1   **Title: Slowed decomposition in ectomycorrhizal ecosystems is independent of plant**

2   **chemistry**

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1   *Abstract:* **Ecosystems dominated by plants in symbiosis with ectomycorrhizal fungi store**

2   **more carbon in soils. There is increasing evidence that this may be due to competition**

3   **between primary producers and microbial decomposers for soil nitrogen, mediated by**

4   **ectomycorrhizal fungi. This competitive interaction inhibits decomposition and increases**

5   **soil carbon storage. However, other work suggests elevated carbon storage is due to**

6   **recalcitrant plant tissue chemistry in ectomycorrhizal ecosystems, rather than**

7   **ectomycorrhizal competition for soil nitrogen. These two frameworks make similar**

8   **predictions for soil carbon storage, making them difficult to distinguish empirically. Here I**

9   **argue that the ectomycorrhizal-recalcitrance hypothesis is not well supported by recent**

10 **developments in the understanding of soil carbon chemistry, or evolutionary relationships**

11 **among ectomycorrhizal plants. Therefore, differences in input chemistry are not sufficient**

12 **to discount alternative mechanisms of carbon stabilization in ectomycorrhizal ecosystems.**

13 **Future work on EM-specific stabilization of soil C should focus on alternative mechanisms**

14 **including competition for N, direct antagonistic interactions, and other microbial**

15 **community driven mechanisms.**

16   *Highlights*

17 1. Ectomycorrhizal ecosystems are associated with slowed decomposition and elevated soil

18 carbon storage.

19 2. This has classically been attributed to recalcitrant plant litter inputs in ectomycorrhizal

20 ecosystems.

21 3. I argue that input chemistry is unlikely explain to this effect.

22 4. Slowed decomposition in ectomycorrhizal ecosystems is more likely due to alternative

23 ecological interactions.

1   Ectomycorrhizal (EM) fungi are plant root symbionts that play a critical role in plant

2 nitrogen (N) nutrition (Read, 1991). This symbiosis is found across the Earth, from arctic to

3 tropical environments (Tedersoo et al., 2014). EM fungi have evolved multiple times from

4 saprotrophic ancestors (Tedersoo et al., 2010), and retain the ability to degrade organic carbon

5 (C) and N compounds in soil (Wolfe et al., 2012). This enables EM fungi to access organic N

6 trapped in soil organic matter directly. Arbuscular mycorrhizal (AM) fungi are the other

7 dominant class of mycorrhizal symbionts, representing a much older monophyletic clade. In

8 contrast to EM fungi, AM fungi seem to lack the capacity to express C and N degrading enzymes

9 (Tisserant et al., 2013). These fungi primarily rely on inorganic N sources, recycled via N-

10 mineralization by saprotrophic microbial decomposers (Hodge and Fitter, 2010; Phillips et al.,

11 2013). This difference in enzymatic capacity generates enormously different predictions of how

12 AM and EM ecosystems cycle C and N in soils.

13   Through multiple lines of evidence it has become clear that EM fungi express N-

14 degrading enzymes to *selectively* mine organic N substrates from soil (Baldrian, 2009; Lindahl

15 and Tunlid, 2015; Rineau et al., 2012; Shah et al., 2015). This allows EM plants to "short-circuit"

16 the traditional N-mineralization pathway (Schimel and Bennett, 2004), and compete directly with

17 free-living microbial decomposers for soil N resources. If this competition is strong enough it

18 may induce or exacerbate N-limitation of free-living decomposers, slowing soil C cycling and

19 increasing soil C storage. In this scenario, increased soil C stabilization is not driven by physical

20 protection, chemical recalcitrance, or changes in primary production. Rather, a competitive

21 interaction between primary producers and decomposers for soil N is mediated by EM fungi and

22 drives soil C stabilization at the ecosystem scale. This is the "EM-competition hypothesis".

23 Multiple lines of evidence suggest that EM dominated ecosystems are associated with slower

1 rates of soil C cycling and elevated soil C storage, consistent with the EM-competition

2 hypothesis (Averill et al., 2014; Averill and Hawkes, 2016; Gadgil and Gadgil, 1975, 1971;

3 Orwin et al., 2011).

4   Alternatively, it has been suggested that more recalcitrant plant chemistry in EM

5 compared to AM ecosystems can explain differences in soil C cycling and storage. Recalcitrant

6 here is defined as organic matter with high C:N and lignin concentrations. This is the "EM-

7 recalcitrance hypothesis". If recalcitrant plant tissues decompose more slowly at initial stages of

8 decay (Melillo et al., 1982), and first order decay dynamics are assumed, then ecosystems

9 dominated by plants with these traits will have greater levels of soil C storage (Parton et al.,

10 1987). If EM-associated plants tend to have more recalcitrant tissues (Cornelissen et al., 2001;

11 Read, 1991), then EM ecosystems will store more C in soils (Phillips et al., 2013). The EM-

12 competition and EM-recalcitrance hypotheses make the same prediction for soil C storage, and

13 are therefore confounded.

