

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

3

4 **Marie-Anne de Graaff¹, Jaron Adkins¹, Paul Kardol³, Heather L. Throop²**

5

6 [1] {Department of Biological Sciences, Boise State University, Boise, ID 83725, USA}

7 [2] {Department of Biology, New Mexico State University, Las Cruces, NM 88003, USA}

8 [3] {Department of Forest Ecol. Manag., Swedish University of Agricultural Sciences, 90183,
9 Umeå, Sweden}

10 Correspondence: Marie-Anne de Graaff

11 Department of Biological Sciences

12 Boise State University

13 1910 University Drive

14 Boise ID, 83725-1515

15 marie-annedegraaff@boisestate.edu

16

17

18 **Abstract**

19 Loss of biodiversity impacts ecosystem functions, such as carbon (C) cycling. Soils are the
20 largest terrestrial C reservoir, containing more C globally than the biotic and atmospheric pools
21 together. As such, soil C cycling, and the processes controlling it, have the potential to affect
22 atmospheric CO₂ concentrations and subsequent climate change. Despite the growing evidence of
23 links between plant diversity and soil C cycling, there is a dearth of information on whether
24 similar relationships exist between soil biodiversity and C cycling. This knowledge gap occurs
25 even though there has been increased recognition that soil communities display high levels of
26 both taxonomic and functional diversity and are key drivers of fluxes of C between the
27 atmosphere and terrestrial ecosystems. Here, we used meta-analysis and regression analysis to
28 quantitatively assess how soil biodiversity affects soil C cycling pools and processes (i.e., soil C
29 respiration, litter decomposition, and plant biomass). We compared the response of process
30 variables to changes in diversity both within and across groups of soil organisms that differed in
31 body size, a grouping that typically correlates with ecological function. When studies that
32 manipulated both within- and across-body size group diversity were included in the meta-
33 analysis, loss of diversity significantly reduced soil C respiration (-27.5%) and plant tissue
34 decomposition (-18%) but did not affect above- or belowground plant biomass. The loss of
35 within-group diversity significantly reduced soil C respiration, while loss of across-group
36 diversity did not. Decomposition was negatively affected both by loss of within-group and
37 across-group diversity. Furthermore, loss of microbial diversity strongly reduced soil C
38 respiration (-41%). In contrast, plant tissue decomposition was negatively affected by loss of soil
39 faunal diversity, but was unaffected by loss of microbial diversity. Taken together, our findings
40 show that loss of soil biodiversity strongly impacts on soil C cycling processes, and highlight the
41 importance of diversity across groups of organisms (e.g., primary consumers and secondary
42 decomposers) for maintaining full functionality of C cycle processes. However, our
43 understanding of the complex relationships between soil biodiversity and C cycling processes is
44 currently limited by the sheer number of methodological concerns associated with these studies,
45 which can greatly overestimate or underestimate the impact of soil biodiversity on soil C cycling,
46 challenging extrapolation to natural field settings. Future studies should attempt to further

47 elucidate the relative importance of taxonomic diversity (species numbers) *versus* functional
48 diversity.
49

50 **1 Introduction**

51 Reductions in biodiversity have been linked with anthropogenic global change drivers such as
52 climatic change, land cover change, reduction and fragmentation of natural areas, and human
53 dependence on synthetic fertilizers (Vitousek and Mooney, 1997; Sanderson et al., 2002; Stevens,
54 2004; Phoenix et al., 2006; Fischer and Lindenmayer, 2007; Clark and Tilman, 2008). Over the
55 past few hundred years, human activities have driven the species extinction rate to ca. 1,000 times
56 the typical background extinction rate (MEA, 2006). This global decline in biodiversity impacts
57 important ecosystem functions, such as net primary production (NPP) and biogeochemical cycles
58 of carbon (C) and nutrients, threatening the services that ecosystems provide to the human
59 population (Wardle et al., 2011; Cardinale et al., 2012).

60 The C cycle is a particularly important ecosystem service because the dynamic balance between
61 C stored in ecosystems and in the atmosphere plays a key regulatory role in the global climate.
62 Although vegetation stores a significant amount of C, soils are the largest terrestrial C reservoir,
63 containing more C globally than the biotic and atmospheric pools combined (Lal, 2004). As such,
64 soil C dynamics, and the processes that influence them, have the potential to impact atmospheric
65 carbon dioxide (CO₂) concentrations and subsequent global change. Perturbations in terrestrial
66 ecosystems that influence soil C dynamics could help mitigate the current rise in atmospheric
67 CO₂ and associated climate change by promoting soil C storage (e.g., Cramer et al., 2001;
68 Johnson and Curtis, 2001). Alternatively, they could exacerbate climate change by causing
69 increased soil CO₂ efflux rates through increased decomposition rates of soil organic C (SOC)
70 (e.g., Mack et al., 2004; Bardgett et al., 2008).

71 Loss of biodiversity has the potential to influence climate change if it alters SOC pools by
72 reducing ecosystem C uptake or by increasing CO₂ outputs from terrestrial ecosystems to the
73 atmosphere (Jastrow et al., 2007). Greater plant species diversity can increase C uptake by
74 promoting biomass production (Tilman et al., 2006; Cardinale et al., 2012), which can enhance
75 SOC storage (Fornara & Tilman, 2008; Steinbeiss et al., 2008; Cong et al., 2014). Conversely,
76 declines in plant species diversity can reduce SOC storage (Hooper et al., 2012). Despite the
77 growing body of evidence suggesting strong links between plant species diversity and soil C
78 cycling, there is a dearth of information on whether similar relationships exist between
79 biodiversity of soil organisms (hereafter ‘soil biodiversity’) and C cycling (Nielsen et al. 2011).

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

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

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

110 case of functional redundancy among soil organisms (Bengtsson, 1998; Andrén and Balandreau,
111 1999; Setälä et al., 2005).

112 To date, studies have assessed soil community diversity impacts on soil C cycling by
113 manipulating diversity within or across multiple organismal groups (specifics of grouping criteria
114 differ among studies, but are often taxonomic, functional, or body size groups). For example,
115 studies have manipulated the diversity within groups of microorganisms [(e.g., bacteria,
116 Bonkowski and Roy, 2005; Griffiths et al., 2000) and mycorrhizal fungi (van der Heijden et al.,
117 1998; Maherali and Klironomos, 2007)], soil mesofauna (e.g., microarthropods, Liiri et al., 2002),
118 and macrofauna (Heemsbergen et al., 2004; Zimmer et al., 2005). Other studies have manipulated
119 the diversity across groups of soil organisms that differ in body size (i.e., microbes, and micro-
120 meso- or macrofauna), or, alternatively, have manipulated diversity of trophic or functional
121 groups (Hedlund and Ohrn, 2000; Ladygina et al., 2010). Although different taxa within soil
122 microbial (Cox et al., 2001; Hanson et al., 2008; Orwin et al., 2006) or faunal (Bignell and
123 Eggleton, 2000; Milcu et al., 2008; Heemsbergen et al., 2004) groups can have unique impacts on
124 the C cycle, functional redundancy among taxa would be expected to be reduced when a more
125 complex food web of organisms is manipulated (e.g., across different size classes or feeding
126 guilds) (Setälä, 2002). Thus, studies assessing biodiversity impacts on ecosystem processes
127 across multiple groups of soil organisms may yield very different answers than studies that probe
128 for biodiversity impacts within single groups.

129 Although our knowledge of relationships between soil biodiversity and soil C cycling processes
130 has increased with expanding research emphasis in this area, a comprehensive understanding to
131 date is hampered by a lack of quantitative synthesis of existing studies. Nielsen et al. (2011)
132 performed the most extensive synthesis on this topic to date, with a qualitative analysis. They
133 found that diversity is often positively correlated with ecosystem function (e.g., soil respiration),
134 although they cautioned that negative relationships between soil biodiversity and C cycling may
135 be related to experimental limitations. In particular, Nielsen et al. (2011) found that strong
136 relationships between soil biodiversity and C cycling were most common under unrealistically
137 low levels of diversity. Further, their synthesis showed that the soil community composition,
138 rather than species richness *per se*, had significant impacts on C cycling processes. This indicates

139 high levels of functional redundancy among soil organisms and suggests that a loss of soil
140 biodiversity may not necessarily impact the C cycle.

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

152

153 **2 Methods**

154 **2.1 Data compilation**

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

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

177 In total we analyzed 45 published studies, of which 8 examined the effects of soil biodiversity on
178 total plant biomass, 10 examined effects on aboveground plant biomass, 9 examined effects on
179 root biomass, 13 examined effects on C respiration, 25 examined effects on decomposition, and 3
180 used laboratory microcosms to examine effects on soil C pools (Table 1). For soil C respiration,
181 we included data that were obtained from either laboratory or *in situ* incubation studies in which
182 the substrate was soil only or soil with organic amendments other than plant tissue (e.g., glucose).
183 Laboratory studies typically estimated potential C mineralization rates, using temperature and
184 moisture conditions assumed to be optimal for microbial activity. These measurements were
185 made in closed microcosms with flux rates estimated from two or more repeated measurements of
186 headspace gas concentrations. *In situ* studies used static or flow-through chambers to measure
187 CO₂ flux rates from the soil surface, and thus would include both microbial heterotrophic and
188 root (autotrophic) respiration (Holland et al., 1999). Plant tissue decomposition data were
189 obtained from studies that measured either litter mass loss through time or C respiration from
190 plant tissues decomposed under controlled laboratory conditions. Litter mass loss analyses used
191 mesh litterbags and measured mass at two or more points in time (Harmon et al., 1999). For
192 studies in which the source of decomposed material (i.e., soil or plant C) could be partitioned,
193 data were separated and included in soil C respiration or plant tissue decomposition data
194 groupings. For all biogeochemical pool and process studies in which data were available from
195 multiple measurement times, we calculated the mean value for all measurement times and used
196 only that value in the meta-analysis.

