**Title:** Interactions among decaying leaf litter, root litter, and soil organic matter vary with mycorrhizal type

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**Summary of Research**

1. Root-derived inputs are increasingly viewed as primary controls of soil organic matter (SOM) formation; however, we have a limited understanding of how root decay rates depend on soil factors, and how decaying roots influence the breakdown of leaf litter and SOM.
2. We incubated root and leaf litter (alone, and in combination) from arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) trees in soils collected from forest plots dominated by AM and ECM trees in a factorial design. In each microcosm, we quantified litter decay rates and the effects of decaying litters on soil C balance. We hypothesized that 1) AM root litters would decompose faster than ECM root litters, 2) root litter decay would be greatest when decomposed in "home" soils (e.g., AM litters in AM soils, ECM litters in ECM soils), and 3) root and leaf litters would decompose faster when decaying in the same microcosms than when decaying in separate microcosms, resulting in the largest $CO_2$ losses.
3. Overall, AM root litter decomposed faster than ECM root litter, and the magnitude of this effect depended on soil origin. AM litters decayed fastest in AM soils, but ECM and mixed AM-ECM litters were unaffected by soil origin. Decaying roots increased leaf litter mass loss, but only in microcosms containing soils of the same origin (e.g., AM litters in AM soils; mixed litters in mixed soils).
4. Carbon losses were dominated by microbial respiration, and the magnitude of this flux depended on litter type and soil origin. When leaves and roots decayed together, respiratory losses exceeded those from microcosms containing leaves and roots alone, with the largest losses occurring in each litters' "home" soil. In AM soils, elevated losses were driven by roots accelerating leaf decay, while in ECM soils elevated losses resulted from roots and leaves accelerating the decay of SOM; in mixed soils, root-induced increases in leaf and SOM decay contributed to elevated C losses.
5. Our results suggest that root, leaf, and SOM decay are intertwined, and that measurements of these processes in isolation may lead to incorrect estimates of the magnitude and source of C gains and losses from soils.

**Keywords:** ecosystem carbon storage, home field advantage, mycorrhizal association, plant-soil interactions, priming effects, root turnover

## 1. Introduction

Litter decomposition is a major component of the global carbon (C) cycle (Cusack et al., 2009), affecting nutrient cycling, soil organic matter (SOM) dynamics and ecosystem C balance (Schmidt et al., 2011, Cotrufo et al., 2013). Most studies of litter decay focus on leaf litter; however, fine root litter can account for 48% of total plant litter inputs, exceeding both leaf litter (41%) and fine stem (11%) inputs in some ecosystems (Freschet et al., 2013). Furthermore, root litter may be selectively preserved in soils to a greater degree than leaf litter (Jackson et al. 2017), such that the majority of stabilized SOM is root-derived (Rasse et al., 2005). Despite the importance of root litter to SOM formation, we have a limited understanding of whether the processes which control root litter decay differ from those that control leaf litter and SOM decay, if at all. Such distinctions are critical given that most terrestrial biosphere models

parameterize root litter decay using data derived from aboveground measurements (McGuire et al., 2001). Thus, our incomplete understanding of root litter decay may limit our ability to predict how global changes impact C and nitrogen (N) cycling in ecosystems.

Tree species that associate with different types of mycorrhizal fungi often differ in their effects on soil biogeochemistry and ecosystem processes (Phillips et al., 2013, Averill et al., 2014, Terrer et al., 2016). Trees associating with arbuscular mycorrhizal (AM) fungi generally possess high quality litters that decompose rapidly (Cornelissen et al., 2001, Midgley et al., 2015), resulting in rapid cycling of C and nutrients in soils (Read and Perez-Moreno, 2003, Lin et al., 2017). In contrast, trees that associate with ectomycorrhizal (ECM) fungi typically have low quality litters that decompose slowly, resulting in slow cycling of C and nutrients and a greater proportion of nutrients in organic forms (Read and Perez-Moreno, 2003). While such differences in litter properties contribute to observed differences between ECM and AM-dominated stands in terms of their soil microbial communities (Cheeke et al., 2017, Rosling et al., 2016) and C and N cycling (Averill et al., 2014, Brzostek et al., 2015, Lin et al., 2017, Midgley and Phillips, 2016), the role of root dynamics in contributing to these biogeochemical syndromes is poorly understood (Langley et al., 2006, Koide et al., 2011, McCormack et al., 2014, Chen et al., 2016, Taylor et al., 2016). Root litter decay rates for a given species often do not mirror the decay rates of their leaf litter (Hobbie et al., 2010, Birouste et al., 2011), and so the faster decay of AM leaf litters (relative to ECM leaf litters) does not necessarily mean that AM root litters decay faster than ECM root litters. Rather, litter decay rates at local scales typically depend on factors such as the chemical quality of the litter and the soil environment (Cornwell et al., 2008, Prescott, 2010, Schmidt et al., 2011, Midgley et al., 2015, Roumet et al., 2016), particularly if soil microbes are best adapted to break down substrates most prevalent in their "home" environment (Hunt et al., 1988, Gholz et al., 2000, Ayres et al., 2006).

Previous investigations of root litter decay have focused primarily on root mass loss over time, with less attention to the effects of root decay on microbial growth and activity. However, roots do not decay in isolation from other soil processes, and decaying roots may influence the decomposition of leaf litter and SOM through priming effects. Priming effects occur when labile C inputs stimulate soil microbes to produce extracellular enzymes that, in turn, lead to the accelerated decay of other substrates in soil. Priming effects are often presumed to result from the release of exudates by living roots (Shahzad et al., 2015, Phillips et al., 2011), but such effects may also be driven by energy and nutrients released during the early stages of litter decay (Parton et al., 2007). This may explain why experimental treatments that result in a pulse of dead roots (e.g., soil trenching or tree girdling) often increase leaf litter decay (Brzostek et al., 2015) and C and N cycling (Averill and Hawkes, 2016). An improved understanding of the interactive effects of root, leaf and SOM decay is clearly needed, as there are still knowledge gaps concerning how differences in litter and SOM quality impact the ability of soil microbes to decompose plant inputs to soils.

While it is well-established that plants control litter decay rates by altering the litter quality of leaves (Melillo et al., 1982) and roots (Silver and Miya, 2001), and soil properties (Vivanco and Austin, 2008, Ward et al., 2015), we have a limited understanding of the interactions that can occur between litter types (leaves vs. roots) and SOM (Hobbie, 2015, Mueller et al., 2015). Here, we examined the extent to which soil provenance (AM vs. ECM), litter type (AM vs. ECM, leaf vs. root), and their interactions affect decomposition rates of leaf litter, root litter, and SOM. Our hypotheses were: (1) AM root litters would decompose faster than ECM root litters, (2) root litter decay would be greatest when decomposed in "home" soils (e.g., AM litters in AM soils, ECM litters in ECM soils), and (3) root and leaf litters would decompose faster when decaying in the same microcosms than when decaying in separate microcosms. To test these hypotheses, we constructed soil microcosms that varied in the mycorrhizal association of the soils, leaf litter, and root litter, and quantified litter mass loss, microbial respiration, and soil C gains and losses over a 16-week incubation. This allowed us to take advantage of the inherent differences between AM and ECM tissue chemistry, as well as the soil microbial communities AM and ECM trees support, in order to identify key drivers of variations in decomposition.

## 2. Materials and Methods

*2.1. Soil and Litter*

We collected root litter and soils from two 15 x 15 meter plots at the Indiana University Griffy Woods Research and Teaching Preserve (RTP) – an approximately 80-year-old forest in south-central Indiana, USA (39.2020° N, 86.5205° W). The RTP is a temperate deciduous forest with elevation ranging from 192 to 246 meters. The climate is humid continental, with mean annual precipitation of 1200 mm and mean annual temperature of 11.6°C. Soils are thin, unglaciated inceptisols, derived primarily from siltstone, shale and in some areas, limestone. One plot was dominated by AM trees and the other dominated by ECM trees with the dominant mycorrhizal type representing greater than 80% of the basal area of each plot. The AM-dominated plot contained a mix of sugar maple (*Acer saccharum* Marsh), tulip poplar (*Liriodendron tulipifera* L.), and sassafras (*Sassafras albidum* Nutt.). The ECM-dominated plot contained American beech (*Fagus grandifolia* Ehrh.), shagbark hickory (*Carya ovata P. Mill.*), and white oak (*Quercus alba* L.). All sampling was performed in a 10 m x 10 m internal plot to avoid edge effects.

