	Not specified	1	Risch et al (2013)
	Microfauna + Mesofauna + Macrofauna	5µm - > 2mm	Nematodes, Enchytraeids, Earthworms	1	Bradford et al (2007)
Decomposition	Microbes	< 5µm	Bacteria	1	Bell et al (2005)

Microbes	< 5µm	Fungi	3	Progar et al (2000),Toljander et al (2006), Lebauer et al (2010)
Microbes	< 5µm	Bacteria, Fungi	3	Griffiths et al (2000), Griffiths et al (2001), Liebich et al (2007)
Mesofauna	100µm - 2mm	Collembola	2	Cragg and Bardgett (2001), Eisenhauer and Schädler (2011)
Macrofauna	> 2mm	Woodlice, Millipedes	1	Collison et al (2013)
Macrofauna	> 2mm	Woodlice, Earthworms	1	Zimmer et al (2005)
Microbes + Microfauna	< 5µm - 100µm	Bacteria, Fungi, Nematodes	2	Mikola and Setälä (1998a), Mikola and Setälä (1998b)
Microbes + Mesofauna	< 5µm, 100µm - 2mm	Microflora, Enchytraeids, Microarthropods	1	Edsberg (2000)
Microbes + Mesofauna	< 5µm, 100µm - 2mm	Fungi, Collembola, Mites	1	Hedlund and Ohrn (2000)
Microbes + Macrofauna	< 5µm , > 2mm	Fungi, Ants, Termites	1	Warren and Bradford (2012)

Microbes + Microfauna + Mesofauna	< 5µm - 2mm	Bacteria, Fungi, Protozoa, Nematodes, Microarthropods, Enchytraeids	1	Sulkava et al (2001)
Microbes + Microfauna + Mesofauna	< 5µm - 2mm	Bacteria, Fungi, Nematoes, Protozoa, Collembola, Enchytraeids, Mites	1	Cortet et al (2003)
Microbes + Microfauna + Mesofauna	< 5µm - 2mm	Not specified	2	Heneghan et al (1999), Wall et al (2008)
Microfauna + Mesofauna + Macrofauna	5µm - > 2mm	Protozoa, Nematodes, Enchytraeids, Arthropods, Earthworms	1	Bradford et al (2002)
Microbes + Microfauna + Mesofauna + Macrofauna	< 5µm - > 2mm	Fungi, Arthropods	1	Araujo et al (2012)

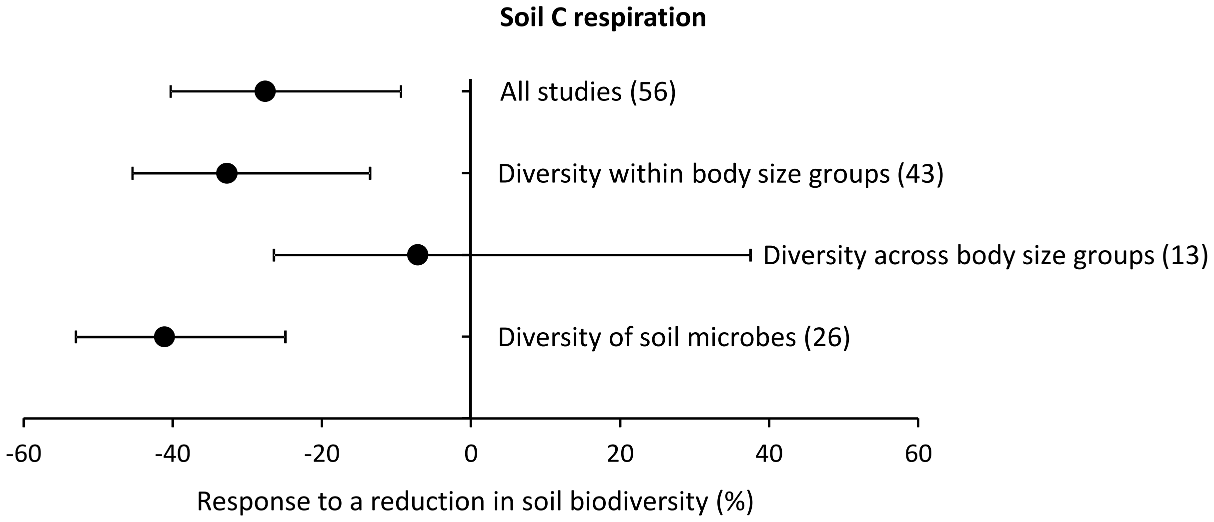
	Microbes + Microfauna + Mesofauna + Macrofauna	5µm - > 2mm	Fungi, Bacteria, Protozoa,Nematodes, Microarthropods	1	Carrillo et al (2011)
	Microbes + Microfauna + Mesofauna + Macrofauna	< 5µm - > 2mm	Not specified	1	Slade and Riutta (2012)
	Microbes + Microfauna + Mesofauna + Macrofauna	< 5µm - > 2mm	Not specified	1	Yang and Chen (2009)
Soil C	Microbes	< 5µm	Bacteria, Fungi	1	Liebich et al (2007)
	Mesofauna	100µm - 2mm	Collembola	1	Cragg and Bardgett (2001)
	Macrofauna	> 2mm	Woodlice, Earthworms	1	Zimmer et al (2005)