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

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

221 **2.2 Statistical analyses**

222 To test how soil microbial and/or soil faunal diversity affects ecosystem C pools (plant biomass)
223 and processes (C respiration and decomposition), and to test whether biodiversity manipulations
224 across multiple body size groups affected C cycling differently from manipulations within
225 groups, we analyzed the data set with meta-analysis (Curtis and Wang, 1998; Hungate et al.,

226 2009), using the statistical software MetaWin 2.0 (Rosenberg et al., 2000). We were unable to use
227 meta-analysis for soil C pools because the number of studies available (3) was inadequate for a
228 meaningful analysis. The response ratio (R) was calculated as the value of a particular response
229 variable at low diversity divided by the value at high diversity. The natural log of the response
230 ratio R (lnR) was used as a metric for all of the response variables (de Graaff et al., 2006; van
231 Groenigen et al., 2006). To ease interpretation of figures, the results for the analyses on lnR were
232 back-transformed to response ratios and reported as percentage change under a reduction in
233 diversity (that is, $100 \times [R-1]$). Thus, for response variables where there was no change between
234 higher and lower diversity communities the change would equal 0. For cases with greater values
235 for response variables in low diversity communities than high diversity communities the percent
236 change would be positive, and lower values for response variables in low diversity
237 communities than high diversity communities would yield negative values for the percent change.

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

250 Further, we tested how a loss of belowground species diversity is linked to changes in C pools
251 and processes by performing linear regressions with percent change in species diversity and the
252 effect size (lnR) of each of the response variables. Percent change in diversity was calculated as
253 $(\text{low diversity} - \text{high diversity})/\text{high diversity} \times 100$. Since the absolute number of species
254 typically manipulated for diversity gradient studies varies among species that differ in body size
255 in absolute terms (i.e. many more species are usually present in studies of microbial diversity than

256 in studies of faunal diversity), we calculated relative differences in species diversity for each
257 treatment. Thus manipulation of microbial diversity might include a low diversity treatment of
258 100 versus a high diversity treatment of 1000 species, while manipulation of soil fauna might
259 span from low diversity of 1 species to high diversity of 10 species. Calculated as relative
260 differences in diversity, both examples would be the same (i.e., low diversity is 10% of the
261 number of species present in high diversity). We performed two sets of regressions. The first
262 included all soil biodiversity levels, and the second included the highest and lowest biodiversity
263 levels only. We used linear regression (SPSS v. 20) to regress lnR against relative change in
264 species diversity. We performed regressions in which we considered lnR (the effect size) between
265 every diversity level, and also regressions in which we only considered lnR between the highest
266 and lowest diversity levels, omitting intermediate diversity levels.

267

268 **3 Results**

269 **3.1 Impacts of soil biodiversity on ecosystem C pools and processes**

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

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

284 analysis and assessed impacts of reductions in soil microbial biodiversity alone on soil C
285 respiration, we found that soil C respiration was reduced by 41% (Fig. 2).

286 Plant tissue decomposition generally responded negatively to reductions in soil biodiversity (Fig.
287 3). Studies that manipulated diversity within soil organismal groups and those that manipulated
288 diversity across organismal groups both led to similar reductions in decomposition (means of
289 23% and 15%, respectively; Fig. 3). Further, whereas reduced soil microbial diversity did not
290 significantly reduce decomposition rates, reduced soil faunal diversity led to a 37% reduction in
291 mean decomposition (Fig. 3).

292 **3.2 Relationships between diversity loss and C cycling processes**

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

305 Regression analysis also revealed a significant response in decomposition to altered biodiversity
306 when all studies were included (Fig. 5a), but not when only the highest and lowest diversity
307 treatments were included (Fig. 5 b). Reductions in biodiversity did not significantly affect
308 decomposition in studies that measured litter mass loss. Conversely, when decomposition was
309 measured via CO₂ efflux, there was a significant relationship between decomposition and
310 biodiversity change when all diversity treatments were included in the analysis ($R^2=0.307$,
311 $p<0.001$; data not shown).

312

313 **4 Discussion**

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

324 **4.1 Biodiversity impacts on C pools**

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

342 biodiversity impacts. Even more likely to provide information on soil biodiversity impacts on soil
343 C cycling are studies assessing diversity effects on short-term C fluxes.

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

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

372 & Tilman, 2008; Steinbeiss et al., 2008), and these benefits of aboveground biodiversity on
373 ecosystem functions are often attributed to increases in plant nutrient uptake resulting from
374 belowground spatial and temporal differentiation in resource use (e.g., McKane et al., 1990;
375 Tilman et al., 1996; Casper and Jackson, 1997; Schenk et al., 1999; van Ruijven and Berendse,
376 2005; van der Heijden et al., 2003). As such, a single limiting resource (e.g., soil N) may be
377 spatially partitioned among co-occurring plant species, which reduces inter-specific competition
378 and thereby facilitates coexistence (McKane et al., 1990). It is reasonable to expect that similar
379 mechanisms occur for soil organisms (Prosser and Nicol, 2012; Sechi et al., 2014), and effects of
380 plant and soil organism diversity on ecosystem functions may not be independent of each other,
381 as increased plant diversity may be accompanied by increased soil biodiversity (Scherber et al.
382 2010, Eisenhauer et al. 2011). If this is the case, soil biodiversity could explain, at least in part,
383 the observed positive relationship between plant diversity and ecosystem C pools and processes.
384 It is noteworthy here to mention that soil fungal pathogens have been found an important driver
385 of observed positive relationships between plant diversity and productivity (Maron et al., 2011).

386 **4.2 Soil biodiversity impacts on soil C processes**

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

401 McLean (2004) used 43 taxa of saprophytic fungi, a large number relative to most manipulative
402 experiments, but a small number relative to the estimated number of fungi in natural soils. In
403 addition, the majority of the studies were conducted under highly controlled and short-term
404 laboratory conditions. Some studies used fumigation or dilution methods to alter soil microbial
405 diversity (Griffiths et al., 2000; 2001; 2004; Wertz et al., 2006), and although it appears that
406 microbial diversity decreases with increased dilution or fumigation, the main impacts of these
407 treatments may be on the community structure by favoring taxa that physiologically withstand the
408 pressures of dilution or fumigation. Studies using this technique showed that with increasing
409 species number, the response of C respiration to an increase in biodiversity leveled off (Bell et al.,
410 2005), and that responses to these treatments are often idiosyncratic, which suggests that they are
411 driven by the soil microbial community structure, rather than by diversity. Thus, although our
412 synthesis indicates that the response of soil C respiration to a reduction in soil biodiversity can be
413 significant, we contend that the response may be an overestimation of what would happen in soils
414 with natural communities.

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

426 Results from the meta-analysis and the regression analysis show that loss of soil biodiversity
427 significantly reduces plant tissue decomposition (-18%). Unlike the other response variables, soil
428 biodiversity impacts on plant tissue decomposition were not dominated by studies that
429 manipulated the soil microbial community. Rather, ca. 84% of decomposition studies in our
430 compilation manipulated soil fauna or multiple groups of soil organisms; soil faunal biodiversity

431 effects on plant tissue decomposition were significant (-37%). The significant impact of soil
432 faunal manipulations on litter decomposition may be due to the strong direct effect of soil fauna
433 on litter decomposition, particularly in the early stages of decomposition (Heemsbergen et al.,
434 2004; Berg & Laskowski, 2006; Milcu & Manning, 2011). By contrast, soil microbial diversity
435 reductions alone did not significantly suppress decomposition rates. This finding is despite
436 individual observations that the diversity of litter-associated microbes increases as decomposition
437 proceeds (e.g., Dilly et al. 2004). Nonetheless, based on our observation that soil faunal diversity
438 has a strong impact on plant tissue decomposition, we propose that diversity of the soil
439 community, and particularly soil faunal diversity, is an important factor driving rates of litter
440 decomposition. This notion is supported by a recent article showing that a reduction in the
441 diversity of detritivores (both microorganisms and invertebrates) slows the rate at which litter is
442 decomposed, regardless of the location of the experiment (Handa et al., 2014).

