SOIL

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

M.-A. de Graaff[1], J. Adkins[1], P. Kardol[3], and H. L. Throop[2]

[1]Department of Biological Sciences, Boise State University, Boise, ID 83725, USA
[2]Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA
[3]Department of Forest Ecol. Manag., Swedish University of Agricultural Sciences, 90183 Umeå, Sweden

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

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, has 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 organisms (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. 1000 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 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 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 straightforward 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 ($100 \, \mu m^{-2}$ mm) such as mites and springtails, microfauna ($< 100 \, \mu m$) 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 and 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 rather "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 the 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; Lady-gina et al., 2010). Although different taxa within soil micro-bial (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 bio-diversity and soil C cycling processes has increased with ex-panding research emphasis in this area, a comprehensive un-derstanding to date is hampered by a lack of quantitative syn-thesis of existing studies. Nielsen et al. (2011) performed the most extensive synthesis on this topic to date, with a quali-tative analysis. They found that diversity is often positively correlated with ecosystem function (e.g., soil respiration), al-though they cautioned that negative relationships between soil biodiversity and C cycling may be related to experimen-tal 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 diver-sity. Further, their synthesis showed that the soil community composition, rather than species richness per se, had signif-icant 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 af-fects soil C cycling pools and processes using meta-analysis. We tested the general hypothesis that soil biodiversity posi-tively 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 ad-dition, we tested whether diversity of soil microbes versus soil fauna (including micro-, meso-, and macrofauna) im-pacts C cycling differently. Finally, since "biodiversity" is a metric that differs greatly in absolute numbers for soil organ-isms 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, respira-tion, or NPP), one soil organism search term (microbes, bac-teria, fungi, microorganism*, soil fauna, soil biota, soil or-ganism*, microfauna, mesofauna, macrofauna, nematode*, collembola, acari, termite*, earthworm*), and the term "*di-versity". We used "*" as a wildcard character such that pa-pers using either singular or plural terms were returned. Ad-ditional relevant studies referenced in those returned by the search engines were also included in the literature compila-tion. While biodiversity sensu stricto includes both species richness and abundance (Magurran, 2005), we follow the re-cent 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 biogeo-chemical 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 rather 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 val-ues from graphical data with image analysis software (Im-ageJ, National Institutes of Health, Bethesda, MD, USA).

In total we analyzed 45 published studies, of which 8 ex-amined the effects of soil biodiversity on total plant biomass, 10 examined effects on aboveground plant biomass, 9 exam-ined effects on root biomass, 13 examined effects on C res-piration, 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 stud-ies in which the substrate was soil only or soil with organic amendments other than plant tissue (e.g., glucose). Labora-tory 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 con-centrations. In situ studies used static or flow-through cham-bers to measure CO_2 flux rates from the soil surface, and thus would include both microbial heterotrophic and root (au-

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	< 5 µm	Ectomycorrhizal fungi	1	Baxter and Dighton (2001)
	Mesofauna	100 µm–2 mm	Microarthropods	2	Liiri et al. (2002), Eisenhauer and Schädler (2011)
	Microbes + microfauna	< 5–100 µm	Microflora, nematodes	1	Bezemer et al. (2005)
	Microbes + macrofauna	< 5 µm, > 2 mm	Fungi, earthworms	2	Eisenhauer et al. (2010), Eisenhauer and Schädler (2011)
	Mesofauna + macrofauna	100 µm–> 2 mm	Collembola, enchytraeids, earthworms	1	Eisenhauer and Schädler (2011)
	Microbes + microfauna + mesofauna	< 5 µm–2 mm	Bacteria, fungi, protozoa, nematodes, microarthropods, enchytraeids	1	Sulkava et al. (2001)
Shoot biomass	Microbes	< 5 µm	Ectomycorrhizal fungi	1	Baxter and Dighton (2001)
	Mesofauna	100 µm–2 mm	Microarthropods	3	Liiri et al. (2002), Cole et al. (2004), Eisenhauer and Schädler (2011)
	Microbes + macrofauna	< 5 µm, > 2 mm	Fungi, earthworms	2	Eisenhauer et al. (2010), Eisenhauer and Schädler (2011)
	Mesofauna + macrofauna	100 µm–> 2 mm	Collembola, enchytraeids, earthworms	1	Eisenhauer and Schädler (2011)
	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, protozoa, microarthropods, enchytraeids	1	Laakso and Setälä (1999)
	Microbes + microfauna + mesofauna + macrofauna	5 µm–> 2 mm	Fungi, nematodes, enchytraeids, microarthropods, wireworms	1	Ladygina et al. (2010)
Root biomass	Microbes	< 5 µm	Ectomycorrhizal fungi	1	Baxter and Dighton (2001)
	Mesofauna	100 µm–2 mm	Microarthropods	3	Liiri et al. (2002), Eisenhauer et al. (2011), Eisenhauer and Schädler (2011)
	Microbes + macrofauna	< 5 µm, > 2 mm	Fungi, earthworms	2	Eisenhauer et al. (2010), Eisenhauer and Schädler (2011)
	Mesofauna + macrofauna	100 µm–> 2 mm	Collembola, enchytraeids, earthworms	1	Eisenhauer and Schädler (2011)
	Microbes + microfauna + mesofauna	< 5 µm–2 mm	Bacteria, fungi, protozoa, nematodes, microarthropods, enchytraeids	1	Sulkava et al. (2001)
	Microbes + microfauna + mesofauna + macrofauna	5 µm–> 2 mm	Fungi, nematodes, enchytraeids, microarthropods, wireworms	1	Ladygina et al. (2010)
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–> 2 mm	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)