Soil samples were collected from the upper 10 cm of the mineral soil from both AM- and ECM-dominated plots in early March, 2014. In ECM soils, where an 2cm O horizon was present,, we collected soils from 10cm beneath this horizon; in AM soils, where no O horizon was present, samples were collected 10 cm beneath the litter layer. In the laboratory, soils were air dried and sieved to 2 mm to remove rocks and roots, and to homogenize the soil. Soils were then combined with 50% sand by dry weight (to facilitate drainage) and placed in microcosms. The soil-sand mixtures from ECM-dominated plots are hereafter referred to as "ECM soils" and those from AM-dominated plots as "AM soils". Thus, the mycorrhizal designations of the soils reflect the soil origin, and assume that any influence of AM and ECM fungi in the soils resulted primarily from their legacy effects in the soils (Taylor et al., 2016).

Terminal fine roots were carefully excavated from the soil samples described above by hand and washed five times with double deionized water to remove adhering soil particles. The roots were then dried at 60° C. We defined 'fine roots' as any root <2 mm in diameter (Freschet et al., 2013). The majority of understory plants in the plots were spice bush (*Lindera benzoin*), which has distinctive roots that were discarded. As AM and ECM tree species represented >80% of the basal area in each plot, respectively, fine roots collected from each plot were assumed to represent AM and ECM roots, respectively. Leaf litter was acquired from a litter basket collection conducted at the RTP in October, 2014. Leaves from trees representing the same AM and ECM associated species listed above were selected and dried at 60° C. Leaves were cut into 1x1 cm squares and roots into 1 cm long segments. An equal mass of litter from each representative tree species was used.

*2.2. Experimental design and treatments*

We conducted a 16 week microcosm incubation experiment that used factorial combinations of leaf litter, root litter, and soils collected from the field plots (Fig. 1). Water was added to the microcosms on a weekly basis and leachate was collected to be analyzed for dissolved organic carbon (DOC). The experiment included three soil treatments: (1) AM-associated soil (AM Soil), (2) ECM-associated soil (ECM Soil), (3) a mixture of 50% AM- and 50% ECM-associated soil (mixed AM/ECM Soil). Mixed AM/ECM soil was included to be representative of areas where AM and ECM trees coexist, and to provide an intermediate treatment, analogous to AM and ECM mixed forest plots.

Litter treatments consisted of combinations of litter types (roots, leaves, or roots and leaves) and litter mycorrhizal associations (AM, ECM, or mixed AM/ECM), along with control treatments with no root or leaf litter additions. The nine litter addition treatments were crossed with each of the four soil treatments and replicated four times, while twelve replicates of each soil type were used for the control treatments, resulting in a total of 144 experimental microcosms (Fig. 1).

*2.3. Microcosm Design*

Microcosms were constructed of 6.35 cm diameter polyvinyl chloride tubing and had a height of 15 cm. 1.5 mm mesh screens were installed on the bottom of each microcosm allowing water to drain. 240 g dry weight of soil was added to each microcosm, with 0.8 g dry weight of either leaf or root litter

added to microcosms receiving single litter treatments and 0.8 g each of both roots and leaves added to microcosms receiving combined litter effect treatments (1.6 g total litter for microcosms receiving both roots and leaves). Root litter was mixed thoroughly into the soil. Leaf litter was placed on a mesh screen, which was used to separate soil from leaf litter, facilitating leaf collection at the end of the experiment. The field capacity of each soil was determined using the method of Bradford et al., (2008). In our micrcosms, 55 ml of water was added in order to reach 60% water holding capacity (WHC) 24 hours after watering, and to generate 15-25 ml of leachate. Microcosms rested on funnels that drained into 50 ml centrifuge tubes. All microcosms were watered with 55 ml of deionized water weekly. The incubation was conducted in an indoor lab space with a diurnal light cycle (~12 hours of light; ~12 hours of dark) and maintained at a temperature of ~22 °C.

*2.4. Gas sampling and analysis*

$CO_2$ flux from each microcosm (i.e., microbial respiration) was determined using an infrared gas analyzer (LI-COR 8100; Lincoln, NE, USA) every seven days for the first 10 weeks, and approximately every 14 days thereafter. A gastight PVC collar was temporarily sealed on the top of each microcosm, and a 10 cm Survey Chamber was placed on the collar before measurement. $CO_2$ accumulation was measured over a two minute period. The rate of $CO_2$ emission was determined, and cumulative C loss as $CO_2$ was calculated by integrating the area under the curve for all dates (i.e., for each microcosm), based on the assumption that rates of $CO_2$ loss scaled linearly between time points. Given that water was added to each microcosm to capture leachate (see below), all respiration measurements were taken one day after each water addition.

*2.5. Dissolved organic carbon sampling and analysis*

Leachate was collected from 50 ml centrifuge tubes resting underneath each microcosm after each weekly watering. Leachate samples were mixed by inversion, after which 10 ml were transferred to 20 ml glass scintillation vials (Thermo Fischer Scientific, Carlsbad, CA, USA) and frozen at -7 °C. Samples were later thawed and filtered through 0.2 μm pore size Whatman Sterile PVDF Syringe Filters (GE Whatman, Maidstone, UK) and analyzed for DOC on a microplate absorbance plate reader (Bartlett and Ross, 1988, Giasson et al., 2014) (BioTek, Winooski, VT, USA). Cumulative DOC leaching losses from each microcosm were calculated by linear interpolation between measurements (as was done for the $CO_2$ fluxes).

*2.6. Litter and soil analysis*

At the beginning and end of the incubation, leaf and root litter was analyzed for C and N%, and soils were analyzed for SOM content (SI Table 1). At the end of the incubation period, leaf litter was collected by removing the screen and gently shaking the litter over 2 mm mesh (to remove residual soil particulates). There was some leaf litter fragmentation at this stage of decomposition, and removing the screen ensured that all visible leaf fragments were collected. Soil was sieved (2 mm mesh) twice in order to collect roots. Both leaves and roots were rinsed with DI water and dried at 60 °C. Dried litter sample weights post-incubation were compared to those of pre-incubation litter samples. Soil and litter samples were ground using a ball mill for 24 hours, and litters were analyzed on a Costech ECS 4010 CHNS-O Elemental Analyzer (Valencia, CA, USA) to determine C and N content. Soils were analyzed for gravimetric moisture content and subsequently heated in a muffle furnace at 450 °C for 48 hours to determine SOM loss on ignition (LOI). Prior to treatment, ECM soils had greater SOM content than AM soils, and ECM roots had higher C:N ratios than AM roots (SI Table 1). Leaf litter C:N was not significantly different between mycorrhizal types (SI Table 1), although a previous analysis from this site found that ECM leaf litter had greater lignin:N ratios, polyphenol content, and tannin content than AM leaf litter (Midgley et al., 2015).

*2.7. Statistics*

Three way analyses of variance (ANOVA), including interactions, were conducted by fitting mixed effect models in SPSS statistical software (SPSS 23.0 for Windows, SPSS Inc., Chicago, IL, USA). $CO_2$ and DOC data were analyzed using repeated measures ANOVA. Single-factor ANOVA was used to compare treatment effects at a given time (i.e. litter mass loss at the end of the incubation). To determine whether microbial respiration from soils containing both roots and leaves was interactive or simply additive (given that the combined treatment comprised more total litter), a custom hypothesis test was carried out using contrast estimates and fixed effects generated from a linear mixed model that included all the respiration data collected. This allowed us to account for the variance in the control soils in our custom hypothesis contrast. Our equation takes the form:

$$H_0: (\mu_{leaves+roots} - \mu_{control}) - [(\mu_{leaves} - \mu_{control}) + (\mu_{roots} - \mu_{control})] = 0$$
$$H_1: (\mu_{leaves+roots} - \mu_{control}) - [(\mu_{leaves} - \mu_{control}) + (\mu_{roots} - \mu_{control})] \neq 0$$

where the mean cumulative $CO_2$ released from each microcosm containing root and leaf litter additions is $\mu_{leaves+roots}$, leaf litter only is $\mu_{leaves}$, root litter only is $\mu_{roots}$, and no litter is $\mu_{control}$.