443 We hypothesized that diversity across multiple organismal groups composed of different body
444 sizes would impact soil C cycling processes to a greater extent than diversity within groups of
445 organisms with a single body size, with the assumption that within-group diversity would be
446 accompanied by a greater degree of functional redundancy (Laakso and Setälä, 1999; Wardle,
447 1999; Cragg and Bardgett, 2001). For example, a higher diversity of feeding guilds has been
448 linked to more effective substrate use (Setälä & Huhta, 1991). Our analysis, however, suggests
449 that for plant tissue decomposition diversity across multiple body size groups has similar impacts
450 on soil C cycling to diversity within body size groups. For soil C respiration, the effect of reduced
451 diversity within groups was even stronger than that of smaller diversity across groups. This may
452 result from the approaches taken to assess community impacts on soil C cycling. First, there is a
453 lack of consistency in approaches taken to study effects of soil biodiversity on C cycling, both for
454 the within- and the across- body size group approach. As such, the level of functional diversity
455 between 'high' diversity and 'low' diversity treatments may have varied across studies, and it is
456 unclear whether shifts in functional diversity were greater for across-group manipulations than
457 for within-group manipulations. Except for Heemsbergen et al. (2004), no studies explicitly tested
458 for the functional dissimilarity among the species manipulated. Second, populations of soil
459 organisms at lower trophic levels may show compensatory growth responses to loss of biomass
460 predation by organisms of higher trophic levels (e.g., Ingham et al., 1985), resulting in no net

461 effect of manipulation of trophic diversity on the processes regulated by lower-trophic level soil
462 organisms. Third, effects of functional or trophic groups of organisms may have opposing effects
463 on the C cycling pools and process rates. For example, Ladygina et al. (2010) showed that
464 arbuscular mycorrhizal fungi and decomposer (enchytraeids and collembolan) cancelled each
465 other out in affecting plant community biomass.

466 **4.3 Methodological concerns**

467 While manipulating diversity of any group of organisms is fraught with challenges, manipulation
468 of soil organism diversity is particularly challenging. A more comprehensive assessment of soil
469 diversity impacts on C cycling will require that some of these challenges are addressed. Nielsen
470 et al. (2011) found that the response to a reduction in diversity was greater if diversity levels were
471 low (i.e. < 10 species included in the analysis) and conducted under more controlled experimental
472 conditions, rather than under high diversity (i.e. >10 species included in the analysis) and more
473 natural experimental conditions. Our analysis set out to quantify how the design of the study
474 affected soil C cycling processes, by comparing studies that manipulated soil biodiversity within
475 a single body size group with studies that manipulated biodiversity across multiple groups.
476 Across body size group manipulations approach the natural complexity of soil food webs to a
477 much greater degree than within-group manipulations. However, even the most complex
478 manipulations accounted only for a fraction of the diversity likely under natural field conditions.
479 As such, to further enhance our understanding of soil community diversity impacts on soil C
480 cycling, studies should incorporate more natural conditions in their design and manipulate more
481 complete soil communities. A recent study by Wagg et al. (2014) used a method for manipulating
482 a broad size range of soil organisms by inoculating sterilized soils with soil communities derived
483 through a series of different sized filters. This method allowed the researchers to successfully
484 obtain a broad soil biodiversity gradient within and across groups of soil organism that span a
485 gradient in body sizes in their grassland microcosms, and showed that soil biodiversity loss and
486 simplification of soil community composition impairs multiple ecosystem functions, including
487 litter decomposition and soil C sequestration. However, filtering groups of organisms based on
488 body size does not allow separating between effects of functional dissimilarity from effects of
489 biodiversity (species richness) *per se*. This underscores the pervasive challenge to truly

490 measuring biodiversity effects on ecosystem processes. A parallel concern is that soil biodiversity
491 typically cuts across multiple trophic groups (e.g., manipulation of nematodes would potentially
492 alter both herbivores and predators in the soil). Aboveground diversity-ecosystem function
493 studies have typically been limited to the primary producer trophic level, but results may yield
494 very different relationships if consumer trophic levels are included in diversity manipulations
495 (Borer et al., 2014). Finally, we caution that measuring soil biodiversity is exceedingly difficult,
496 and in many cases treatments were assumed to affect biodiversity for the duration of the
497 experiment, but this was often not measured. It is also possible that a change in the relative
498 abundance of organisms is an important component of biodiversity and studies in our compilation
499 typically equated species richness with diversity, whereas biodiversity *sensu stricto* includes both
500 species richness and abundance (Magurran, 2005). To fully comprehend how biodiversity
501 impacts ecosystem function, an attempt should be made at manipulating and maintaining different
502 levels of soil community diversity, in the strict sense of the definition.

503

504 **5 Conclusions**

505 If we are to fully understand how anthropogenic-induced changes in biodiversity affect the
506 terrestrial C cycle, we must dig deeper and embrace the challenges associated with studying the
507 belowground world. Understanding the complex relationships between soil biodiversity and C
508 cycling processes is currently limited by the sheer number of methodological concerns associated
509 with these studies, which can greatly overestimate or underestimate the impact of soil
510 biodiversity on soil C cycling, challenging extrapolation to natural field conditions. Nonetheless,
511 our data point towards a definite importance of soil community diversity on key C cycling
512 processes. Our quantitative analysis revealed significant negative effects of loss of soil
513 biodiversity on rates of soil respiration and litter decomposition. If this is the case, declines in soil
514 biodiversity could significantly affect the rates and dynamics of C cycling. However, biodiversity
515 effects were not always consistent across groups of organisms. Differential responses of groups
516 of organisms could be related to their functional role in the respective processes. It is however
517 important to emphasize that we are still lacking full understanding of the underlying changes in
518 soil community functioning (or the lack of) with shifts in soil biodiversity (Nielsen et al. 2011;
519 Briones, 2014). Future studies should therefore attempt to further elucidate the relative

520 importance of taxonomic diversity (species numbers) *versus* functional diversity. Effects of loss
521 of soil biodiversity on ecosystem C cycling should depend on the degree of functional
522 dissimilarity of the organisms involved (Heemsbergen et al. 2004). Hence, unraveling the level of
523 variation in functional traits among soil organisms, both within and across feeding groups, should
524 be a future research priority. Such studies would improve predictions on the global C cycling in
525 the face of future environmental changes. Given the importance of the soil community in
526 regulating the direction and magnitude of C fluxes between the atmosphere and terrestrial
527 ecosystems, advancing our understanding of soil biodiversity impacts on biogeochemical cycles
528 may enhance the efficacy of climate change mitigation efforts.

529
530 **Acknowledgements:** This work was supported by the National Institute of Food and Agriculture
531 (2012-67010-20069) to MA de Graaff, and HT's participation was supported by US National
532 Science Foundation grants DEB-0953864 and DEB-1235828.

533
534 **Author contribution:** All authors contributed to conceiving the idea, compilation of the data and
535 preparation of the manuscript. Analyses were performed by MA de Graaff and J Adkins.

536
537 **References**

- 538 Adams, D.C., Gurevitch, J., and Rosenberg, M.S.: Resampling tests for meta-analysis of
539 ecological data, *Ecology*, 78, 1277-1283, 1997.
- 540 Andren, O., and Balandreau, J.: Biodiversity and soil functioning - from black box to can of
541 worms? *Appl. Soil Ecol.*, 13, 105-108, 1999.
- 542 Araujo, P.I.,Yahdjian L., and Austin, A.T.: Do soil organisms affect aboveground litter
543 decomposition in the semiarid Patagonian steppe, Argentina? *Oecologia*, 168, 221-230, 2012.
- 544 Balvanera P., Pfisterer A.B., Buchmann N., He J.S., Nakashizuka T., Raffaelli D., and Schmid
545 B.: Quantifying the evidence for biodiversity effects on ecosystem functioning and services, *Ecol.*
546 *Lett.*, 9, 1146-1156, 2006.

547 Bardgett, R.: *The Biology of Soil*, Oxford University Press, New York, U.S.A., 2005.

548 Bardgett R., Freeman C., and Ostle N.J.: Microbial contributions to climate change though
549 carbon cycle feedbacks, *ISME J*, 2, 805-814, 2008.

550 Baxter, J.W., and Dighton J.: Ectomycorrhizal diversity alters growth and nutrient acquisition of
551 grey birch (*Betula populifolia*) seedlings in host-symbiont culture conditions, *New*
552 *Phytol.*, 152,139-149, 2001.

553 Bell, T., Newman, A.J., Silverman, B.W., Turner, S.L., and Lilley, A.K.: The contribution of
554 species richness and composition to bacterial services, *Nature*, 436, 1157-1160, 2005.

555 Bengtsson, J.: Which species? What kind of diversity? Which ecosystem function? Some
556 problems in studies of relationships between biodiversity and ecosystem functioning, *Appl. Soil*
557 *Ecol.*, 10, 191–199, 1998.

558 Berg, B., and Laskowski, R.: Advances in ecological research, in: *Litter decomposition: A guide*
559 *to carbon and nutrient turnover*, Elsevier Academic Press, San Diego, California, USA, 2006.

560 Bezemer, T.M., De Deyn, G.B., Bossinga, T.M., van Dam, N.M., Harvey, J.A., and Van der
561 Putten, W.H.: Soil community composition drives aboveground plant-herbivore-parasitoid
562 interactions, *Ecol. Lett.*, 8, 652-661, 2005.

563 Bignell, D.E., and Eggleton, P.: Termites in ecosystems, In: *Termites: Evolution, Sociality,*
564 *Symbiosis, Ecology*, T. Abe, D.E. Bignell & M. Higashi (eds.), Kluwer Academic, Dordrecht,
565 Netherlands, 363–387, 2000.

566 Bonkowski M., and Roy J.: Soil microbial diversity and soil functioning affect competition
567 among grasses in experimental microcosms, *Oecologia* 143(2), 232–240, 2005.

568 Borer, E.T., Seabloom, E.W., Mitchell, C.E., and Cronin, J.P.: Multiple nutrient and herbivores
569 interact to govern diversity, productivity, composition, and infection in a successional grassland,
570 *Oikos*, 123, 214-224, 2014.