Fig. 1

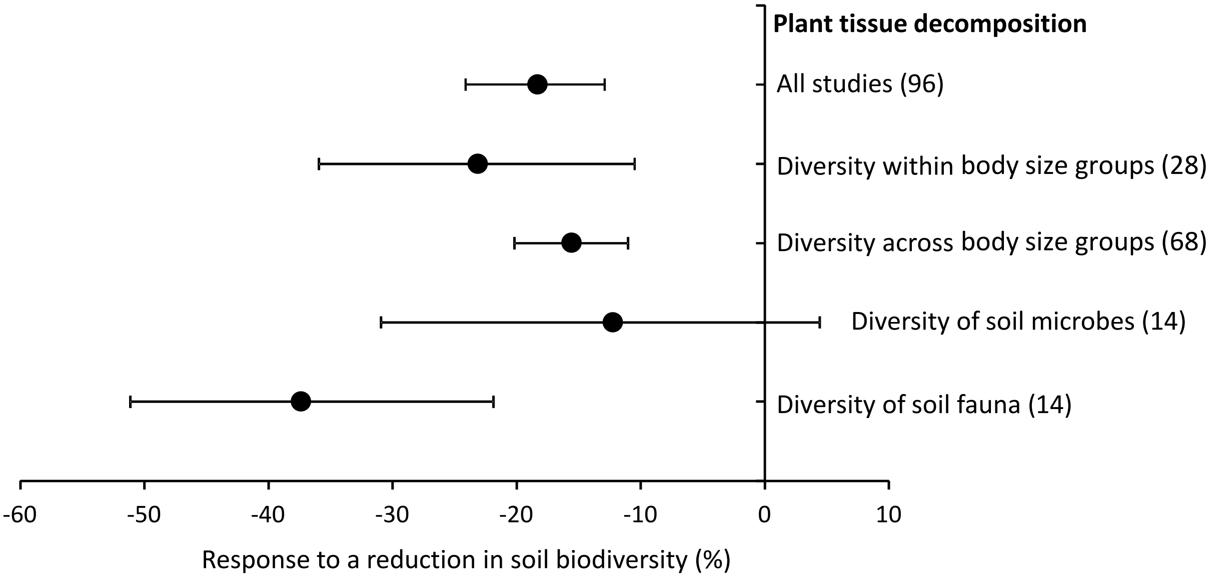


Plant biomass
Total biomass (17)
Aboveground biomass (20)
Belowground biomass (22)
-40
-30
-20
-10
0
10
20
Response to a reduction in soil biodiversity (%)

Fig. 2


Soil C respiration
All studies (56)
Diversity within body size groups (43)
Diversity across body size groups (13)
Diversity of soil microbes (26)
-60
-40
-20
0
20
40
60
Response to a reduction in soil biodiversity (%)