Mass loss rates were compared between roots and leaves decomposing alone versus decomposing together. T-tests were performed to test the hypothesis that leaf or root litter respectively would decompose at a faster rate when decomposing with the other litter type than when decomposing alone. One-tail p-values were used in this test, as the alternate hypothesis was that the mean mass loss of leaves or roots decomposing together is greater than that of leaves or roots decomposing alone, rather than merely testing a difference in the means in either direction.

Tukey adjusted post-hoc differences of least square means were used to compare treatments, and confidence intervals were generated to observe graphical differences in means. Regression analyses were calculated using the Regression Wizard function in SigmaPlot Version 13 (Systat Software, San Jose, CA).

## 3. Results

*Litter mass loss*

AM litters lost more mass than either ECM or mixed AM/ECM litters across all litter types ($P < 0.05$), and mixed AM/ECM litters lost more mass than ECM litters across all litter types ($P < 0.05$, Fig. 2). Mass loss from leaves was less than that from roots across all soils ($P < 0.05$). Analysis of variance showed significant interactions between soil mycorrhizal type and litter type ($P = 0.001$, $F_{(5, 102)} = 4.102$), litter type and litter mycorrhizal association ($P = 0.007$, $F_{(5, 102)} = 3.706$), and soil mycorrhizal type, litter type, and litter mycorrhizal association ($P < 0.001$, $F_{(8, 99)} = 4.085$). These interactions varied in direction and magnitude, but the significant interaction between litter type, litter mycorrhizal association, and soil mycorrhizal type indicated that litter mass loss was influenced by a combination of these three factors.

Across all soil mycorrhizal types, AM roots incubating alone decomposed 46% faster than ECM roots incubating alone ($P < 0.05$, Fig. 2), while AM leaves incubating alone decomposed 110% faster than ECM leaves incubating alone ($P < 0.05$, Fig. 2). AM root litter decay was sensitive to soil origin, decomposing 43% faster in AM soil compared to ECM soil ($P < 0.05$), while ECM root litter decay was not influenced by soil origin (Fig. 2). However, AM leaf litter incubated alone lost 32% more mass in ECM soil than in AM soil ($P = 0.03$). In AM soil, AM leaves lost significantly more mass when roots were also present ($P = 0.016$, Fig. 2a). In ECM soil, leaf and root litter mass loss did not differ between incubations where litters were separated or combined (Fig. 2b). In mixed soils, mixed leaves lost significantly more mass when roots were also present ($P = 0.047$; Fig. 2c).

*Microbial respiration and litter effects*

Averaged across all litter treatments, microbial respiration was significantly greater in ECM soils than in AM or mixed soils ($P < 0.05$, Figure S1). Additionally, microbial respiration in ECM control soils (without litter additions) was greater than in AM or mixed control soils ($P < 0.05$, Fig. 3). Microbial

247 respiration did not differ significantly between AM and mixed soils across litter treatments ($P > 0.05$), or
248 between AM and mixed control soils ($P > 0.05$).
249 The effects of litter type on microbial respiration varied by soil mycorrhizal type. In AM soils,
250 additions of leaf litter only, and both root and leaf litter, stimulated microbial respiration, whereas root
251 litter alone did not ($P < 0.05$, Fig. 3a). By contrast, in ECM soils, only additions of both roots and leaves
252 stimulated microbial respiration ($P < 0.05$, Fig. 3b). Leaf litter alone had no effect and root litter actually
253 suppressed soil respiration relative to control in ECM soil ($P < 0.05$, Fig. 3b). Only in the mixed
254 AM/ECM soil did all litter types significantly stimulate soil respiration with the microcosms containing
255 roots and leaves having the largest effect ($P < 0.05$, Fig. 3c)
256 Averaged across soil and litter mycorrhizal types, the addition of root litter did not produce a
257 significant increase in respiration compared to control soils (Figure S1). The addition of leaf litter
258 produced an increase in respiration compared to either soil controls or soils with root additions across all
259 soils ($P < 0.05$, Figure S1), and the addition of both roots and leaves produced a significant increase in
260 soil respiration compared to all other litter additions ($P < 0.05$, Figure S1).
261 Microcosms with both leaf and root litter additions were expected to have larger increases in
262 respiration rates relative to individual root or litter additions because the total amount of litter added was
263 greater (1.6 g for the roots + leaves treatment, and 0.8 g for the roots or leaves alone treatments). For
264 some treatments, respiration in the microcosms containing roots and leaves exceeded the sum of
265 respiration in the roots alone and leaves alone micrococms, indicating interactive effects among root litter,
266 leaf litter and SOM decomposition (Fig. 4). AM-associated roots and leaves interacted to produce a
267 significant non-additive increase in microbial respiration when incubated in either AM soil ($P = 0.035$) or
268 ECM soil ($P = 0.023$). ECM associated roots and leaves interacted to produce a significant non-additive
269 increase in respiration in ECM soil ($P < 0.001$), but did not produce significant interactive effects in AM
270 or mixed soils. In the mixed soils, there was a trend toward an interactive effect of the mixed litters ($P <$
271 0.1) but no interactive effects with the addition of AM or ECM litters.
272
273 *Soil C loss*
274 Across all soil types, ECM soils lost more soil C (as a % of the total) than the either AM or mixed
275 AM/ECM soils ($P < 0.05$, Fig. 5; SI Table 2). Moreover, in ECM soils, there was a significant
276 enhancement of soil C loss when ECM roots and leaves were present ($P < 0.05$). This effect was not
277 observed in AM soils. In mixed AM/ECM soils, there was a significant enhancement of soil C loss when
278 mixed AM/ECM roots and leaves were present ($P < 0.05$).
279
280 *Dissolved organic carbon*
281 There was no difference in dissolved organic carbon (DOC) losses among soil types (SI Fig. 1).
282 Regardless of soil type, litter type, or litter mycorrhizal association, litter addition did not significantly
283 increase DOC fluxes compared to soil controls. However, cumulative DOC losses were negatively
284 correlated with cumulative respiration losses for AM soil with AM leaf litter addition ($P = 0.033$, SI Fig.
285 2a). Although only marginally significant, a similar trend was observed when ECM roots and leaves were
286 decomposed in ECM soils ($P = 0.07$, SI Fig. 2b).
287
288 **4. Discussion**
289 Root litter represents a significant C input to SOM (Rasse et al., 2005, Brzostek et al., 2015,
290 Iversen et al., 2017; Jackson et al. 2017); however, few studies have considered how soil environment
291 affects root litter decay rates, or how decaying roots influence the decay of leaf litter and SOM (Silver
292 and Miya, 2001, Dornbush et al., 2002, Cusack et al., 2009, Harmon et al., 2009, Fan and Guo, 2010,
293 Goebel et al., 2011, Li et al., 2015, Santos et al., 2016, Taylor et al., 2016). In this study, we investigated
294 the degree to which AM and ECM roots decay differently from AM and ECM leaves, the impacts of litter
295 and soil origin on soil C losses, and potential interactions between litter types. We hypothesized that: (1)
296 AM root litters would decompose faster than ECM root litters, (2) root litter decay would be greatest
297 when decomposed in "home" soils (e.g., AM litters in AM soils, ECM litters in ECM soils), and (3) root

and leaf litters would decompose faster when decaying in the same microcosms than when decaying in separate microcosms, such that C losses would be greatest in microcosms containing roots and leaves decaying together in their home soil. We found at least partial support for all three hypotheses. AM roots, on average, decayed faster than ECM roots, and the magnitude of this effect was greatest when roots decayed in their home soil. Across all soil types, microcosms containing roots and leaves drove an interactive (i.e., non-additive) increase in microbial respiration, indicating that the presence of decaying roots may have primed the decomposition of other organic substrates in soil. Collectively, our results indicate that root detritus may play an underappreciated role in elevating C losses from soils, though the mechanisms responsible for the enhanced losses depend on mycorrhizal type.