571 Bradford, M.A., Jones, T.H., Bardgett, R.D., Black, H.I.J., Boag, B., Bonkowski, M., Cook, R.,
572 Eggers, T., Gange, A.C., Grayston, S.J., Kandeler, E., McCaig, A.E., Newington, J.E., Prosser,
573 J.I., Setälä, H., Staddon, P.L., Tordoff, G.M., Tscherko, D., and Lawton, J.H.: Impacts of soil
574 faunal community composition on model grassland ecosystems, *Science*, 298, 615-618, 2002.

575 Bradford, M.A., Tordoff, G.M., Black, H.I.J Cook, R., Eggers, T., Garnett, M.H., Grayston, S.J.,
576 Hutcheson, K.A., Ineson, P., Newington, J.E., Ostle, N., Sleep, D., Stott, A., and Jones, T.H.:
577 Carbon dynamics in a model grassland with functionally different soil communities, *Funct.*
578 *Ecol.*, 21, 690-697, 2007.

579 Briones, M.J.I.: Soil fauna and soil functions: a jigsaw puzzle, *Frontiers in Environmental*
580 *Science*, 2, 1-22, 2014.

581 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A.,
582 Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B.,
583 Larigauderie, A., Srivastava, D.S., and Naeem, S.: Biodiversity loss and its impact on humanity,
584 *Nature*, 486, 59–67, 2012.

585 Carrillo, Y., Ball, B.A., Bradford, M.A., Jordan, C.F., and Molina, M.: Soil fauna alter the effects
586 of litter composition on nitrogen cycling in a mineral soil, *Soil Biol. Biochem.*, 43, 1440-1449,
587 2011.

588 Casper, B. B., and Jackson, R.B.: Plant competition underground, *Annu. Rev. Ecol. Syst.*, 28,
589 545-570, 1997.

590 Clark, C.M., and Tilman, D.: Loss of plant species after chronic low-level nitrogen deposition to
591 prairie grasslands, *Nature*, 451, 712–715, 2008.

592 Cole, L., Dromph, K.M., Boaglio, V., and Bardgett, R.D.: Effect of density and species richness
593 of soil mesofauna on nutrient mineralisation and plant growth, *Biol. Fert. Soils*, 39, 337-343,
594 2004.

595 Collison, E.J., Riutta, T., and Slade, E.M.: Macrofauna assemblage composition and soil moisture
596 interact to affect soil ecosystem functions, *Acta Oecol.*, 47, 30-36, 2013.

597 Conen F., Yakutin M., and Sambuu A.: Potential for detecting changes in soil organic carbon
598 concentrations resulting from climate change, *Glob. Change Biol.*, 9, 1515–1520, 2003.

599 Cong, W.F., van Ruijven, J., Mommer, L., De Deyn, G.B., Berendse, F., and Hoffland, E.: Plant
600 species richness promotes soil carbon and nitrogen stocks in grasslands without legumes, *J. Ecol.*,
601 102, 1163-1170, 2014.

602 Cortet, J., Joffre, R., Elmholt, S., and Krogh, P.H.: Increasing species and trophic diversity of
603 mesofauna affects fungal biomass, mesofauna community structure and organic matter
604 decomposition processes, *Biol. Fert. Soils*, 37, 302-312, 2003.

605 Cox, P., Wilkinson, S.P., and Anderson, J.M.: Effects of fungal inocula on the decomposition of
606 lignin and structural polysaccharides in *Pinus sylvestris* litter, *Biol. Fert. Soils*, 33, 246–251,
607 2001.

608 Cragg, R.G., and Bardgett R.D.: How changes in soil faunal diversity and composition within a
609 trophic group influence decomposition processes, *Soil Biol. Biochem.*, 33, 2073-2081, 2001.

610 Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M.,
611 Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S.,
612 Smith, B., White, A., and Young-Molling, C.: Global response of terrestrial ecosystem structure
613 and function to CO₂ and climate change: results from six dynamic global vegetation models,
614 *Glob. Change Biol.*, 7, 357-373, 2001.

615 Curtis, P. S., and Wang, X.Z.: A meta-analysis of elevated CO₂ effects on woody plant mass,
616 form, and physiology, *Oecologia*, 113, 299-313, 1998.

617 de Deyn, G.B., and Van der Putten, W.H.: Linking aboveground and belowground diversity,
618 *Trends Ecol. Evol.*, 20, 625-633, 2005.

619 de Graaff, M-A., van Groenigen K.J., Six J., Hungate B., and van Kessel C.: Interactions between
620 plant growth and soil nutrient cycling under elevated CO₂: a Meta-Analysis. *Glob. Change*
621 *Biol.*, 12, 1-15, 2006.

622 De Vries, F.T., Thébault, E., Liiri, M., Birkhofer, K, Tsiafouli, M.A., Bjørnlund, L., Bracht H.,
623 Jørgensen, Brady, M.V., Christensen, S., de Ruyter, P.C., d’Hertefeldt, T., Frouzk, J., Hedlund,
624 K., Hemerik, L., Hol, W.H.G., Hotes, S., Mortimer, S.R., Setälä, H., Sgardelis, S.P., Uteseny, K.,
625 van der Putten W.H., V., Wolters, R.D., and Bardgett.: Soil food web properties explain
626 ecosystem services across European land use systems. *P Natl. Acad. Sci. USA*, 110, 14296-
627 14301, 2013.

628 Dilly, O., Bloem, J., Vos, A., and Munch, J.C.: Bacterial diversity in agricultural soils during
629 litter decomposition, *Appl. Environ. Microb.*, 70, 468–474, 2004.

630 Edsberg, E.: The quantitative influence of enchytraeids (Oligochaeta) and microarthropods on
631 decomposition of coniferous raw humus in microcosms, *Pedobiologia*, 44, 132-147, 2000.

632 Edwards, C.A.: Soil invertebrate controls and microbial interactions in nutrient and organic
633 matter dynamics in natural and agroecosystems, in: *Invertebrates as Webmasters in Ecosystems*,
634 Coleman, D., Hendrix, P. (Eds.), CAB International, Wallingford, UK, 141-159, 2000.

635 Eisenhauer, N., and Schadler, M.: Inconsistent impacts of decomposer diversity on the stability of
636 aboveground and belowground ecosystem functions, *Oecologia*, 165, 403-415, 2011.

637 Eisenhauer, N., Horsch, V., Moeser, J., and Scheu, S.: Synergistic effects of microbial and animal
638 decomposers on plant and herbivore performance, *Basic Appl. Ecol.*, 11, 23-34, 2010.

639 Eisenhauer, N., Milcu, A., Sabais, A.C.W., Bessler, H., Brenner, J., Engels, C., Klärner, B.,
640 Maraun, M., Partsch, S., Roscher, C., Schonert, F., Temperton, V.M., Thomisch, K., Weigelt, A.,
641 Weisser, W.W., and Scheu, S.: Plant Diversity Surpasses Plant Functional Groups and Plant
642 Productivity as Driver of Soil Biota in the Long Term, *Plos One*, 6, 2011.

643 Eisenhauer, N., Sabais, A.C.W., and Scheu, S.: Collembola species composition and diversity
644 effects on ecosystem functioning vary with plant functional group identity, *Soil Biol.*
645 *Biochem.*, 43, 1697-1704, 2011.

646 Fischer J., and Lindenmayer D.B.: Landscape modification and habitat fragmentation: A
647 synthesis, *Global Ecol. Biogeogr.*, 16, 265–280, 2007.

648 Fitter, A. H., Gilligan, C.A., Hollingworth, K., Kleczkowski, A., Twyman, R.M., Pitchford, J.W.,
649 and Programme, N.S.B.: Biodiversity and ecosystem function in soil, *Funct. Ecol.*, 19, 369-377,
650 2005.

651 Fornara, D.A., and Tilman, D., Plant functional composition influences rates of soil carbon and
652 nitrogen accumulation, *J. Ecol.*, 96, 314-322, 2008.

653 Griffiths, B.S., Ritz, K., Bardgett, R.D., Cook, R., Christensen, S., Ekelund, F., Sorensen, S.J.,
654 Baath, E., Bloem, J., de Ruiter, P.C., Dolfing, J., and Nicolardot, B.: Ecosystem response of
655 pasture soil communities to fumigation-induced microbial diversity reductions: an examination of
656 the biodiversity-ecosystem function relationship, *Oikos*, 90, 279-294, 2000.

657 Griffiths, B. S., Ritz, K., Wheatley, R., Kuan, H.L., Boag, B., Christensen, S., Ekelund, F.,
658 Sorensen, S.J., Muller, S., and Bloem, J.: An examination of the biodiversity-ecosystem function
659 relationship in arable soil microbial communities, *Soil Biol. Biochem.*, 33, 1713-1722, 2001.

660 Griffiths, B. S., Kuan, H.L., Ritz, K., Glover, L.A., McCaig, A.E., and Fenwick, C.: The
661 relationship between microbial community structure and functional stability, tested
662 experimentally in an upland pasture soil, *Microb. Ecol.*, 47, 104-113, 2004.

663 Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Bruder, A., Butenschoen, O., Chauvet, E.,
664 Gessner, M.O., Jabiou, J., Makkonen, M., McKie, B.G., Malmqvist, B., Peeters, E.T.H.M., Scheu,
665 S., Schmid, B., van Ruijven, J., Vos V.C.A., and Hättenschwiler, S.: Consequences of
666 biodiversity loss for litter decomposition across biomes. *Nature*, 509, 218-221, 2013.

