

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

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

**M.-A. de Graaff<sup>1</sup>, J. Adkins<sup>1</sup>, P. Kardol<sup>2</sup>, and H. L. Throop<sup>3</sup>**

<sup>1</sup>Department of Biological Sciences, Boise State University, Boise, ID 83725, USA

<sup>2</sup>Department of Forest Ecol. Manag., Swedish University of Agricultural Sciences, 90183, Umeå, Sweden

<sup>3</sup>Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA

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Correspondence to: M.-A. de Graaff (marie-annedegraaff@boisestate.edu)

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## Abstract

Loss of biodiversity can impact ecosystem functioning, such as altering carbon (C) cycling rates. 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<sub>2</sub> 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 biodiversity of soil organisms (microbes and soil fauna) and C cycling. This is despite increasing 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 pool and process variables to changes in biodiversity both within and across trophic groups of organisms. Overall, loss of soil diversity significantly reduced soil C respiration (−27.5%) and plant tissue decomposition (−18%), but did not affect above- and belowground plant biomass. Detailed analyses showed that loss of within-group biodiversity significantly reduced soil C respiration, while loss of across-group diversity did not. Decomposition was negatively affected by losses of both within-group and across-group diversity. Further, 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 can strongly affect soil C cycling processes, and highlight the importance of diversity across organismal groups for maintaining full C cycling functionality. 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.

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These limitations present challenges to extrapolation to natural field settings. Future studies should attempt to further elucidate the relative importance of taxonomic diversity vs. functional diversity.

## 1 Introduction

5 Reductions in biodiversity have been linked with anthropogenic global change drivers such as land cover change, reduction and fragmentation of natural areas (Vitousek and Mooney, 1997; Sanderson et al., 2002; Fischer and Lindenmayer, 2007), and human dependence on synthetic fertilizers (Stevens, 2004; Phoenix et al., 2006; Clark and Tilman, 2008). Over the past few hundred years, human activities have caused  
10 the species extinction rate to increase by as much as 1000 times the background extinction rates typical over the planet's history (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.,  
15 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<sub>2</sub>) concentrations and subsequent global change. Perturbations in terrestrial ecosystems that influence soil C dynamics could help mitigate the current rise in atmospheric CO<sub>2</sub> and associated climate change by promoting soil C storage (e.g., Cramer et al., 2001;  
20 Johnson and Curtis, 2001). Alternatively, they could exacerbate climate change by causing increased soil CO<sub>2</sub> efflux rates through increased decomposition rates of soil organic C (SOC) (e.g., Mack et al., 2004; Bardgett et al., 2008).

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Loss of biodiversity has the potential to influence climate change if it alters SOC pools, by reducing ecosystem C uptake or by increasing CO<sub>2</sub> 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 and 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 impacts global C cycling processes.

Soil communities are highly diverse, with 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 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. 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 and Van der Putten, 2005; Fitter et al., 2005; Wall et al., 2010). 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. For example, studies have manipulated the diversity within organismal groups for 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), or macrofauna (Heemsbergen et al., 2004; Zimmer et al., 2005). Other studies have manipulated the diversity of soil organisms across multiple organismal groups, or, alternatively, have manipulated the number of organism groups (e.g., trophic group diversity; Hedlund and Ohn, 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 greater than when a more complex food web of organisms is manipulated (i.e. across organismal groups of different size classes, or feeding guilds) (Setälä, 2002). Thus, studies assessing biodiversity impacts

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on ecosystem processes across multiple organismal groups 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 increased diversity is often correlated with increased ecosystem functions (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 soil biodiversity may not necessarily impact the C cycle.

Using meta-analysis, we aimed to quantitatively assess how soil biodiversity affects soil C cycling pools and processes. We tested the general hypothesis that soil biodiversity positively influences soil C pools and processes rates, while reductions in diversity decrease soil C pools and process rates. 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). 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.