947 Fig 3.



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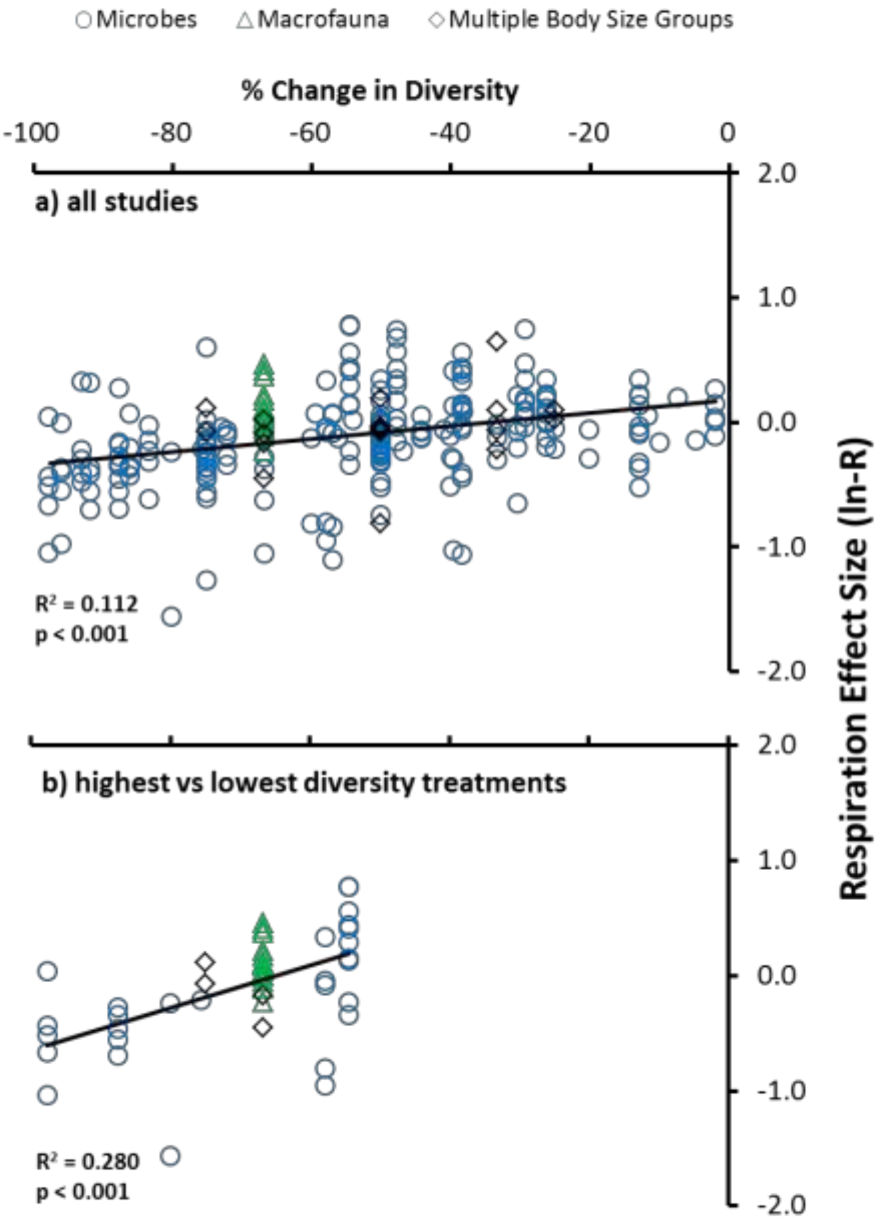
950 Figs. 4a, and b