667 Hanson, C.A., Allison, S.D., Bradford, M.A., Wallenstein, M.D., and Treseder, K.K.: Fungal taxa
668 target different carbon sources in forest soil, *Ecosystems*, 11, 1157–1167, 2008.

669 Harmon M.E., Nadelhoffer K.J., and Blair J.M. Measuring decomposition, nutrient turnover, and
670 stores in plant litter, in: *Standard Soil Methods for Long-Term Ecol. Res.*, Robertson G.P.,
671 Coleman D.C., Bledsoe C.S., Sollins P. (Eds.), Oxford University Press, New York, U.S.A, 202–
672 240, 1999.

673 Heal, O.W., Anderson, J.M., and Swift, M.J.: Plant litter quality and decomposition: an historical
674 overview, in: *Driven by Nature: plant Litter Quality and Decomposition*, Cadisch, G., Giller, K.E.
675 (Eds.), CAB International, Wallingford, England, 3-30, 1997.

676 Hedges, L.V., and Olkin, I.: *Statistical Methods for Meta-Analysis*, Academic Press, San Diego,
677 California, U.S.A., 1985.

678 Hedlund K., and Ohm M.S.: Tritrophic interactions in a soil community enhance decomposition
679 rates, *Oikos*, 88, 585–591, 2000.

680 Heemsbergen, D.A., Berg, M.P., Loreau, M., van Haj, J.R., Faber, J.H., and Verhoef, H.A.:
681 Biodiversity effects on soil processes explained by interspecific functional dissimilarity, *Science*,
682 306, 1019–1020, 2004.

683 Heneghan, L., Coleman, D.C., Zou, X., Crossley, D.A., and Haines, B.L.: Soil microarthropod
684 contributions to decomposition dynamics: Tropical-temperate comparisons of a single substrate,
685 *Ecology*, 80, 1873-1882, 1999.

686 Hol, W. H., De Boer, W., Termorshuizen, A.J., Meyer, K.M., Schneider, J.H.M., van Dam, N.M.,
687 van Veen, J.A., and Van Der Putten W.H.: Reduction of rare soil microbes modifies plant–
688 herbivore interactions. *Ecol. Lett.*, 13, 292-301, 2010.

689 Holland, E.A., Robertson, G.P., Greenberg, J., Groffman, P.M., Boone, R.D., and Gosz, J.R.: Soil
690 CO₂, N₂O, and CH₄ exchange, in: *Standard Soil Methods for Long-term Ecol. Res.*, Robertson,
691 G.P., Bledsoe, C.S., Coleman, D.C., and Sollins P. (Eds.), Oxford University Press, New York,
692 U.S.A., 185-201, 1999.

693 Hooper, D.U., Bignell, D.E., Brown, V.K., Brussaard, L., Dangerfield, J.M., Wall, D.H., Wardle,
694 D.A., Coleman, D.C., Giller, K.E., Lavelle, P., Van der Putten, W.H., De Ruiter, P.C., Rusek, J.,
695 Silver, W.L., Tiedje, J.M., and Wolters, V.: Interactions between aboveground and belowground
696 biodiversity in terrestrial ecosystems: Patterns, mechanisms, and feedbacks, *Bioscience*, 50,
697 1049-1061, 2000.

698 Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L.,
699 Gonzalez, A., Duffy, J.E., Gamfeldt, L., and O'Connor, M.I.: A global synthesis reveals
700 biodiversity loss as a major driver of ecosystem change, *Nature*, 486, 105-U129, 2012.

701 Huang C.Y., Hendrix P.F., Fahey T.J., Bohlen P.J., and Groffman P.M.: A simulation model to
702 evaluate the impacts of invasive earthworms on soil carbon dynamics, *Ecol. Model*, 221, 2447-
703 2457, doi:10.1016/j.ecolmodel.2010.06.023, 2010.

704 Hungate, B.A., Jackson, R.B., Field, C.B., and Chapin, F.S.: Detecting changes in soil carbon in
705 CO₂ enrichment experiments, *Plant Soil*, 187, 135-145, 1996.

706 Hungate, B.A., van Groenigen, K.J., Six, J., Jastrow, J.D., Luo, Y.Q., de Graaff, M.A., van
707 Kessel, C., and Osenberg, C.W.: Assessing the effect of elevated carbon dioxide on soil carbon: a
708 comparison of four meta-analyses, *Glob. Change Biol.*, 15, 2020-2034, 2009.

709 Ingham, R.E., Trofymow, J. A., Ingham, E.R., and Coleman, D.C.: Interactions of bacteria, fungi
710 and their nemotode grazers: effects on nutrient cycling and plant growth, *Ecol. Monogr.*, 20

711 55, 119–140, 1985.

712 Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen,
713 M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., and
714 Loreau, M.: High plant diversity is needed to maintain ecosystem services, *Nature*, 477, 199-
715 U196, 2011.

716 Jastrow, J.D., Amonette, J.E., and Bailey, V.L.: Mechanisms controlling soil carbon turnover and
717 their potential application for enhancing carbon sequestration, *Climatic Change*, 80, 5-23, 2007.

718 Johnson D.W., and Curtis P.S.: Effects of forest management on soil C and N storage: meta
719 analysis, *Forest Ecol. Manag.*, 140, 227-238, 2001.

720 Laakso J., and Setälä H.: Sensitivity of primary production to changes in the architecture of
721 belowground food webs, *Oikos*, 87(1), 57–64, 1999.

722 Ladygina, N., Henry, F., Kant, M.R., Koller, R., Reidinger, S., Rodriguez, A., Saj, S.,
723 Sonnemann, I., Witt, C., and Wurst, S.: Additive and interactive effects of functionally dissimilar
724 soil organisms on a grassland plant community, *Soil Biol. Biochem.*, 42, 2266-2275, 2010.

725 Lal R.: Soil carbon sequestration to mitigate climate change, *Geoderma*, 123, 1-22, 2004.

726 LeBauer, D.S.: Litter degradation rate and beta-glucosidase activity increase with fungal
727 diversity, *Can. J. Forest Res.*, 40, 1076-1085, 2010.

728 Liebich, J., Schloter, M., Schaffer, A., Vereecken, H., and Burauel, P.: Degradation and
729 humification of maize straw in soil microcosms inoculated with simple and complex microbial
730 communities, *Eur. J. Soil Sci.*, 58, 141-151, 2007.

731 Liiri, M., Setala, H., Haimi, J., Pennanen, T., and Fritze, H.: Relationship between soil
732 microarthropod species diversity and plant growth does not change when the system is disturbed,
733 *Oikos*, 96, 137-149, 2002.

734 Mack M.C., Schuur E.A.G., Bret-Harte M.S., Shaver G.R., and Chapin F.S., III.: Ecosystem
735 carbon storage in Arctic tundra reduced by long-term nutrient fertilization, *Nature*, 431, 440-443,
736 2004.

737 Magurran, A.E.: Species abundance distributions: pattern or process? *Funct. Ecol.*, 19, 177-181,
738 2005.

739 Maherali H., and Klironomos J.N.: Influence of phylogeny on fungal community assembly and
740 ecosystem functioning, *Science*, 316(5832), 1746–1748, 2007.

741 Maron, J.L., Marlet, M., Klironomos, J.N., and Cleveland, C.C.: Soil fungal pathogens and the
742 relationship between plant diversity and productivity, *Ecol. Lett.*, 14, 36–41, 2001.

743 McKane, R. B., Grigal, D.F., and Russelle, M.P.: Spatiotemporal differences in N-15 uptake and
744 the organization of an old-field plant community, *Ecology*, 71, 1126-1132, 1990.

745 Mikola, J., and Setälä, H.: Productivity and trophic-level biomasses in a microbial-based soil food
746 web, *Oikos*, 82, 158-168, 1998a.

747 Mikola, J., and Setälä, H.: Relating species diversity to ecosystem functioning: mechanistic
748 backgrounds and experimental approach with a decomposer food web, *Oikos*, 83, 180-194,
749 1998b.

750 Milcu, A., Partsch, S., Scherber, C., Weisser, W.W., and Scheu, S.: Earthworms and legumes
751 control litter decomposition in a plant diversity gradient, *Ecology*, 89, 1872–1882, 2008.

752 Milcu, A, and Manning, P.: All size classes of soil fauna and litter quality control the acceleration
753 of litter decay in its home environment, *Oikos*, 120, 1366–1370, 2011.

754 Millennium Ecosystem Assessment, *Ecosystems and Human Well-being: Synthesis*
755 www.millenniumassessment.org/documents/document.356.aspx.pdf, 2006.

756 Nielsen, U.N., Ayres, E., Wall, D.H., and Bardgett, R.D.: Soil biodiversity and carbon cycling: a
757 review and synthesis of studies examining diversity-function relationships, *Eur. J. Soil Sci.*, 62,
758 105-116, 2011.

759 Orwin, K.H., Wardle, D.A., and Greenfield, L.G.: Ecological consequences of carbon substrate
760 identity and diversity in a laboratory study, *Ecology*, 87, 580–593, 2006.

761 Peters, R.H., 1983. *The Ecological Implications of Body Size*. Cambridge University Press,
762 Cambridge, UK.

763 Petersen, H., and Luxton, M.: A comparative-analysis of soil fauna populations and their role in
764 decomposition processes, *Oikos*, 39, 287-388, 1982.