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## 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 pools and/or processes. Biogeochemical pool measurements were plant biomass and soil C pools (in some cases this was measured as total soil C, but in others it was measured as dissolved organic C (DOC), or as 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).

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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, and 25 examined effects on decomposition (Table 1). All soil C pool data were derived from laboratory microcosms. 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, generally 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<sub>2</sub> 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 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



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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). We also categorized the studies by organismal groups: 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 organismal groups affected C cycling differently, while also enabling us to compare the relative impacts of diversity within the soil microbial community vs. soil biodiversity within the soil faunal community.

Many of the studies we compiled assessed soil biodiversity impacts on C cycling by assessing 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*” vs. “*a* + *b* + *c*”, (2) “*b*” vs. “*a* + *b* + *c*”, and (3) “*c*” vs. “*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 organismal groups affected C cycling differently from manipulations within a single organismal group, 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 natural log of the response ratio, “ $r$ ”, was used as a metric for all of the response variables (Eq. 1).

$$r = \left( \left( \frac{\text{response at high diversity}}{\text{response at low diversity}} \right) - 1 \right) \times 100 \quad (1)$$

Thus, for response variables where there was no change between higher and lower diversity communities,  $r$  would equal 0. For cases with greater values for response variables in high diversity communities than low diversity communities  $r$  would be positive, and lower values for response variables in high diversity communities than low diversity communities would yield negative values for  $r$ .

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 response ratios 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 response ratio of each of the response variables. Since the absolute

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number of species typically manipulated for diversity gradient studies varies among organismal groups 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 the response ratio against relative change in species diversity. We performed regressions in which we considered the response ratios between every diversity level, and also regressions in which we only considered the response ratios 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 organismal groups) corresponded to a mean 27.5% reduction in soil C respiration (Fig. 2) and a mean 18% reduction in decomposition (Fig. 3).

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When soil C respiration responses were partitioned into studies that manipulated diversity within organismal groups vs. those that manipulated diversity across organismal groups, we found a significant effect only for within organismal 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 vs. 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 the soil microbial community on soil C respiration alone, 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 species loss and C cycling processes

Regression analyses revealed that a decline in soil biodiversity significantly reduced soil C respiration rates (Fig. 4). This relationship was significant when we regressed the percent change in soil biodiversity and the C respiration response ratios based on all diversity treatments in the compiled studies (Fig. 4a), and when we calculated the response ratios for the highest and lowest diversity treatments only (Fig. 4b). We further examined how a decline in diversity within organismal groups (microorganisms, microfauna, mesofauna, or macrofauna) was related to soil C respiration. 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).

Regression analysis also revealed a significant response in decomposition to altered biodiversity when all studies were included, but not when only the highest and lowest diversity treatments were included (Fig. 5a and b). Reduced





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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 and 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; van Ruijven and Berendse, 2005; van der Heijden et al., 2003; Casper and Jackson, 1997; Schenk et al., 1999; Tilman et al., 1996). 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 (Sechi et al., 2014; Prosser and Nicol, 2012), 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

5 Results from the 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  
10 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  
15 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  
20 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  
25 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

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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. As such a loss of soil biodiversity may not impact the C cycle to the extent suggested by our analysis.

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 earthworm-mediated changes in the abundance of other organisms, such as microbes (Szlavec 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 a greater number of studies that manipulates soil fauna is 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, and manipulation of soil faunal biodiversity on plant tissue decomposition was significant ( $-37\%$ ). The significant impact of soil faunal manipulations on litter decomposition may be due to the strong direct effect on litter decomposition by

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soil fauna, particularly in the early stages of decomposition (Heemsbergen et al., 2004; Berg and Laskowski, 2006; Milcu and 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.