In this study, we used microcosms to address key knowledge gaps about interactions between decaying leaves, roots and SOM, and the consequences for these dynamics on soil C balance. This enabled us to avoid common pitfalls related to measuring root litter decay *in situ* (Hobbie et al., 2010, Beidler and Pritchard, 2017). However, microcosms, like all lab-based incubation approaches, have potential biases as well. In our study, root litter was added as a one-time input, which differs from temperate forests where roots of varying orders turn-over throughout the year (McCormack et al., 2014). Additionally, our excised roots may have differed chemically from those decaying *in situ* owing to the absence of active mycorrhizal fungi, which can alter root decay rates (Langley et al., 2006) but see Taylor et al., 2016). Finally, the litter and soils used in our microcosms were collected from a single forest in south-central Indiana, which may limit the generality of our findings. Given these limitations, we view our results as being most useful for testing hypotheses about litter-SOM interactions and as a way to identify novel mechanisms that necessitate further exploration *in situ*.

*Mass loss differences between AM and ECM litters*

We hypothesized that AM roots would decompose faster than ECM roots, based on reports that AM leaves tend to decompose faster than ECM leaves (Cornelissen et al., 2001; Midgley et al., 2015; Taylor et al., 2016), and suggestions that plants possess coordinated nutrient use traits such that species with fast-decaying leaves also have fast-decaying roots (Reich, 2014). While we found support for this hypothesis (Fig. 2), there is conflicting evidence on whether roots from varying mycorrhizal types decay differently. In a microcosm experiment similar to this study, Taylor et al. (2016) reported greater respiratory fluxes from soils containing AM roots than from soils containing ECM roots (Taylor et al., 2016) – consistent with our results. However, two common garden studies reported no differences in fine root lifespan (McCormack et al., 2012) and turnover rate (McCormack et al., 2014, Kubisch et al., 2016) between AM and ECM trees. What factors might explain this discrepancy? One possibility is differences in experimental systems (i.e., lab vs. common garden). For example, the lack of observed differences in AM and ECM root decay in the McCormack et al., (2012; 2014) and Kubisch et al., (2016) studies may reflect the young age of the trees' root systems, in that there was insufficient time for unique AM and ECM root-decaying microbial communities to develop. While our study was not designed to address this issue, we anticipate that the development of root trait databases (e.g., FRED; Iversen et al. 2017), will provide more clarity about the relationship between mycorrhizal type, microbial community structure, and root decay.

We found partial support for our second hypothesis. AM roots (C:N = 62; Table S1) decayed fastest in AM soils, while ECM roots (C:N = 66; Table S1) and mixed roots (C:N = 63) decomposed similarly independent of soil type. The AM root result is consistent with the "home-field advantage" hypothesis, which predicts that litters tend to decompose faster in "home" soils than in "away" soils (Hunt et al., 1988, Gholz et al., 2000, Ayres et al., 2006), and with an extension of this hypothesis, which predicts that low quality litters decompose fastest in low fertility soils (e.g., wide C:N), and vice versa for high quality litters (Freschet et al., 2012). However, the acceleration of AM and mixed leaf litter decay in ECM soils was inconsistent with this hypothesis, and may reflect differences in microbial community characteristics (e.g. fungal:bacterial ratio) between soil types (Rosling et al. 2016; Cheeke et al 2017). One possible explanation for the ECM litter result is that the ECM litter was of such low chemical quality (e.g., high polyphenolic content), that its slow decay rate was not affected by the soil environment during

the short-term incubation time period. This is consistent with findings that low quality ECM litters may decay slowly regardless of their soil environment (Midgley et al. 2015).

*Interactions between leaf, root, and SOM decay*

$CO_2$ flux responses to combined leaf and root litter addition supported our third hypothesis that the presence of decomposing roots accelerated the decay of other organic matter. However, patterns of litter and SOM mass loss differed with mycorrhizal type and were clearer in AM and ECM soils compared to mixed soils. Based on mass loss measurements, the primary source of increased respiration in AM systems was enhanced leaf litter decomposition (Fig. 2a), with no significant change in soil C loss. These results suggest that microbes in AM soils preferentially used the products of root decay to degrade leaf litter. In contrast, leaf litter decomposition in ECM and mixed systems was insensitive to root additions (Fig. 2b,c), while soil C losses increased with combined leaf/root additions when litter mycorrhizal association matched soil origin. Differences in litter and SOM quality may explain these patterns: ECM litters often have higher C:N ratios, higher lignin:N ratios, and lower degradation rates than AM litters (Cornelissen et al., 2001, Midgley et al., 2015, Taylor et al., 2016). To the extent that more chemically recalcitrant litters release less energy and nutrients during decay (Parton et al., 2007), ECM leaf litter may have been a less preferred substrate for decomposition than SOM. ECM soils lost significantly more C than AM soils (Fig. 5), suggesting a higher availability of decomposable substrates, which is plausible given theory suggesting that low quality substrates typically result in less physical protection of SOM (Cotrufo et al., 2013). Another potential explanation is that the microbial community shifted during the course of the experiment, causing community-level properties such as carbon use efficiency to increase. The lower soil C losses from mixed AM/ECM soils could also be explained by similar shifts in microbial communities, although we cannot rule out the possibility in mixed soils that there were antagonistic responses between divergent microbial functional groups that specialize on AM vs. ECM litter. Our measurements could not directly assess microbial community properties, but the role of microbial community shifts warrants further testing.

The result that soil C loss was enhanced in ECM soils with ECM litter and in mixed soils with mixed litter supports our second hypothesis, and with previous measurements showing enhanced microbial activity when the mycorrhizal identity of litter matched that of the soil (Midgley et al., 2015, Taylor et al., 2016). This extends the home field advantage framework discussed above to include dynamic interactions between root litter, leaf litter, and SOM. Our results thus add to previous findings by suggesting that interactions between root and leaf decomposition can accelerate decomposition of SOM in ECM-dominated but not AM-dominated systems.

Acceleration of SOM decomposition with litter addition has been suggested as an explanation for the lack of soil C accumulation under enhanced litter inputs at the ecosystem scale (e.g. Lajtha et al., 2014; van Groenigen et al., 2017). Our results suggest that in addition to priming effects associated with leaf litter addition or exudation from live roots, decaying root litter can also prime decomposition post-mortem. Most estimates of priming effects have focused on the effects of living roots, mostly in short-term pot studies where root turnover was negligible (Cheng et al., 2014); as such, priming effects in ecosystems may be greater than previously considered. Additionally, our results provide a mechanistic explanation for why experimental treatments such as soil trenching or tree girdling that increase root detrital inputs to soil may accelerate leaf litter decay (Brzostek et al., 2015) and microbial C and N cycling (Averill and Hawkes, 2016). This important synergistic effect is largely absent from our current conceptual understanding of the fate of plant detritus. Our results are consistent with the view that priming effects tend to be greater in ECM than in AM soils (Terrer et al., 2017; Sulman et al., 2017). However, there is contrasting evidence from a seedling study that reported that AM roots induced greater SOC losses than ECM roots (Wurzburger and Brookshire, 2017). Due to the inherent limitations of our microcosm study, we suggest further investigation of whether the litter-induced priming effects suggested by our results also occur in the field and at the ecosystem scale.

There has been relatively little research on whether AM and ECM soils differ in the form and rate of DOC leaching. Given known differences in decomposition rates and nutrient economies (Phillips et

al., 2013), we expected that leaching losses in AM soils would likely exceed those in ECM soils. However, our results indicate that C loss via leaching of DOC was a minor C flux, equivalent to only about 6-7% of the C loss via $CO_2$ production (SI Fig. 1, SI Fig. 2). These losses did not vary by treatment but in some cases DOC losses were correlated negatively with $CO_2$ losses, indicating that DOC production was partially constrained by decomposition activity. Our measured ratios were slightly lower than recent measurements by Soong et al. (2015), who also found that DOC mass loss as a fraction of total mass loss varied with litter quality.

*Conclusion*

While studies explicitly investigating interactions between root litter, leaf litter and SOM during decomposition are rare, it is clear that soil decomposition processes do not occur in isolation (Schmidt et al., 2011). Here we found that root litter decomposition is dependent on both root litter properties (as indicated by mycorrhizal association) and the soil environment, and that the presence and mycorrhizal type of root litter can influence the decomposition of leaf litter. These observations support the need for an integrative approach to studying decomposition. Studies of decomposition should account for multiple litter sources (including both leaves and roots), variations in litter chemistry, and interactions between inputs and soil chemistry. Moreover, the observed interactions between root, leaf, and SOM decomposition suggest that environmental change factors (such as N deposition or rising atmospheric $CO_2$ levels) that enhance root production, turnover, and inputs to soils could have cascading effects on leaf and SOM decomposition.