765 Phoenix, G. K., Hicks W. K., Cinderby, S., , Kuylenstierna, J.C.I. Stock, W.D., Dentener, F.J.,
766 Giller, K.E., Austin, A.T., Lefroy, R.D.B., Gimeno, B.S., Ashmore, M.R., and Ineson, P.:
767 Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global
768 perspective in assessing N deposition impacts, *Glob. Change Biol.*, 12, 470-476, 2006.

769 Progar, R.A., Schowalter, T.D., Freitag, C.M., and Morrell, J.J.: Respiration from coarse woody
770 debris as affected by moisture and saprotroph functional diversity in Western Oregon,
771 *Oecologia*, 124, 426-431, 2000.

772 Prosser, J.I., and Nicol, G.W.: Archaeal and bacterial ammonia oxidisers in soil: the quest for
773 niche specialisation and differentiation, *Trends Microbiol.*, 20, 523-531, 2012.

774 Reich, P.B., Tilman, D., Isbell, F., Mueller, K., Hobbie, S.E., Flynn, D.F.B., and Eisenhauer, N.:
775 Impacts of biodiversity loss escalate through time as redundancy fades, *Science*, 336, 589-592,
776 2012.

777 Risch, A.C., Haynes, A.G., Busse, M. D., Filli, F., and Schutz, M.: The Response of Soil CO₂
778 Fluxes to Progressively Excluding Vertebrate and Invertebrate Herbivores Depends on
779 Ecosystem Type, *Ecosystems*, 16, 1192–1202, 2013.

780 Roesch, L.F., Fulthorpe, R.R., Riva, A., Casella, G., Hadwin, A.K.M., Kent, A.D., Daroub, S.H.,
781 Camargo, F.A.O., Farmerie, W.G., and Triplett E.W.: Pyrosequencing enumerates and contrasts
782 soil microbial diversity, *ISME J*, 1, 283-290, 2007.

783 Rosenberg, M.S., Adams, D.C., and Gurevitch, J.: *MetaWin: Statistical Software for Meta-*
784 *Analysis, Version 2.0*, Sinauer Associates, Sunderland, Massachusetts, U.S.A., 2000.

785 Sanderson, E. W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., and Woolmer, G.: The
786 human footprint and the last of the wild, *Bioscience*, 52, 891-904, 2002.

787 Schenk, H. J., Callaway, R.M., and Mahall, B.E.: Spatial root segregation: Are plants territorial?
788 *Adv. Ecol. Res.*, 28, 145-180, 1999.

789 Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.D.,
790 Roscher, C., Weigelt, A., Allan, E., Bessler, H., Bonkowski, M., Buchmann, N., Buscot, F.,
791 Clement, L.W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.M., Koller, R., König,
792 S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova,
793 V.D., Milcu, A., Müller, R., Partsch, S., Petermann, J.S., Renker, C., Rottstock, T., Sabais, A.,
794 Sechi, V., D'Annibale, A., Ambus, P., Sárosy, Z., Krogh, P.H., Eriksen, J., and Holmstrup, M.:
795 Collembola feeding habits and niche specialization in agricultural grasslands of different
796 composition, *Soil Biol. Biochem.*, 74, 3138, 2014.

797 Scheu, S., Schlitt, N., Tiunov, A.V., Newington, J.E., and Jones, T.H.: Effects of the presence and
798 community composition of earthworms on microbial community functioning, *Oecologia*, 133,
799 254-260, 2002.

800 Setälä, H.: Sensitivity of ecosystem functioning to changes in trophic structure, functional group
801 composition and species diversity in belowground food webs, *Ecol. Res.*, 17, 207-215, 2002.

802 Setälä, H. and Huhta, V.: Soil fauna increase *Betula pendula* growth: laboratory experiments with
803 coniferous forest floor, *Ecology*, 72, 665–671, 1991.

804 Setälä, H., and McLean, M.A.: Decomposition rate of organic substrates in relation to the species
805 diversity of soil saprophytic fungi, *Oecologia*, 139, 98-107, 2004.

806 Setälä, H., Berg, M.P., and Jones, T.H.: Trophic structure and functional redundancy in soil
807 communities, in: *Biological diversity and function in soils*. Bardgett, R.D., Hopkins, D.W., and
808 Usher, M.B. (Eds.), Cambridge University Press, 236-249, 2005.

809 Six, J., Conant, R.T., Paul, E.A., and Paustian, K.: Stabilization mechanisms of soil organic
810 matter: Implications for C-saturation of soils, *Plant Soil*, 241, 155-176, 2002.

811 Slade, E. M., and Riutta, T.: Interacting effects of leaf litter species and macrofauna on
812 decomposition in different litter environments, *Basic Appl. Ecol.*, 13, 423-431, 2012.

813 Smith, P.: How long before a change in soil organic carbon can be detected? *Glob. Change Biol.*,
814 10, 1878–1883, 2004.

815 Steinbeiss, S., Bessler, H., Engels, C., Temperton, V.M., Buchmann, N., Roscher, C., Kreuziger,
816 Y., Baade, J., Habekost, M., and Gleixner, G.: Plant diversity positively affects short-term soil
817 carbon storage in experimental grasslands, *Glob. Change Biol.*, 14, 2937-2949, 2008.

818 Stevens, C.J.: Impact of nitrogen deposition on the species richness of grasslands, *Science*, 303,
819 1876–1879, 2004.

820 Sulkava, P., Huhta, V., Laakso, J., and Gyllen, E.R.: Influence of soil fauna and habitat patchiness
821 on plant (*Betula pendula*) growth and carbon dynamics in a microcosm experiment,
822 *Oecologia*, 129, 133-138, 2001.

823 Szlavecz, K., McCormick, M., Xia, L.J., Saunders, J., Morcol, T., Whigham, D.T., and
824 Csuzdi, C.: Ecosystem effects of non-native earthworms in Mid-Atlantic deciduous forests, *Biol.*
825 *Invasions*, 13, 1165-1182, 2011.

826 Tilman, D., Wedin, D., and Knops, J.: Productivity and sustainability influenced by biodiversity
827 in grassland ecosystems, *Nature*, 379, 718-720, 1996.

828 Tilman, D., Hill, J., and Lehman, C.: Carbon-negative biofuels from low-input high-diversity
829 grassland biomass, *Science*, 314, 1598-1600, 2006.

830 Tiunov, A.V., and Scheu, S.: Facilitative interactions rather than resource partitioning drive
831 diversity-functioning relationships in laboratory fungal communities, *Ecol. Lett.*, 8, 618–625,
832 2005.

833 Toljander, Y.K., Lindahl, B.D., Holmer, L., and Hogberg, N.O.S.: Environmental fluctuations
834 facilitate species co-existence and increase decomposition in communities of wood decay fungi,
835 *Oecologia*, 148, 625-631, 2006.

836 van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R.,
837 Boller, T., Wiemken, A., and Sanders, I.R.: Mycorrhizal fungal diversity determines plant
838 biodiversity, ecosystem variability and productivity, *Nature*, 396, 69-72, 1998.

839 van der Heijden, M.G.A., Wiemken, A., and Sanders, I.R.: Different arbuscular mycorrhizal fungi
840 alter coexistence and resource distribution between co-occurring plant, *New Phytol.*, 157, 569-
841 578, 2003.

842 van der Heijden, M.G.A., Bardgett, R.D., and van Straalen, N.M.: The unseen majority: soil
843 microbes as drivers of plant diversity and productivity in terrestrial ecosystems, *Ecol. Lett.*, 11,
844 296-310, 2008.

845 van Groenigen, K.J., Six, J., Hungate, B., de Graaff, M-A., van Breemen, N. and van Kessel, C.
846 Element interactions limit soil carbon storage. *Proceedings of the National Academy of Sciences*,
847 103, 6571-6574, 2006.

848 van Ruijven, J., and Berendse, F.: Diversity-productivity relationships: Initial effects, long-term
849 patterns, and underlying mechanisms, *P Natl. Acad. Sci. USA*, 102, 695-700, 2005.

850 Vitousek P.M., and Mooney H.A.: Human domination of earth's ecosystems, *Science*, 277, 494,
851 1997.

852 Wagg, C., Bender, S.F., Widmer, F., and van der Heijden, M.G.A.: Soil biodiversity and soil
853 community composition determine ecosystem multifunctionality, *P Natl. Acad. Sci. USA*, 111,
854 5266-5270, 2014.

855 Wall, D.H., Bradford, M.A., St John, M.G., Trofymow, J.A., Behan-Pelletier, V., Bignell,
856 D.D.E., Dangerfield, J.M., Parton, W.J., Rusek, J., Voigt, W., Wolters, V., Gardel, H.Z., Ayuke,
857 F.O., Bashford, R., Beljakova, O.I., Bohlen, P.J., Brauman, A., Flemming, S., Henschel, J.R.,
858 Johnson, D.L., Jones, T.H., Kovarova, M., Kranabetter, J.M., Kutny, L., Lin, K.C., Maryati, M.,
859 Masse, D., Pokarzhevskii, A., Rahman, H., Sabara, M.G., Salamon, J.A., Swift, M.J., Varela, A.,
860 Vasconcelos, H.L., White, D., and Zou X.M.: Global decomposition experiment shows soil
861 animal impacts on decomposition are climate-dependent, *Glob. Change Biol.*, 14, 2661-2677,
862 2008.