We hypothesized that diversity across multiple organismal groups would impact soil C cycling processes to a greater extent than diversity within organismal groups, with the assumption that within organismal 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 and Huhta, 1991). Our analysis, however, suggests that diversity across multiple organismal groups has similar impacts on soil C cycling to diversity within organismal 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-group approach and the across-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. Remarkably, 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

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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 organisms is fraught with challenges, manipulation of soil organisms 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 organismal group with studies that manipulated biodiversity across multiple organismal groups. Across-group manipulations approach the natural complexity of soil food webs to a much larger 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 an innovative 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 organismal groups 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. 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

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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 changes in the relative abundance of organisms is an important component of biodiversity and studies in our compilation typically equated species richness with diversity.

## 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 settings. 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) vs. functional diversity. Effects of loss of soil biodiversity on ecosystem C

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cycling should depend on the degree of functional dissimilarity of the organisms involved (Heemsbergen et al., 2004). Hence, unravelling the level of variation in functional traits among soil organisms, both within and across feeding groups, should be a future research priority.

5 *Author contributions.* All authors contributed to conceiving the idea, compilation of the data and preparation of the manuscript. Analyses were performed by M.-A. de Graaff and J. Adkins.

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**Table 1.** Overview of studies used in the analyses.

| Response variable                              | Organismal group                               | Size class                 | Taxonomic group   | Number of studies     | Reference   |
|--|--|----------------------------|---|-----------------------|---|
| Total plant biomass                            | Microbes                                       | < 5 $\mu\text{m}$          | Ectomycorrhizal fungi   | 1                     | Baxter and Dighton (2001)   |
|  | Mesofauna                                      | 100 $\mu\text{m}$ –2 mm    | Microarthropods   | 2                     | Liiri et al. (2002), Eisenhauer and Schädler (2011)                           |
|  | Microbes + Microfauna                          | < 5–100 $\mu\text{m}$      | Microflora, Nematodes   | 1                     | Bezemer et al. (2005)   |
|  | Microbes + Macrofauna                          | < 5 $\mu\text{m}$ , > 2 mm | Fungi, Earthworms   | 2                     | Eisenhauer et al. (2010), Eisenhauer and Schädler (2011)                      |
|  | Mesofauna + Macrofauna                         | 100 $\mu\text{m}$ –> 2 mm  | Collembola, Enchytraeids, Earthworms                                | 1                     | Eisenhauer and Schädler (2011)  |
|  | Microbes + Microfauna + Mesofauna              | < 5 $\mu\text{m}$ –2 mm    | Bacteria, Fungi, Protozoa, Nematodes, Microarthropods, Enchytraeids | 1                     | Sulkava et al. (2001)   |
| Shoot biomass                                  | Microbes                                       | < 5 $\mu\text{m}$          | Ectomycorrhizal fungi   | 1                     | Baxter and Dighton (2001)   |
|  | Mesofauna                                      | 100 $\mu\text{m}$ –2 mm    | Microarthropods   | 3                     | Liiri et al. (2002), Cole et al. (2004), Eisenhauer and Schädler (2011)       |
|  | Microbes + Macrofauna                          | < 5 $\mu\text{m}$ , > 2 mm | Fungi, Earthworms   | 2                     | Eisenhauer et al. (2010), Eisenhauer and Schädler (2011)                      |
|  | Mesofauna + Macrofauna                         | 100 $\mu\text{m}$ –> 2 mm  | Collembola, Enchytraeids, Earthworms                                | 1                     | Eisenhauer and Schädler (2011)  |
|  | Microbes + Microfauna + Mesofauna              | > 5 $\mu\text{m}$ –2 mm    | Bacteria, Fungi, Protozoa, Nematodes, Microarthropods, Enchytraeids | 1                     | Sulkava et al. (2001)   |
|  | Microbes + Microfauna + Mesofauna              | < 5 $\mu\text{m}$ –2 mm    | Bacteria, Fungi, Protozoa, Microarthropods, Enchytraeids            | 1                     | Laakso and Setälä (1999)  |
|  | Microbes + Microfauna + Mesofauna + Macrofauna | 5 $\mu\text{m}$ –> 2 mm    | Fungi, Nematodes, Enchytraeids, Microarthropods, Wireworms          | 1                     | Ladygina et al. (2010)  |
|  | Root biomass                                   | Microbes                   | < 5 $\mu\text{m}$   | Ectomycorrhizal fungi | 1   |
| Mesofauna                                      |  | 100 $\mu\text{m}$ –2 mm    | Microarthropods   | 3                     | Liiri et al. (2002), Eisenhauer et al. (2011), Eisenhauer and Schädler (2011) |
| Microbes + Macrofauna                          |  | < 5 $\mu\text{m}$ , > 2 mm | Fungi, Earthworms   | 2                     | Eisenhauer et al. (2010), Eisenhauer and Schädler (2011)                      |
| Mesofauna + Macrofauna                         |  | 100 $\mu\text{m}$ –> 2 mm  | Collembola, Enchytraeids, Earthworms                                | 1                     | Eisenhauer and Schädler (2011)  |
| Microbes + Microfauna + Mesofauna              |  | < 5 $\mu\text{m}$ –2 mm    | Bacteria, Fungi, Protozoa, Nematodes, Microarthropods, Enchytraeids | 1                     | Sulkava et al. (2001)   |
| Microbes + Microfauna + Mesofauna + Macrofauna |  | 5 $\mu\text{m}$ –> 2 mm    | Fungi, Nematodes, Enchytraeids, Microarthropods, Wireworms          | 1                     | Ladygina et al. (2010)  |