totrophic) 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 ($\ln R$) was used as a metric for all of the response variables (de Graaff et al., 2006; van Groenigen et al., 2006). To ease interpretation of figures, the results for the analyses on $\ln R$ were back-transformed to response ratios and reported as percentage change under a reduction in diversity (that is, $100 \times [R - 1]$). 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 be 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, 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 ($\ln R$) of each of the response variables. Percent change in diversity was calculated as (low diversity – high diversity/high diversity) $\times 100$. Since the absolute number of species typically manipulated for diversity gradient studies varies among species that differ in body size
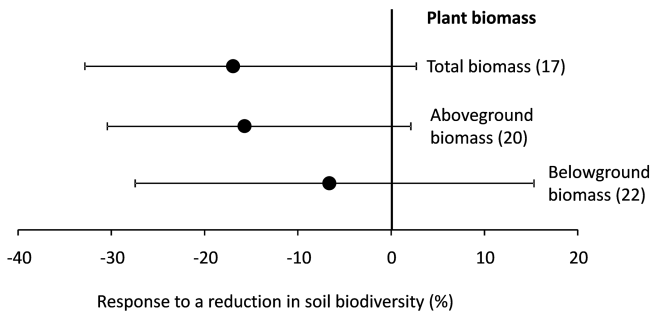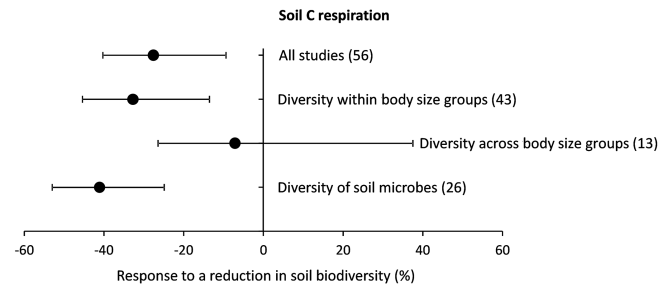
Figure 1. The percent response of total plant biomass, shoot biomass, and root biomass to a change in soil community diversity (i.e., "high" vs. "low" diversity). Studies included in the analysis manipulated diversity of the soil microbial community, the soil micro-, meso, or macrofaunal community or 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.

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 $\ln R$ against relative change in species diversity. We performed regressions in which we considered $\ln R$ (the effect size) between every diversity level, and also regressions in which we only considered $\ln R$ 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

Figure 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.
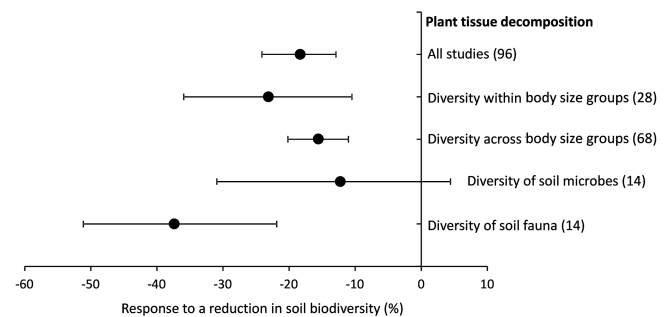
Figure 3. The percent response of decomposition to a change in soil community diversity (i.e., "high" vs. "low" diversity). Studies included in the analysis manipulated diversity of the soil microbial community; the soil micro-, meso, or macrofaunal community; or a combination of these trophic groups ("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.