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**Authors' contributions:** All authors designed the experiment. LMJ and JJF carried out the incubation and soil/tissue analysis. LMJ conducted the statistical analysis. LMJ, BNS, ERB, and RPP interpreted the results and wrote and edited the manuscript. All authors gave final approval for publication.

**Data accessibility:** Archived data will be made available (upon acceptance) to FigShare.

**Figure legends**

Fig 1. Factorial design of the microcosm experiment (144 total microcosms)

Fig 2. Percentage of root, leaf or root+leaf litter mass loss in AM (a), ECM (b), and AM/ECM (c) soils (N=4 replicates for all values). Asterisks indicate significant differences ($P < 0.05$) between roots and leaves decomposing alone or in the presence of the other litter type. 'Roots with leaves' is the average

mass loss of roots (in the presence of leaves) whereas "leaves with roots" is the average mass loss of leaves (in the presence of roots). Error bars represent the standard deviation from the mean.

Fig 3. Total $CO_2$ efflux from microcosms containing AM (a), ECM (b), or mixed AM/ECM (c) soils (N=12 replicates for each soil-litter combination). For each treatment, litter mycorrhizal types (AM vs. ECM vs mixed) are averaged. Error bars represent 95% confidence intervals. Different letters indicate significant differences between the means for each soil type ($P < 0.05$).

Fig 4. Interactive vs. additive effects of root and leaf litter decay on $CO_2$ efflux (N=12 discreet mesocosms x 10 time points for each soil type control; N=4 discreet mesocosms x 10 time points for each soil type-litter type-litter mycorrhizal combination). Bars indicate the size of the mean interactive effect relative to the mean additive effect (*see Methods for details about how both terms were calculated*). A value of zero indicates that $CO_2$ efflux from microcosms containing roots and leaves was equal to the sum of $CO_2$ efflux from the microcosms containing roots and leaves alone. Error bars represent the 95% confidence interval associated with the effect. Significantly different interactive effects (relative to additive effects), are denoted by asterisks ($P < 0.05$) and the ŧ symbol ($P < 0.1$).

Fig 5. Percent loss of soil C over the course of the experiment (N = 4 for each litter treatment except controls which were N = 12). Asterisks indicate changes in soil C that differ significantly from controls ($P < 0.05$). Error bars represent the standard deviation of the mean.

**Supplemental figures & tables**

SI Fig. 1. Cumulative losses of C (top and bottom rows) and biomass (middle row) from microcosms over the course of the experiment. Bars are mean values of C or mass loss from microcosms containing roots, leaves or roots + leaves (of AM, ECM and mixed litters) in AM, ECM or mixed soils. Cumulative C loss was calculated by linear interpolation between weekly measurements of dissolved organic C (DOC) leached and CO2 respired (N = 12; 3 mycorrhizal litter types x 4 replicates), assuming that measured rates of C flux scale linearly between time points. Mass loss was calculated by weighing litters prior to and following the incubation period (N = 12; 3 mycorrhizal litter types x 4 replicates). Error bars represent standard deviations of the mean.

Sl Fig 2. Cumulative C losses (as $CO_2$ and DOC) from select microcosms. $CO_2$ and DOC fluxes were significantly correlated ($P < 0.05$) for AM soils containing AM leaves (a) and marginally significant for ECM soils containing ECM roots and leaves (b). Other soil-litter combinations did not show significant relationships.

Table S1. AM, ECM, and mixed AM/ECM litter C:N and percent soil SOM before the experiment. Value and (SD). Asterisks indicate significant differences ($P < 0.05$) between averages. N = 12 for all values.

Table S2. AM, ECM, and mixed AM/ECM litter C:N and percent SOM after the experiment in each litter treatment. Values are means and values in parentheses indicate standard deviation from the mean. N = 4 unless indicated otherwise.

Table S3. Initial, final, and net changes in SOM and litter pools across all treatments. Values in parentheses indicate standard deviation from the mean. N = 12 for initial and final Soil SOM means in the no litter treatment. N= 4 for all other means.

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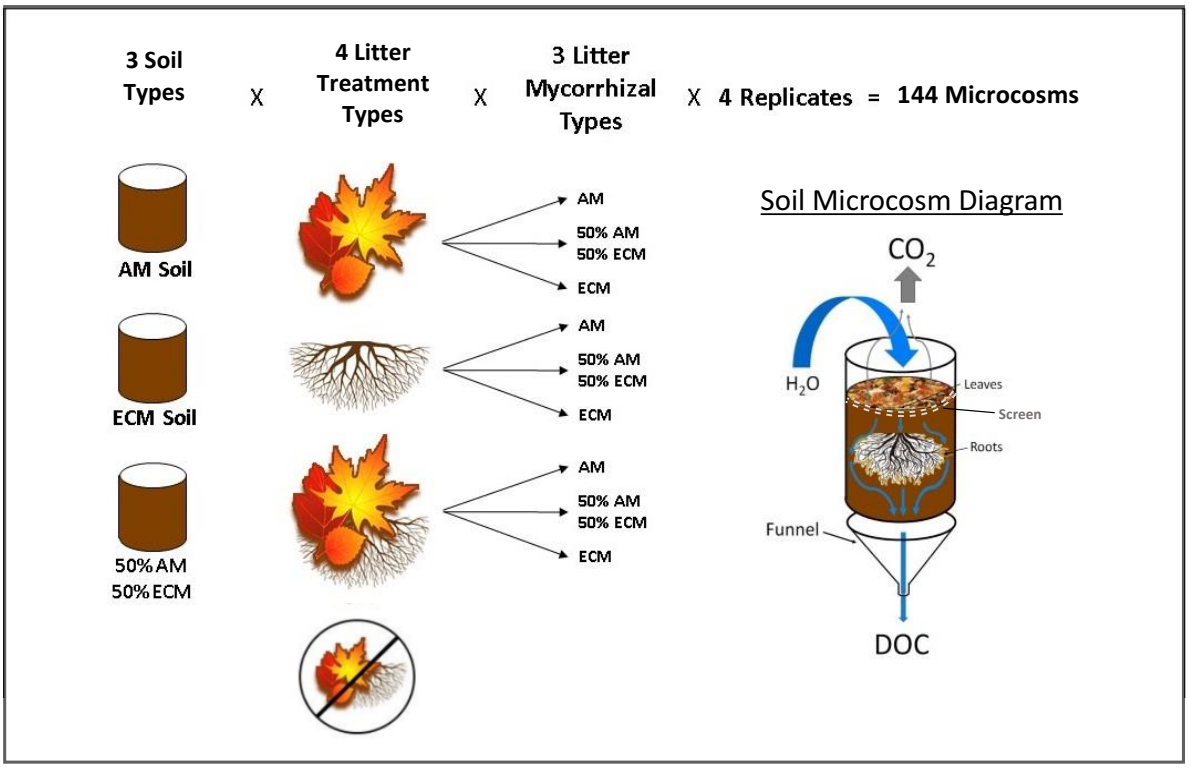



Figure 1. Factorial design of the microcosm experiment (144 total microcosms)