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**Table 1. Continued.**

| Response variable | Organismal group                               | Size class          | Taxonomic group   | Number of studies | Reference  |                           |
|-------------------|--|---------------------|---|-------------------|--|---------------------------|
| Respiration       | Microbes                                       | < 5 µm              | Bacteria  | 1                 | Wertz et al. (2006)  |                           |
|                   | Microbes                                       | < 5 µm              | Bacteria, Fungi   | 3                 | Griffiths et al. (2000, 2001, 2004)  |                           |
|                   | Microbes                                       | < 5 µm              | Fungi   | 5                 | Wilkinson et al. (2010, 2011, 2012), Tiunov and Scheu (2005), Setälä and McLean (2004) |                           |
|                   | Macrofauna                                     | > 2 mm              | Earthworms  | 1                 | Scheu et al. (2002)  |                           |
|                   | Microbes + Mesofauna                           | < 5 µm, 100 µm–2 mm | Microflora, Enchytraeids, Microarthropods                             | 1                 | Edsberg (2000)   |                           |
|                   | Mesofauna + Macrofauna                         | 100 µm–> 2 mm       | Not specified   | 1                 | Risch et al. (2013)  |                           |
|                   | Microfauna + Mesofauna + Macrofauna            | 5 µm–> 2 mm         | Nematodes, Enchytraeids, Earthworms                                   | 1                 | Bradford et al. (2007)   |                           |
| Decomposition     | Microbes                                       | > 5 µm              | Bacteria  | 1                 | Bell et al. (2005)   |                           |
|                   | Microbes                                       | < 5 µm              | Fungi   | 3                 | Progar et al. (2000), Toljander et al. (2006), Lebauer et al. (2010)                   |                           |
|                   | Microbes                                       | < 5 µm              | Bacteria, Fungi   | 3                 | Griffiths et al. (2000, 2001), Liebich et al. (2007)                                   |                           |
|                   | Mesofauna                                      | 100 µm–2 mm         | Collembola  | 2                 | Cragg and Bardgett (2001), Eisenhauer and Schädler (2011)                              |                           |
|                   | Macrofauna                                     | > 2 mm              | Woodlice, Millipedes  | 1                 | Collison et al. (2013)   |                           |
|                   | Macrofauna                                     | > 2 mm              | Woodlice, Earthworms  | 1                 | Zimmer et al. (2005)   |                           |
|                   | Microbes + Microfauna                          | < 5 µm–100 µm       | Bacteria, Fungi, Nematodes  | 2                 | Mikola and Setälä (1998a, b)   |                           |