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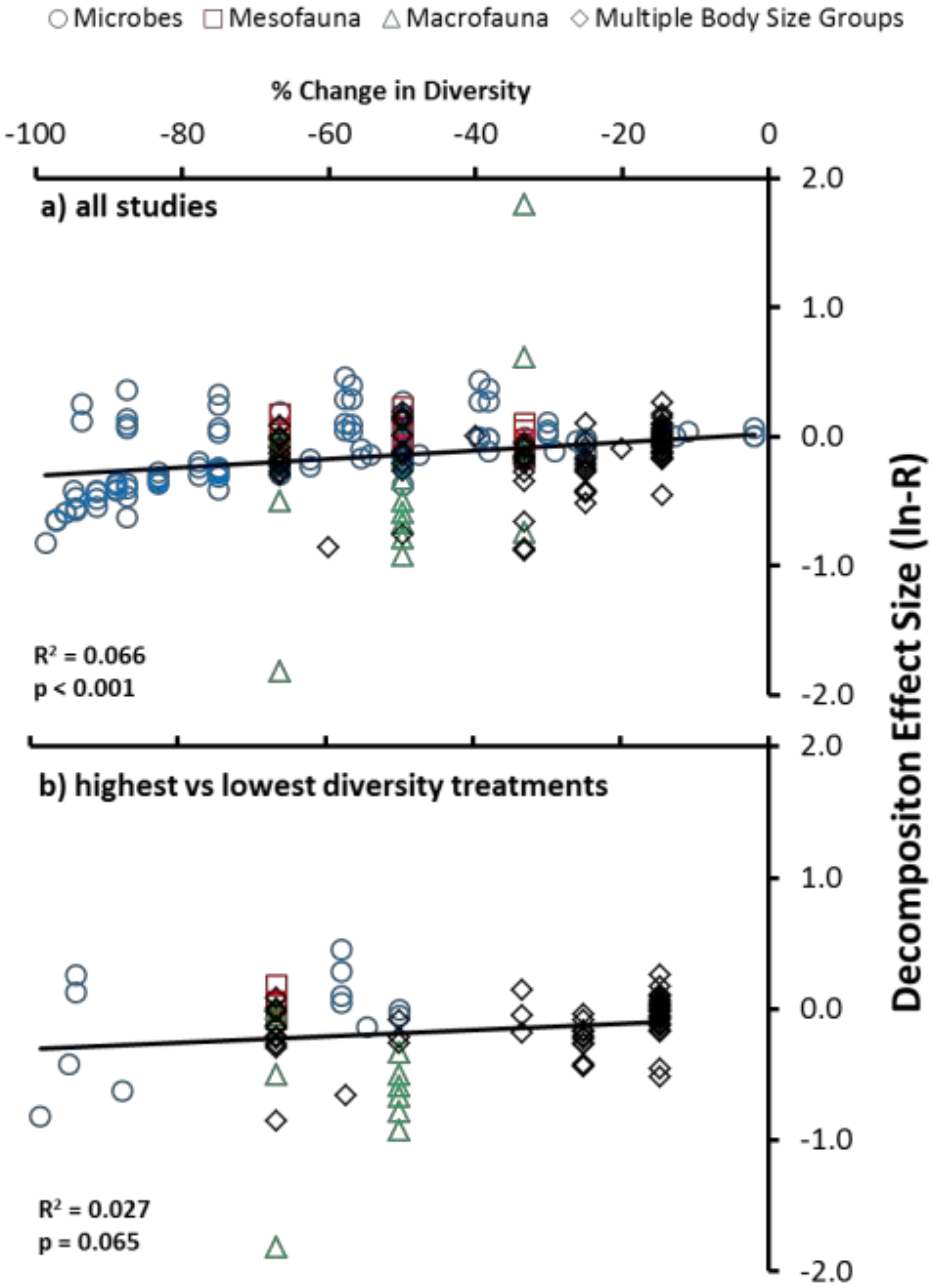
Figs. 5a and b


○ Microbes
□ Mesofauna
△ Macrofauna
◇ Multiple Body Size Groups
% Change in Diversity
-100
-80
-60
-40
-20
0
a) all studies
R² = 0.066
p < 0.001
b) highest vs lowest diversity treatments
R² = 0.027
p = 0.065
2.0
1.0
0.0
-1.0
-2.0
Decompositon Effect Size (ln-R)