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 $\ln R$ for soil C respiration (Fig. 4). This relationship was significant when we regressed the percent change in soil biodiversity and $\ln R$ for C respiration based on all diversity treatments in the compiled studies (Fig. 4a) and also when we calculated $\ln R$ 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. 5b). 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. Us-
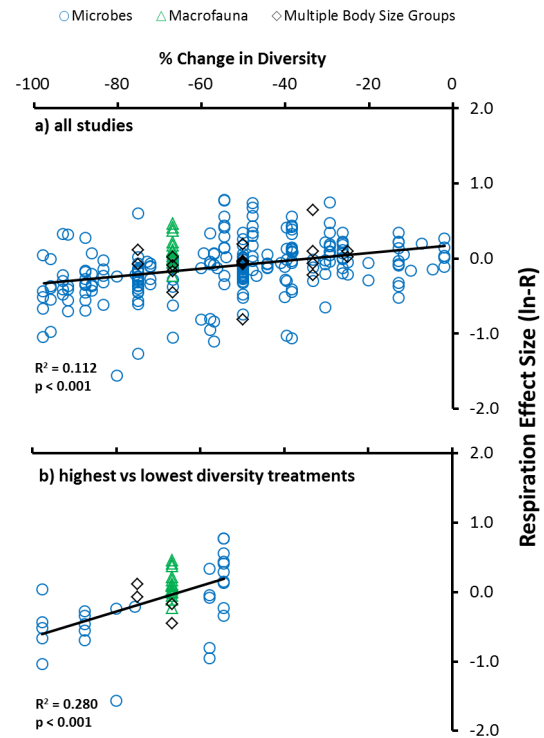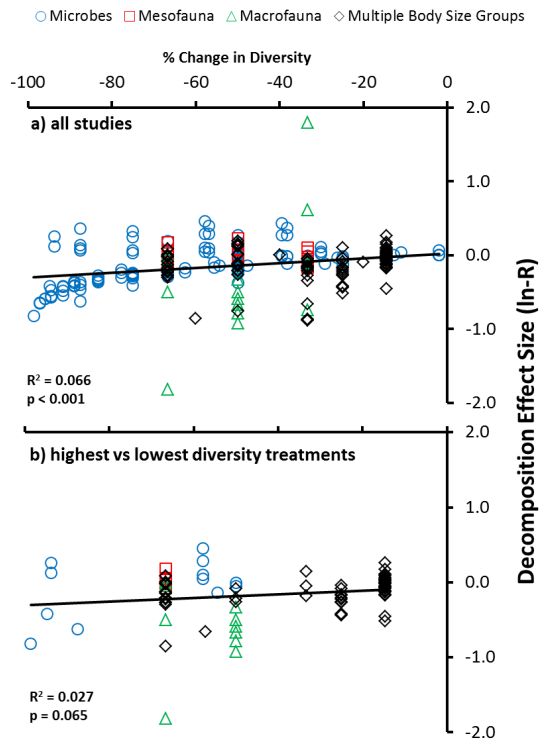

Figure 4. Regressions between a percent change in the soil microbial, soil macrofaunal, or soil microbial and soil faunal communities (i.e., multiple organismal groups) and the natural log of the response ratio of soil C respiration ($\ln R$; calculated as the natural log of the response ratio, R, which 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 respiration included manipulation of only soil microfauna or mesofauna, so these body size groups are not included in the figure. Percent change in diversity was calculated as (low diversity – high diversity/high diversity) $\times 100$. **(a)** includes all possible comparisons across diversity gradients in studies, whereas **(b)** includes the comparisons between the lowest and highest diversity levels only.

ing 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 shortcomings and 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

Figure 5. 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 ($\ln R$; 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 manipulation only of soil microfauna, so this body size group is not included in the figure. Percent change in diversity was calculated as (low diversity – high diversity/high diversity) ×100. **(a)** includes all possible comparisons across diversity gradients in studies, whereas **(b)** includes the comparisons between the lowest and highest diversity levels only.

and Bardgett, 2001); and soil organic C concentration (Zimmer et al., 2005). All three studies were of short duration (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 (Eisenhauer and Schädler, 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; Eisenhauer et al., 2010; Eisenhauer and Schädler, 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 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 re-

sulting 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., 2015), 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., 2011a, b). 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 worthy of mention here 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 the response of C respiration to an increase in biodiversity leveled off (Bell et al., 2005) with increasing species number, 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 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. This notion is supported by a recent article showing that a reduction in the diversity of detritivores (both microorganisms and invertebrates) 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 and 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-" 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 have 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 collembola) canceled 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 manip-

ulated 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 for 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 anthropogenically 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 a 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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