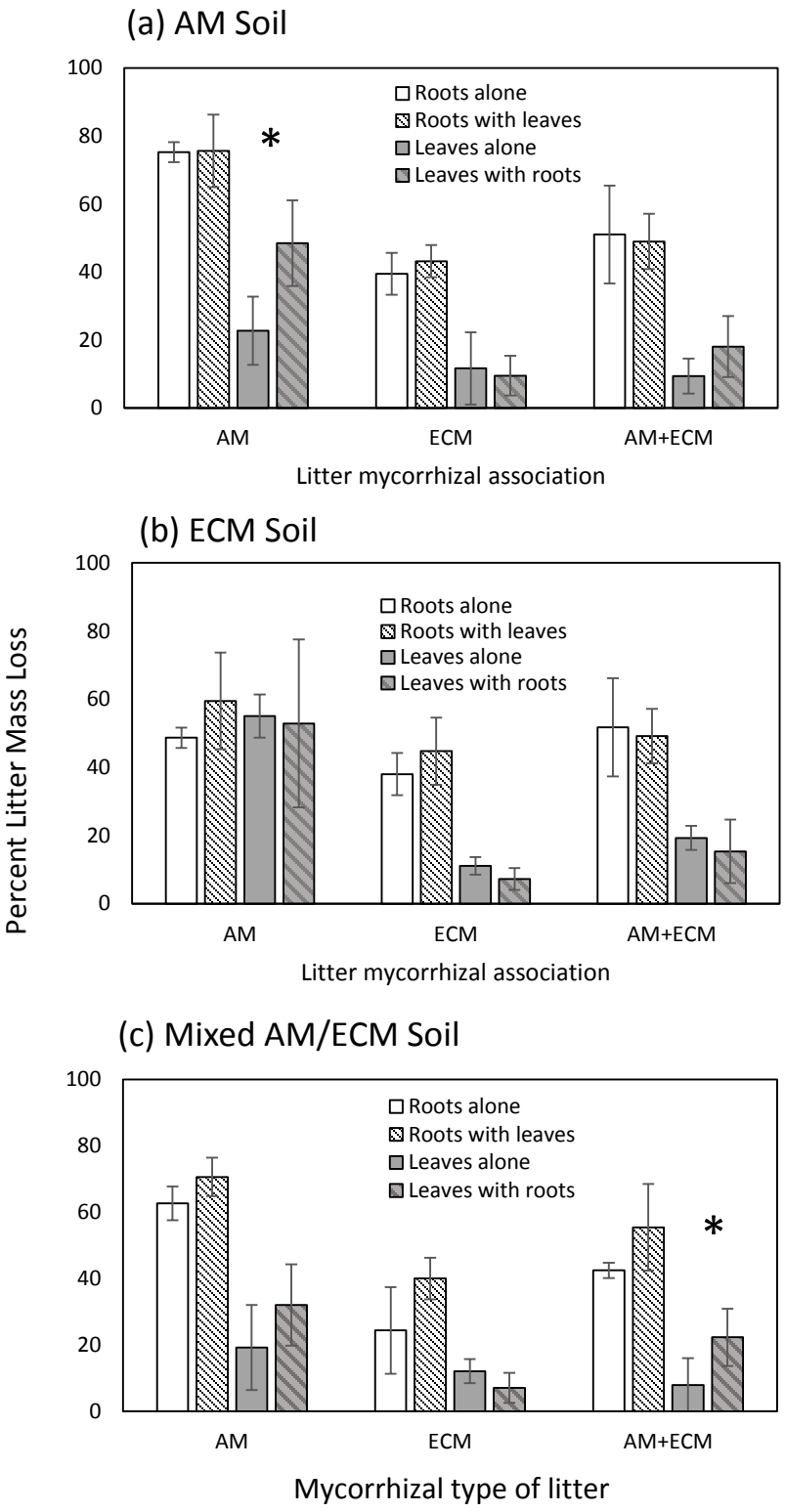



Figure 2. Percentage of root, leaf or root+leaf litter mass loss in AM (a), ECM (b), or AM/ECM (c) soils (N=4 replicates for all values). Asterisks indicate significant differences ($P < 0.05$) between roots and leaves decomposing alone vs. in the presence of the other litter type. 'Roots with leaves' is the average mass loss of roots (in the presence of leaves) whereas "leaves with roots" is the average mass loss of leaves (in the presence of roots). Error bars represent the standard deviation from the mean.

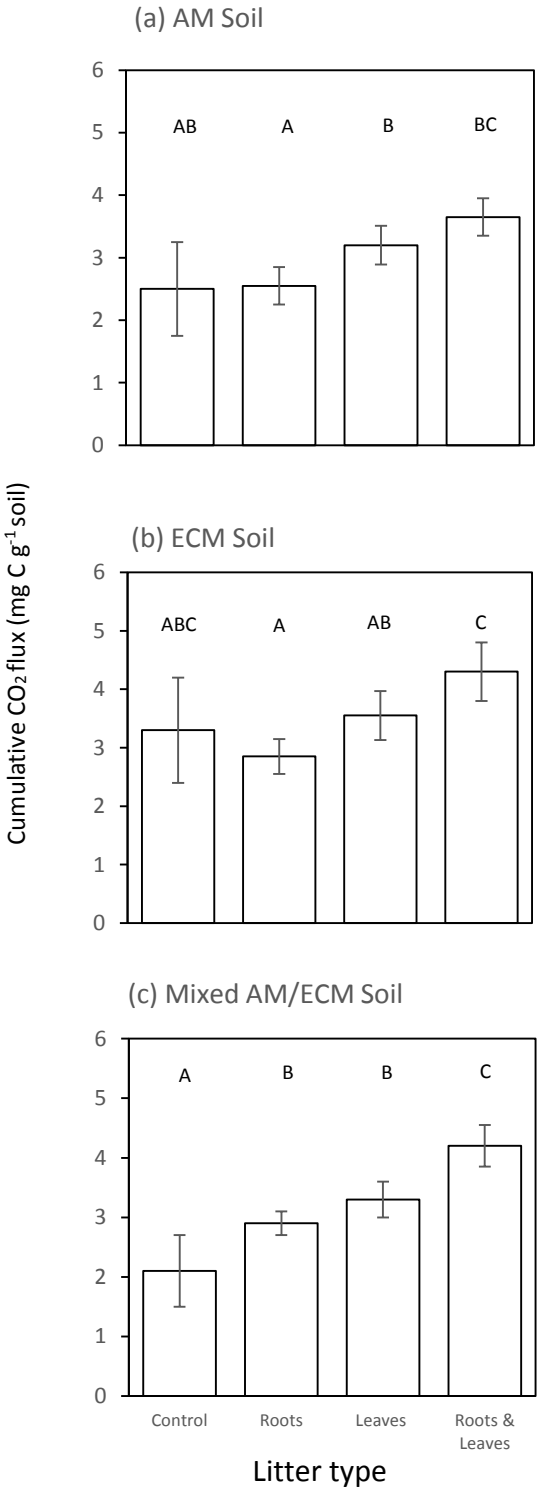



Figure 3. Total CO2 efflux from microcosms containing AM (a), ECM (b), or mixed AM/ECM (c) soils (N=12 replicates for each soil-litter combination). For each treatment, litter mycorrhizal types (AM vs. ECM vs mixed) are averaged. Error bars represent 95% confidence intervals. Different letters indicate significant differences between the means for each soil type ($P < 0.05$).