14   The problem with the EM-recalcitrance hypothesis is that its core premises are unlikely

15 to be true. Recalcitrant plant traits are not correlated with plants' ability to form an EM

16 symbiosis. Recalcitrant organic matter input does not drive greater C storage, and first order

17 decay dynamics cannot be assumed. In fact, if the EM-recalcitrance association were assumed,

18 new soil organic matter theory would make the opposite prediction: EM ecosystems should store

19 less C, rather than more.

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21 **Plant association with EM fungi and recalcitrant foliar chemistry do not emerge as a trait**

22 **syndrome.**

1   The idea that EM plants are selected to have recalcitrant tissues is old (Read, 1991), and is still

2   common today (Phillips et al., 2013). Researchers hypothesize EM plants exhibit low leaf

3   nutrients and high concentrations of lignin as a trait syndrome (Cornelissen et al., 2001).

4   However, this generalization is based on a limited number of EM host plants, primarily from the

5   Pinaceae and Fagales, despite a much broader diversity of EM hosts (Dickie and Moyersoen,

6   2008). Koele *et al.* (2012) use phylogenetic independent contrasts to determine if foliar nutrient

7   content (%N, %P) is actually correlated with mycorrhizal association, or emerges as an artifact

8   of phylogeny. They demonstrate that once phylogeny is taken into account, there is no difference

9   in plant foliar nutrient content between AM and EM associated hosts. Congeneric AM and EM

10   plants do not differ in these aspects foliar chemistry. Therefore, the hypothesis that mycorrhizal

11   association and recalcitrant tissue chemistry occur as a trait syndrome is unsupported, at least in

12   regard to foliar nutrient content.

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14   **Recalcitrant organic matter inputs do not increase soil C storage.**

15   It may still be the case that the most abundant EM plants have more recalcitrant tissues,

16   even if this is not due to a trait syndrome reinforcing EM association and tissue recalcitrance.

17   However, this does not support the argument that EM ecosystems should store more C. Recent

18   work has demonstrated that most soil organic matter is chemically labile (e.g. amino acids and

19   simple sugars), that recalcitrant and labile organic matter have similar turnover times, and that

20   recalcitrant organic matter inputs are not associated with increases in soil C storage (Schmidt et

21   al., 2011). Expanding on these findings, the recently developed MEMS-framework hypothesizes

22   that recalcitrant organic matter inputs reduce microbial carbon use efficiency, and therefore

23   decrease soil C storage (Cotrufo et al., 2013). This framework is supported by long term (>5yr)

1 leaf litter decomposition experiments (Berg, 2000; Berg and Ekbohm, 1991). Interactions

2 between substrate chemistry and microbial carbon use efficiency may decouple the *rate* at which

3 plant tissues are decomposed, and the *efficiency* with which they are retained in the soil carbon

4 pool. Given new conceptual developments, the EM-recalcitrance hypothesis should argue EM

5 ecosystems should store less carbon, not more (Figure 1, reproduced and modified with

6 permission from Cotrufo et al. 2013).

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8   Soil organic matter cycling is a fundamentally ecological process, with major control

9 exerted by the organisms that execute decay reactions and the interactions among those

10 community members. A new class of non-linear decomposition models is emerging that

11 embraces these features of decomposition and is transforming how we understand the process of

12 carbon cycling (Allison, 2012; Allison et al., 2010; Averill, 2014; Cotrufo et al., 2015; Hawkes

13 and Keitt, 2015; Sulman et al., 2014; Waring et al., 2013; Wieder et al., 2014). The insight

14 generated from these models, as well as the current upheaval in the understanding of soil C

15 chemistry (Lehmann and Kleber, 2015), requires us to completely rethink our classic

16 understanding of decomposition (Melillo et al., 1982; Parton et al., 1987). While I have

17 emphasized the EM-competition mechanism here, other mechanisms may contribute to

18 differences in C-cycling and storage between C-cycling and storage between AM and EM

19 ecosystems (Fernandez and Kennedy, 2016). Given the present state of understanding, future

20 research should de-emphasize idea that EM ecosystems store more C due to correlations with

21 input chemistry, and seriously consider alternative C-stabilization mechanisms unique to EM

22 ecosystems, including competitive interactions within and across trophic levels.

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Figure Legend

2 Figure 1: Predicted mass loss trajectories of labile (high nutrient, low lignin) vs. recalcitrant (low

3 nutrient, high lignin) litter types, based on Cotrufo et al 2013, Berg and Ekbohm 1991.

4 Arbuscular mycorrhizal litters are classically thought to be labile, while ectomycorrhizal litters

5 are thought to be recalcitrant. Reproduced and modified with permission from Cotrufo et al.

6 (2013).