|                   | Microbes + Mesofauna                           | < 5 µm, 100 µm–2 mm | Microflora, Enchytraeids, Microarthropods                             | 1                 | Edsberg (2000)   |                           |
|                   | Microbes + Mesofauna                           | < 5 µm, 100 µm–2 mm | Fungi, Collembola, Mites  | 1                 | Hedlund and Ohrn (2000)  |                           |
|                   | Microbes + Macrofauna                          | < 5 µm, > 2 mm      | Fungi, Ants, Termites   | 1                 | Warren and Bradford (2012)   |                           |
|                   | Microbes + Microfauna + Mesofauna              | < 5 µm–2 mm         | Bacteria, Fungi, Protozoa, Nematodes, Microarthropods, Enchytraeids   | 1                 | Sulkava et al. (2001)  |                           |
|                   | Microbes + Microfauna + Mesofauna              | < 5 µm–2 mm         | Bacteria, Fungi, Nematodes, Protozoa, Collembola, Enchytraeids, Mites | 1                 | Cortet et al. (2003)   |                           |
|                   | Microbes + Microfauna + Mesofauna              | < 5 µm–2 mm         | Not specified   | 2                 | Heneghan et al. (1999), Wall et al. (2008)   |                           |
|                   | Microfauna + Mesofauna + Macrofauna            | 5 µm–> 2mm          | Protozoa, Nematodes, Enchytraeids, Arthropods, Earthworms             | 1                 | Bradford et al. (2002)   |                           |
|                   | Microbes + Microfauna + Mesofauna + Macrofauna | < 5 µm–> 2 mm       | Fungi, Arthropods   | 1                 | Araujo et al. (2012)   |                           |
|                   | Microbes + Microfauna + Mesofauna + Macrofauna | 5 µm–> 2 mm         | Fungi, Bacteria, Protozoa, Nematodes, Microarthropods                 | 1                 | Carrillo et al. (2011)   |                           |
|                   | Microbes + Microfauna + Mesofauna + Macrofauna | < 5 µm–> 2 mm       | Not specified   | 1                 | Slade and Riutta (2012)  |                           |
|                   | Microbes + Microfauna + Mesofauna + Macrofauna | < 5 µm–> 2 mm       | Not specified   | 1                 | Yang and Chen (2009)   |                           |
|                   | Soil C   | Microbes            | < 5 µm  | Bacteria, Fungi   | 1  | Liebich et al. (2007)     |
|                   |  | Mesofauna           | 100 µm–2 mm   | Collembola        | 1  | Cragg and Bardgett (2001) |
| Macrofauna        |  | > 2 mm              | Woodlice, Earthworms  | 1                 | Zimmer et al. (2005)   |                           |

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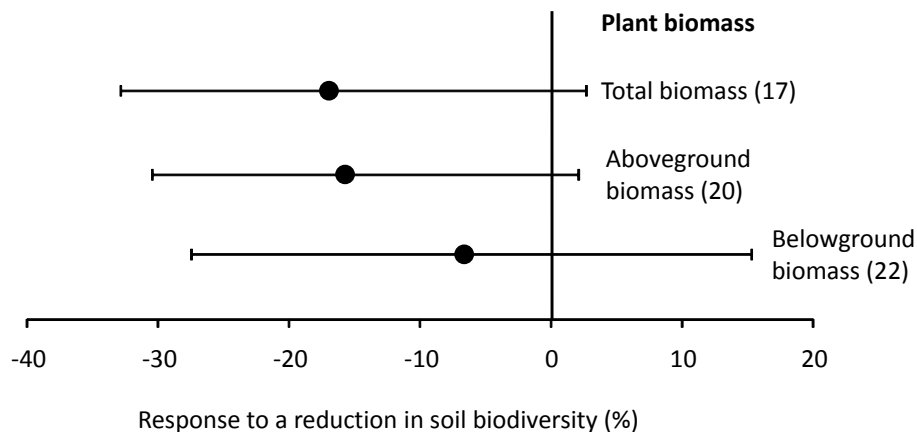
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**Figure 1.** The percent response of total plant biomass, shoot biomass and root biomass to a change in soil biodiversity (i.e., “high” vs. “low” diversity). Studies included in the analysis manipulated diversity of the soil microbial community, the 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.