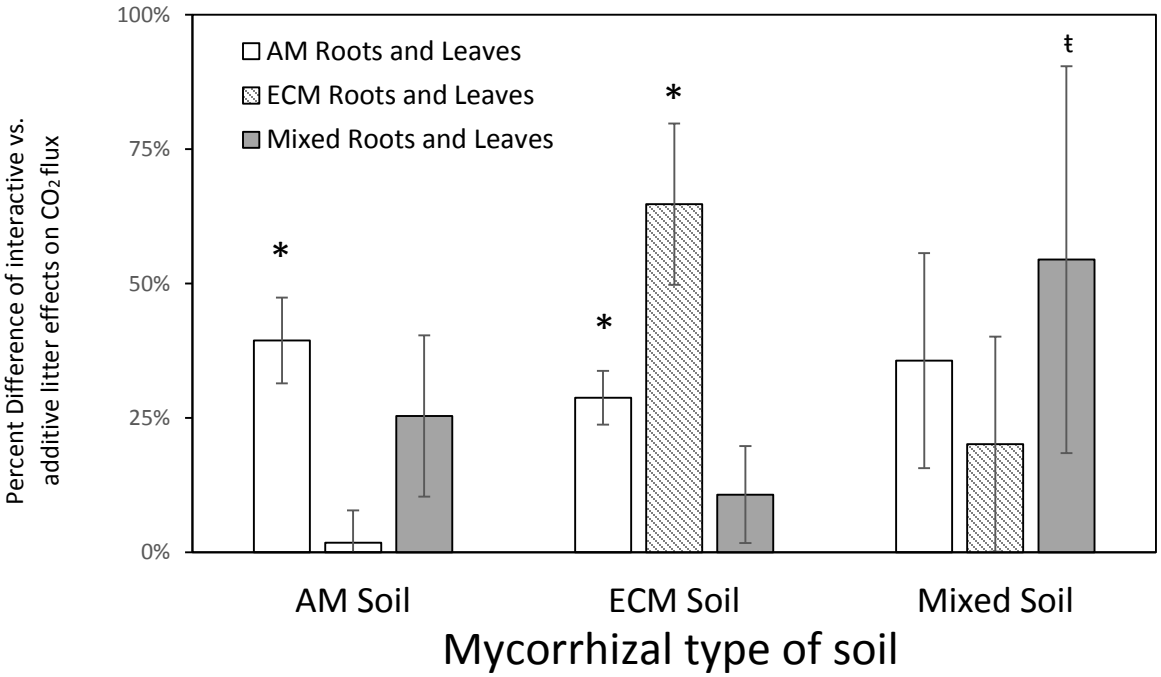



Fig. 4. Interactive vs. additive effects of root and leaf litter decay on CO2 efflux (N=12 discreet microcosms x 10 time points for each soil type control; N=4 discreet microcosms x 10 time points for each soil type-litter type-litter mycorrhizal combination). Bars indicate the size of the mean interactive effect relative to the mean additive effect (see Methods for details about how both terms were calculated). A value of zero indicates that CO2 efflux from microcosms containing roots and leaves was equal to the sum of CO2 efflux from the microcosms containing roots and leaves alone. Error bars represent the 95% confidence interval associated with the effect. Significantly different interactive effects (relative to additive effects), are denoted by asterisks ($P < 0.05$) and the ŧ symbol ($P < 0.1$).

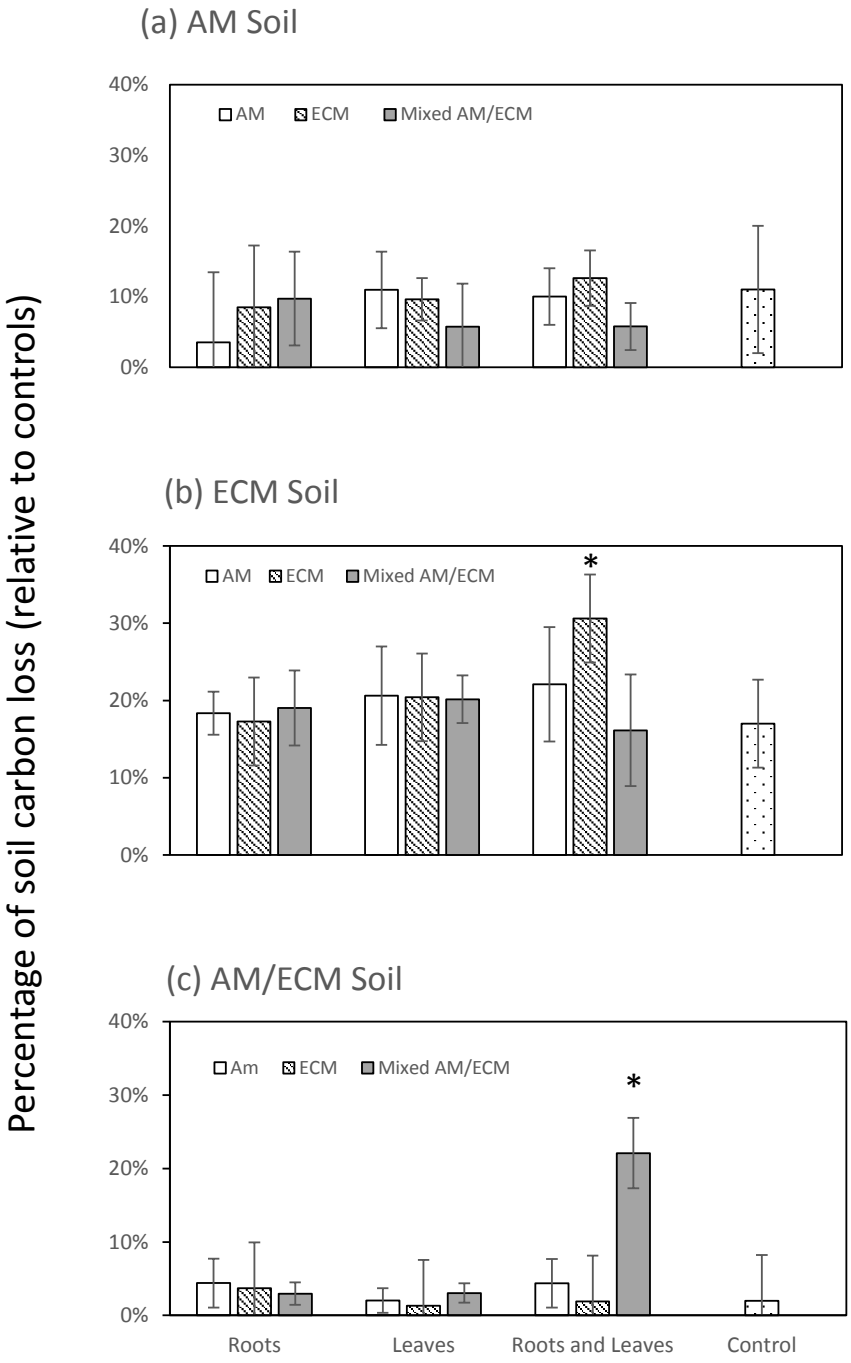
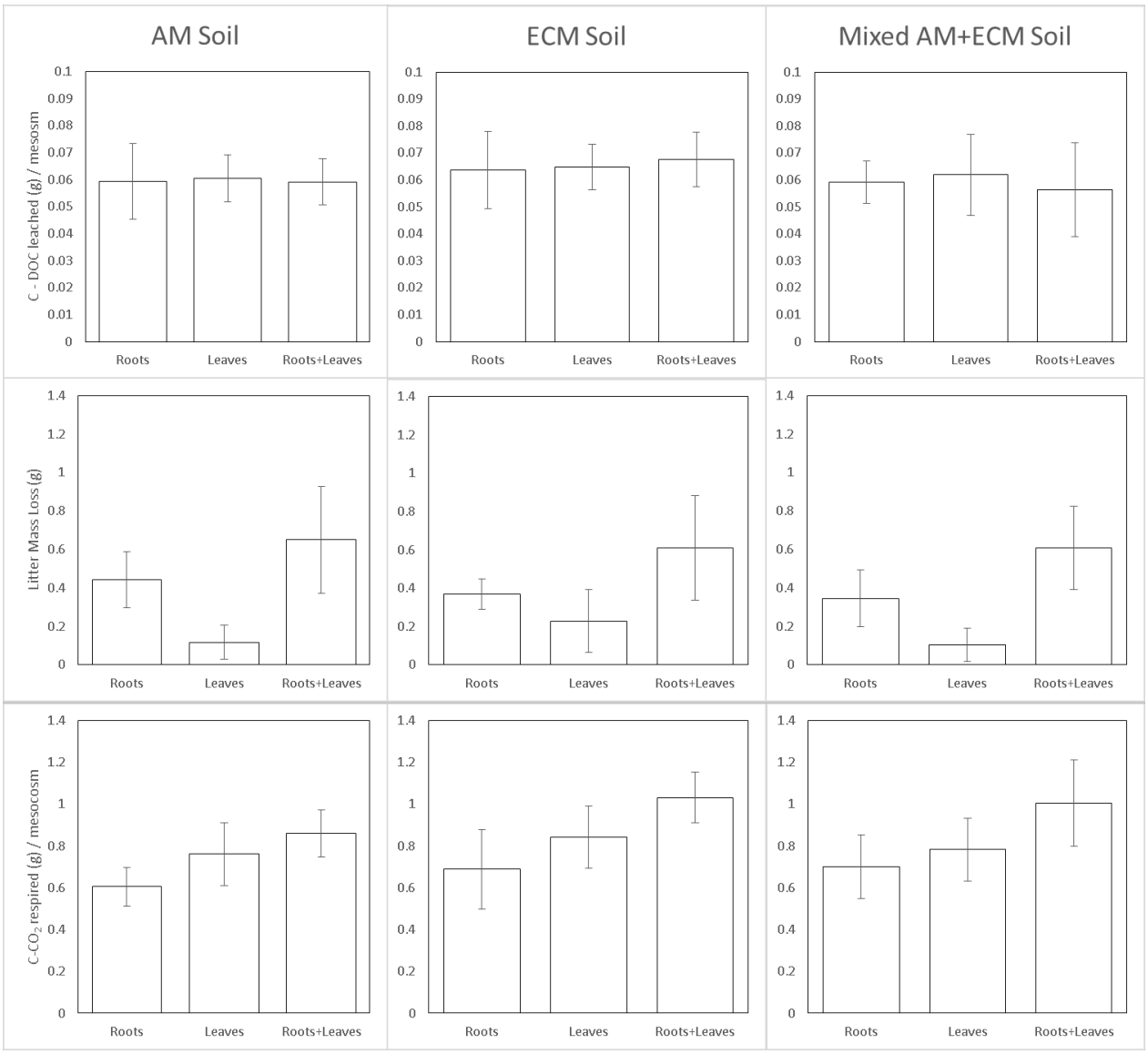
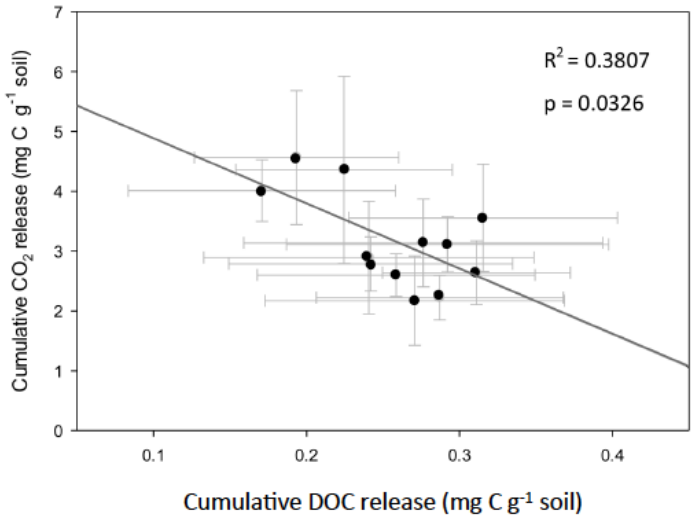