863 Wall, D. H., Bardgett, R.D., and Kelly, E.F.: Biodiversity in the dark, *Nat. Geosci.*, 3, 297-298,
864 2010.

865 Wardle, D.A.: Is "sampling effect" a problem for experiments investigating biodiversity-
866 ecosystem function relationships? *Oikos*, 87, 403-407, 1999.

867 Wardle, D.A., K. I. Bonner, G. M. Barker, G. W. Yeates, K. S. Nicholson, R. D. Bardgett, R. N.
868 Watson, and Ghani A.: Plant removals in perennial grassland: Vegetation dynamics,
869 decomposers, soil biodiversity, and ecosystem properties, *Ecol. Monogr.*, 69, 535-568, 1999.

870 Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., and Wall, D.H.:
871 Ecological linkages between aboveground and belowground biota, *Science*, 304, 1629-1633,
872 2004.

873 Wardle, D.A., Bardgett, R.D., Callaway, R.M., and Van der Putten, W.H.: Terrestrial Ecosystem
874 Responses to Species Gains and Losses, *Science*, 332, 1273-1277, 2011.

875 Warren, R.J. and Bradford, M.A.: Ant colonization and coarse woody debris decomposition in
876 temperate forests, *Insect. Soc.*, 59, 215–221, 2012.

877 Wertz, S., Degrange, V., Prosser, J.I., Poly, F., Commeaux, C., Freitag, T., Guillaumaud, N., and
878 Le Roux, X.: Maintenance of soil functioning following erosion of microbial diversity, *Environ.*
879 *Microbiol.*, 8, 2162-2169, 2006.

880 Wilkinson, A., Solan, M., Taylor, A.F.S., Alexander, I.J., and Johnson, D.: Intraspecific Diversity
881 Regulates Fungal Productivity and Respiration, *Plos One*, 5, 2010.

882 Wilkinson, A., Alexander, I.J., and Johnson, D.: Species richness of ectomycorrhizal hyphal
883 necromass increases soil CO₂ efflux under laboratory conditions, *Soil Biol. Biochem.*, 43, 1350-
884 1355, 2011.

885 Wilkinson, A., Solan, M., Alexander, I., and Johnson, D.: Species richness and nitrogen supply
886 regulate the productivity and respiration of ectomycorrhizal fungi in pure culture, *Fungal Ecol.*, 5,
887 211-222, 2012.

888 Yang, X.D., and Chen, J.: Plant litter quality influences the contribution of soil fauna to litter
889 decomposition in humid tropical forests, southwestern China, *Soil Biol. Biochem.*, 41, 910-918,
890 2009.

891 Zimmer, M., Kautz, G. and Topp, W.: Do woodlice and earthworms interact synergistically in
892 leaf litter decomposition? *Funct. Ecol.*, 19, 7-16, 2005.

893

894 **Figure legends**

895

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

901

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

910

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

919

920 **Figs. 4a and b** Regressions between a percent change in the soil microbial, soil macrofaunal or
921 soil microbial and soil faunal communities (i.e. multiple organismal groups) and the natural log

922 of the response ratio of soil C respiration ($\ln R$; calculated as the natural log of the response ratio,
923 R , which was the value of the response variable at low diversity divided by the value at high
924 diversity). No studies in our literature compilation of soil C respiration included manipulation of
925 only soil microfauna or mesofauna, so these body size groups are not included in the figure.
926 Percent change in diversity was calculated as $(\text{low diversity} - \text{high diversity}) / \text{high diversity} * 100$.
927 Figure 4a includes all possible comparisons across diversity gradients in studies, whereas 4b
928 includes the comparisons between the lowest and highest diversity levels only.

929
930 **Figs. 5a and b** Regressions between a percent change in the soil microbial, mesofaunal,
931 macrofaunal, or soil microbial and soil faunal communities (i.e. multiple organismal groups) and
932 the natural log of the response ratio of litter decomposition ($\ln R$; calculated as the natural log of
933 the response ratio, R , which was the value of the response variable at low diversity divided by the
934 value at high diversity). No studies in our literature compilation of litter decomposition included
935 manipulation only of soil microfauna, so this body size group is not included in the figure.
936 Percent change in diversity was calculated as $(\text{low diversity} - \text{high diversity}) / \text{high diversity} * 100$.
937 Figure 5a includes all possible comparisons across diversity gradients in studies, whereas 5b
938 includes the comparisons between the lowest and highest diversity levels only.

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

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

Enchytraeids

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

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

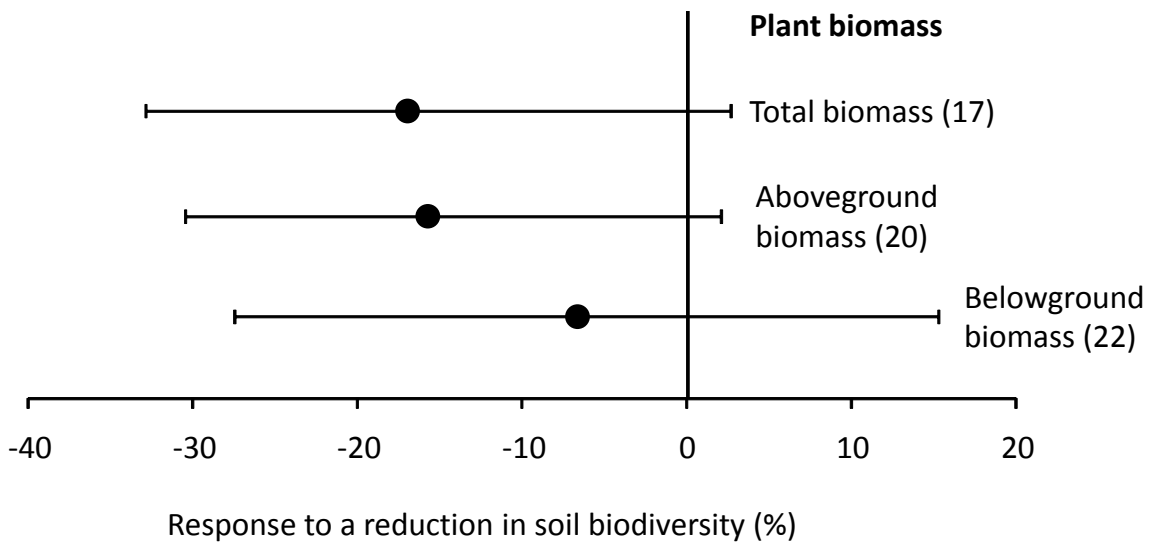
	Microfauna	+		Enchytraeids,		
	Mesofauna	+		Microarthropods,		
	Macrofauna			Wireworms		
Respiration	Microbes		< 5µm	Bacteria	1	Wertz et al (2006)
	Microbes		< 5µm	Bacteria, Fungi	3	Griffiths et al (2000, 2001 and 2004)
	Microbes		< 5µm	Fungi	5	Wilkinson et al (2010, 2011 and 2012), Tiunov and Scheu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