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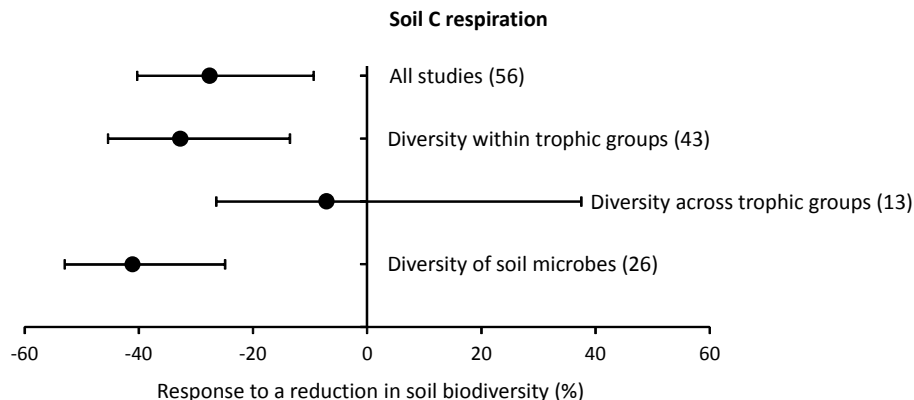
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**Figure 2.** The percent response of soil C respiration to a change in soil biodiversity (i.e., “high” vs. “low” diversity). Studies included in the analysis manipulated diversity of the soil microbial community, the soil micro-, meso, or macrofaunal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

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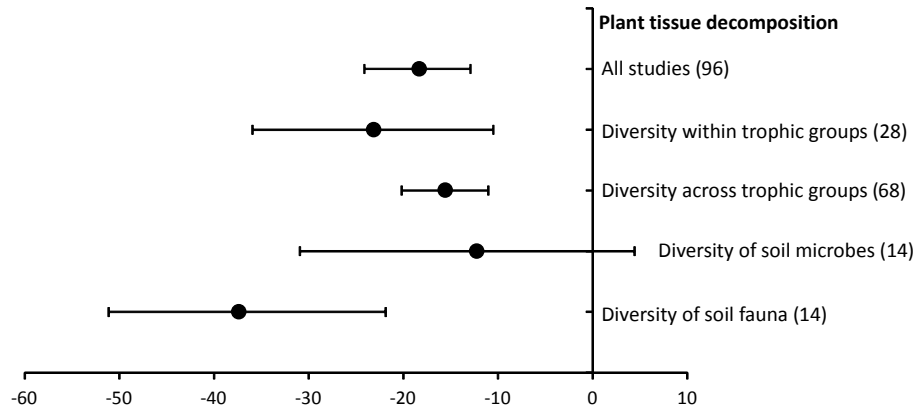
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**Figure 3.** The percent response of plant tissue decomposition to a change in soil biodiversity (i.e., “high” vs. “low” diversity). Studies included in the analysis manipulated diversity of the soil microbial community, the soil micro-, meso, or macrofaunal community or a combination of these trophic groups (“all studies”). Further studies are categorized by studies that manipulated species diversity within or across trophic 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.