Figure 5. Percent loss of soil C over the course of the experiment (N=4 for each litter treatment except controls where N = 12). Asterisks indicate changes in soil C that differ significantly from controls ($P<0.05$). Error bars represent the standard deviation of the mean.

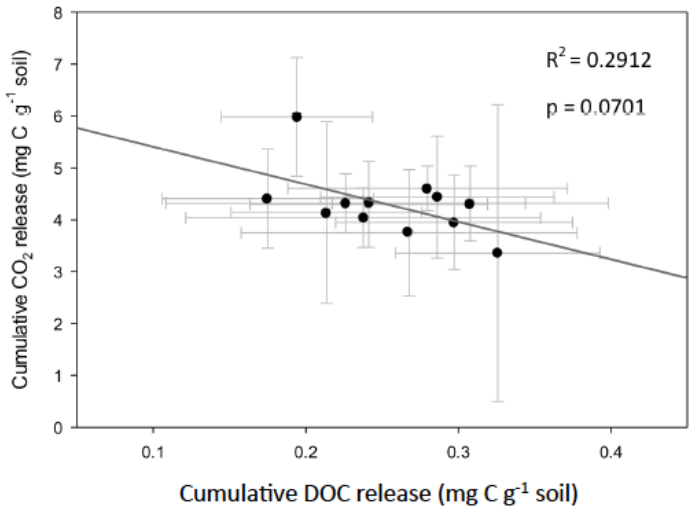



SI Figure 1. Cumulative losses of C (top and bottom rows) and biomass (middle row) from microcosms over the course of the experiment. Bars are mean values of C or mass loss from microcosms containing roots, leaves or roots + leaves (of AM, ECM and mixed litters) in AM, ECM or mixed soils. Cumulative C loss was calculated by linear interpolation between weekly measurements of dissolved organic C (DOC) leached and CO2 respired (N = 12; 3 mycorrhizal litter types x 4 replicates), assuming that measured rates of C flux scale linearly between time points. Mass loss was calculated by weighing litters prior to and following the incubation period (N = 12; 3 mycorrhizal litter types x 4 replicates). Error bars represent standard deviations of the mean.

(a) AM Soil with AM leaves




(b) ECM soil with ECM roots & leaves




Sl Fig 2. Cumulative C losses (as CO2 and DOC) from select microcosms. CO2 and DOC fluxes were significantly correlated ($P < 0.05$) for AM soils containing AM leaves (a) and marginally significant for ECM soils containing ECM roots and leaves (b). Other soil-litter combinations did not show significant relationships.

Table S1. Soil and litter properties (means) prior to incubation. Standard deviations are in parentheses. Asterisks denote significant differences ($P < 0.05$) between mycorrhizal types ($N = 12$ replicates).

| **Mycorrhizal association** | Organic matter (%) | **Roots C:N** | **Leaves C:N** |
|---|---|---|---|
| AM | 2.93 (0.32)* | 61.51(4.8)* | 45.55 (2.45) |
| ECM | 3.33 (0.24)* | 65.75 (2.71)* | 44.48 (1.97) |
| AM/ECM | 3.13 (0.22) | 63.33 (3.97) | 45.04 (2.73) |

Table S2. AM, ECM, and mixed AM/ECM litter C:N and percent SOM after the experiment in each litter treatment. Values are means and values in parentheses indicate standard deviation from the mean. N = 4 unless indicated otherwise.

| Soil Type | Litter mycorrhizal association | Litter Treatment | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | No litter | | Roots | | Leaves | | Roots + Leaves | | |
| | | Soil SOM (%) | *n* | Soil SOM (%) | C:N | Soil SOM (%) | C:N | Soil SOM (%) | Roots C:N | Leaves C:N |
| AM | AM | 2.61 +/- 0.27 | 12 | 2.83 +/- 0.34 | 40.39 +/- 1.61 | 2.61 +/- 0.18 | 40.58 +/- 7.89 | 2.64 +/- 0.14 | 40.51 +/- 1.55 | 40.08 +/- 9.53 |
| | ECM | | | 2.68 +/- 0.30 | 39.91 +/- 4.53 | 2.65 +/- 0.10 | 43.81 +/- 1.82 | 2.56 +/- 0.13 | 38.71 +/- 4.27 | 36.59 +/- 2.73 |
| | AM/ECM | | | 2.65 +/- 0.22 | 43.11 +/- 15.74 | 2.76 +/- 0.21 | 37.58 +/- 4.54 | 2.76 +/- 0.11 | 35.71 +/- 4.94 | 41.88 +/- 6.67 |
| ECM | AM | 2.77 +/- 0.22 | 12 | 2.72 +/- 0.11 | 38.74 +/- 9.42 | 2.64 +/- 0.19 | 40.30 +/- 7.70 | 2.74 +/- 0.26 | 36.42 +/- 8.47 | 39.63 +/- 10.15 |
| | ECM | | | 2.75 +/- 0.25 | 39.93 +/- 5.80 | 2.51 +/- 1.33 | 43.57 +/- 5.48 | 2.65 +/- 0.13 | 53.06 +/- 15.04 | 41.53 +/- 4.84 |
| | AM/ECM | | | 2.70 +/- 0.28 | 31.72 +/- 7.61 | 2.76 +/- 0.21 | 37.58 +/- 4.54 | 2.79 +/- 0.28 | 35.83 +/- 18.02 | 36.08 +/- 11.18 |
| AM/ECM | Am | 3.06 +/- 0.20 | 12 | 3.27 +/- 0.12 | 38.20 +/- 6.24 | 3.19 +/- 0.06 | 41.74 +/- 11.16 | 3.27 +/- 0.12 | 36.87 +/- 2.21 | 45.46 +/- 9.45 |
| | ECM | | | 3.01 +/- 0.21 | 32.93 +/- 9.12 | 3.09 +/- 0.15 | 45.32 +/- 4.80 | 3.07 +/- 0.22 | 37.57 +/- 18.87 | 42.54 +/- 12.77 |
| | AM/ECM | | | 3.22 +/- 0.06 | 34.72 +/- 7.41 | 3.03 +/- 0.05 | 35..75 +/- 16.12 | 2.64 +/- 0.87 | 33.75 +/- 17.01 | 40.81 +/- 12.07 |