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

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

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

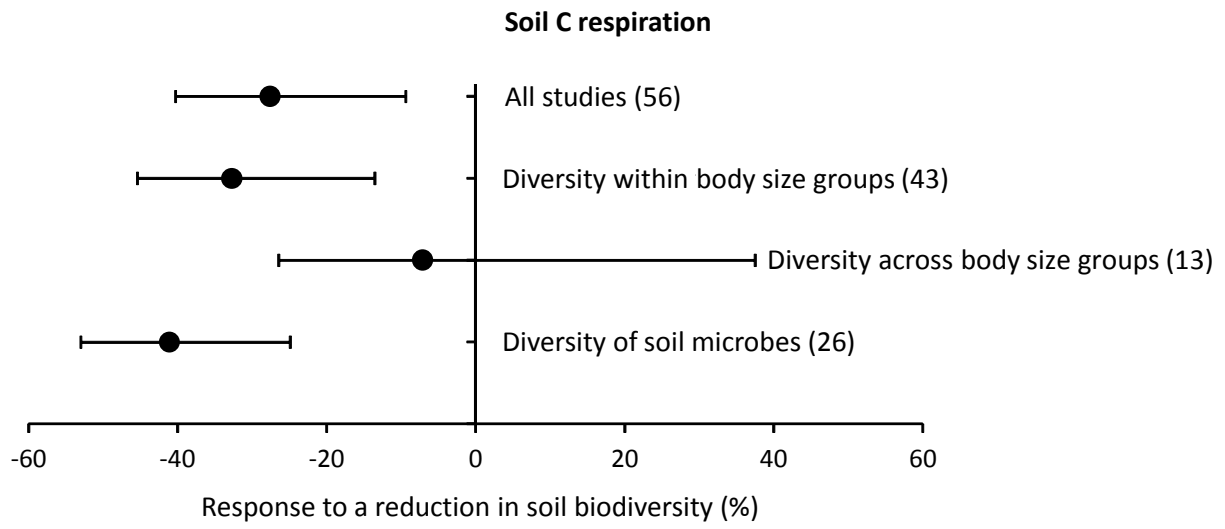
941 Fig. 1



942

943

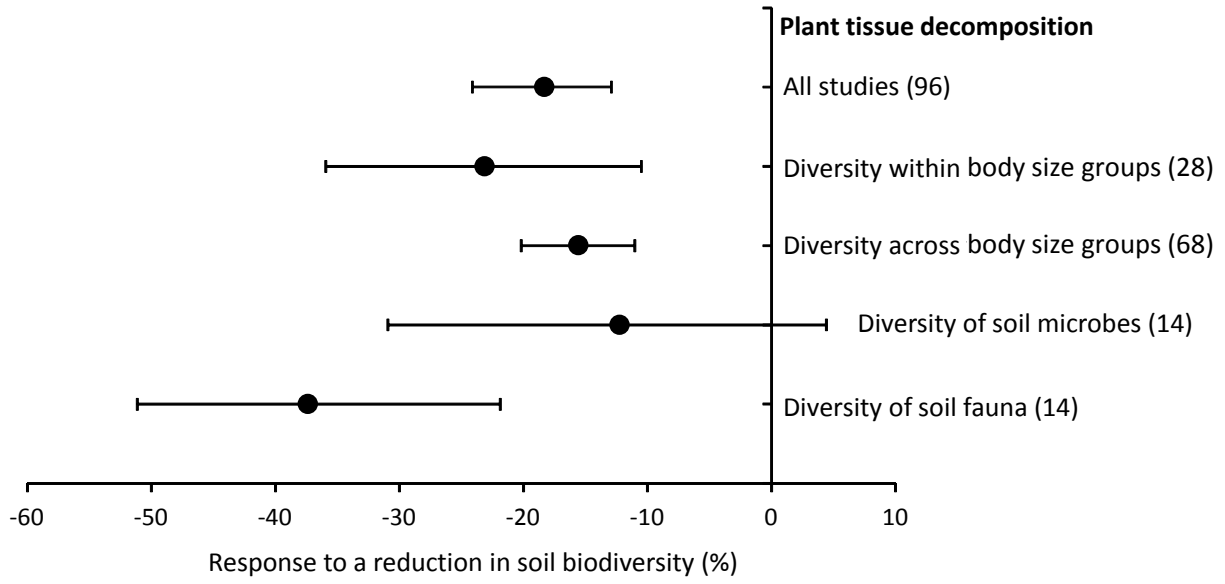
944 Fig. 2



945

946

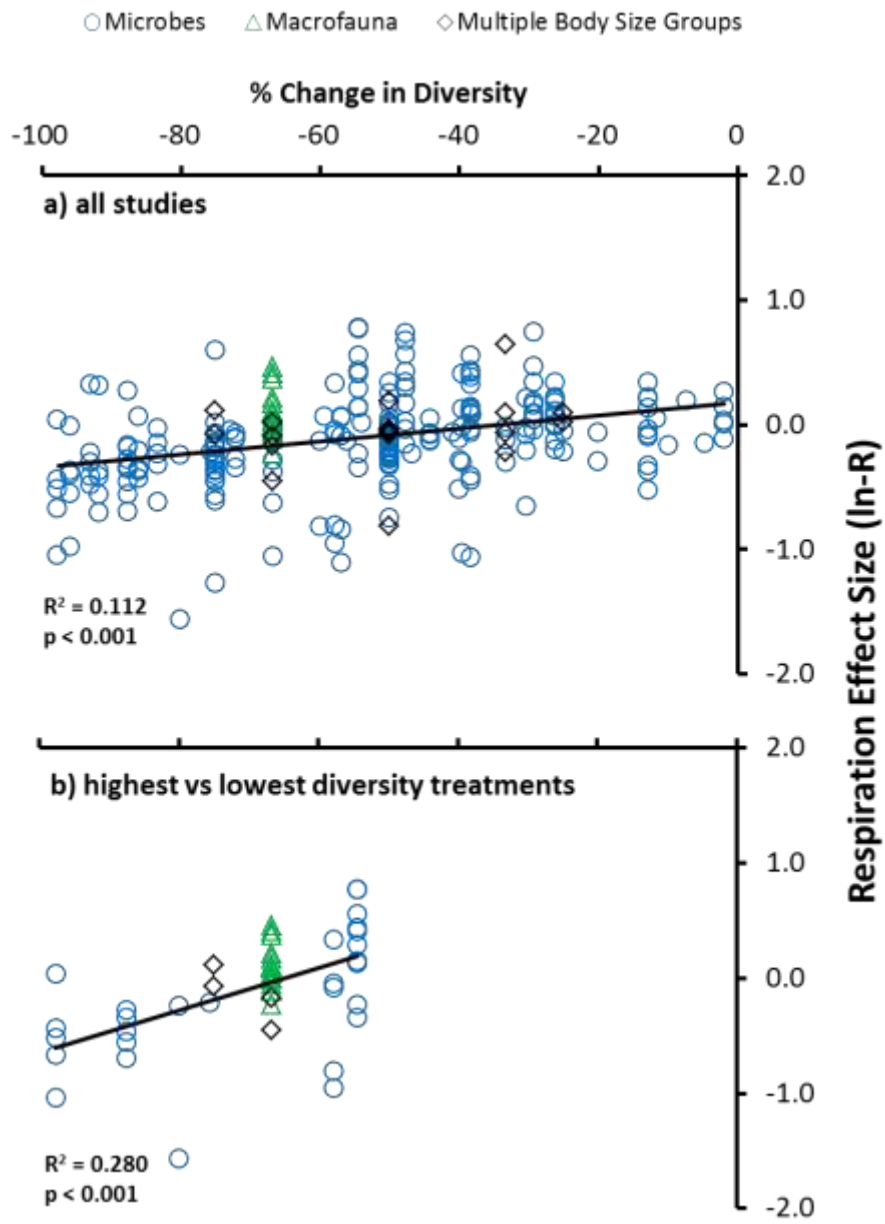
947 Fig 3.



948

949

950 Figs. 4a, and b

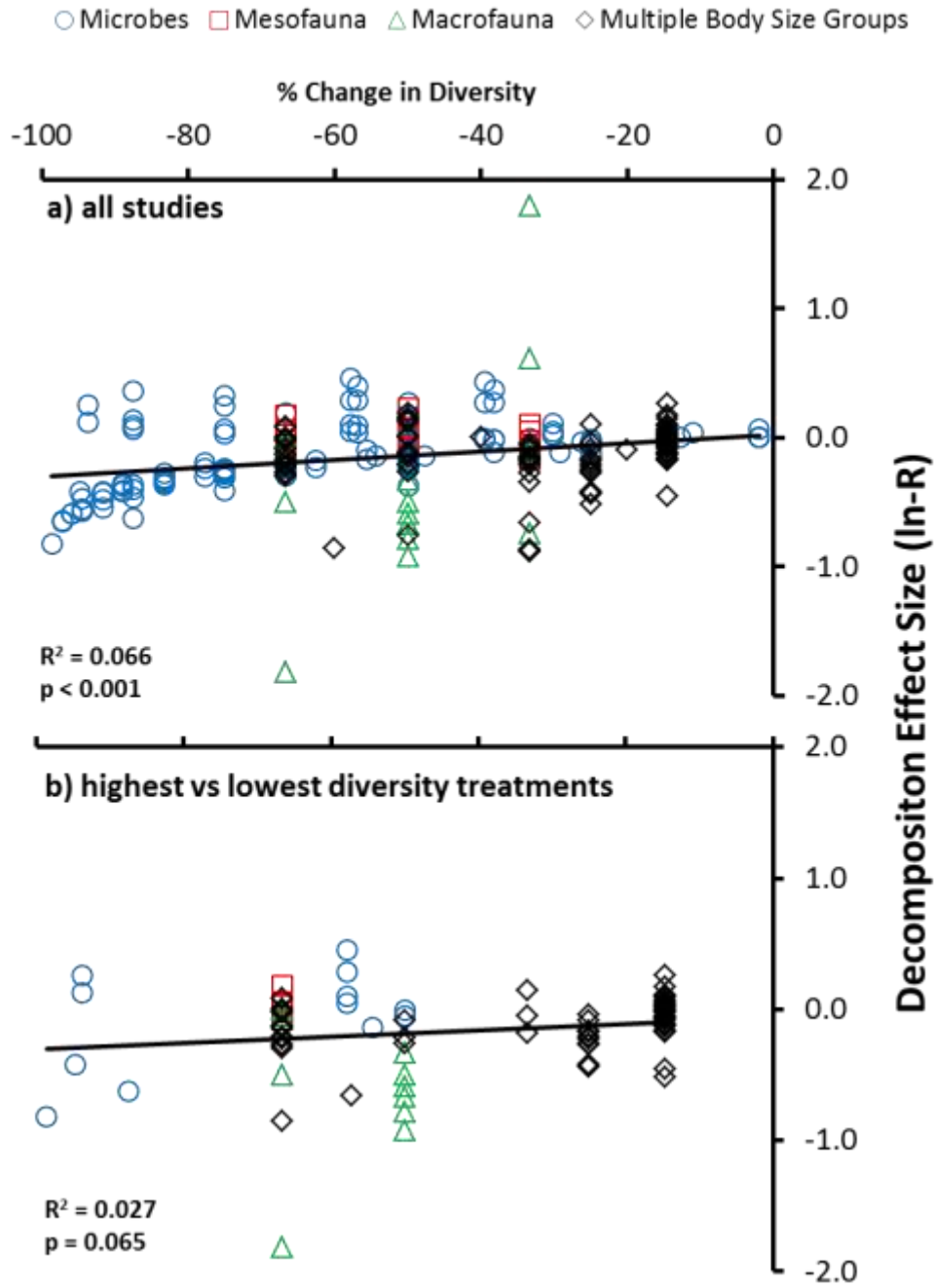


951

952

953

954 Figs. 5a and b



955

956

957

958