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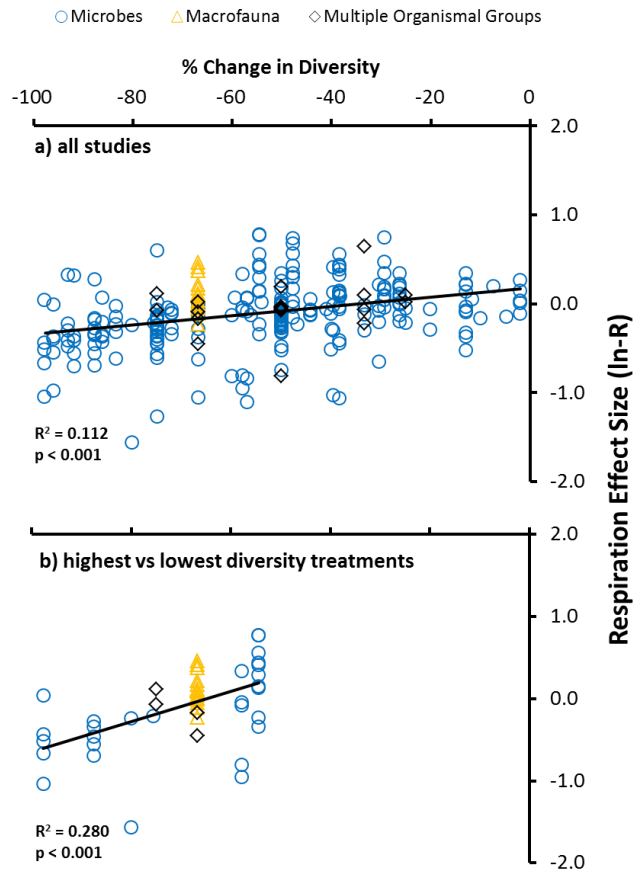
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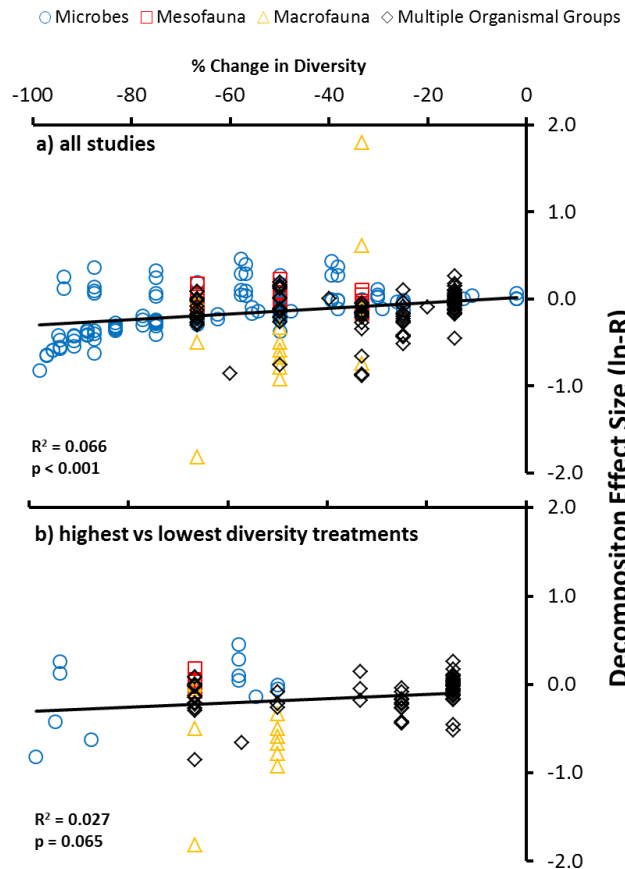
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**Figure 4.** Regressions between a percent change in the soil microbial, soil faunal or soil microbial and soil faunal communities (i.e. multiple organismal groups) and the response ratio of soil C respiration. **(a)** includes all possible comparisons across diversity gradients in studies, whereas **(b)** includes the comparisons between the lowest and highest diversity levels only.



**Figure 5.** Regressions between a percent change in the soil microbial, soil faunal or soil microbial and soil faunal communities (i.e. multiple organismal groups) and the response ratio of litter decomposition. **(a)** includes all possible comparisons across diversity gradients in studies, whereas **(b)** includes the comparisons between the lowest and highest diversity levels only.