

## Commentary

# Moving beyond the black-box: fungal traits, community structure, and carbon sequestration in forest soils

More carbon (C) is stored globally in soils than biotic and atmospheric pools combined (Lal, 2004). As such, the biogeochemical processes affecting the amount of C sequestered in soil have major implications for global climate change. Despite the fact that most plants associate with mycorrhizal fungi and allocate significant amounts of C to these symbionts in order to gain access to soil nutrients and water (Godbold *et al.*, 2006; Hobbie, 2006; Allen & Kitajima, 2014), the input of mycorrhizal fungal biomass, its turnover, and potential contribution to C sequestration in soil organic matter (SOM) has been largely overlooked until recently (Langley & Hungate, 2003). The significance of mycorrhizal fungal inputs, however, was convincingly demonstrated by Clemmensen *et al.* (2013), who used bomb carbon-14 ( $^{14}\text{C}$ ) modeling coupled with biomarker analysis to show that the majority of C stored in SOM in a boreal forest system was of root and fungal origin. In this issue of *New Phytologist*, Clemmensen *et al.* (2015, pp. 1525–1536) explore the link between community composition of mycorrhizal fungi and soil C sequestration in the same study system. Their results clearly indicate that simplistic ‘black-box’ approaches to studying soil fungal communities miss important ecological patterns and that shifts in species traits, both within and among fungal guilds, may be key determinants of C sequestration in forest soils.

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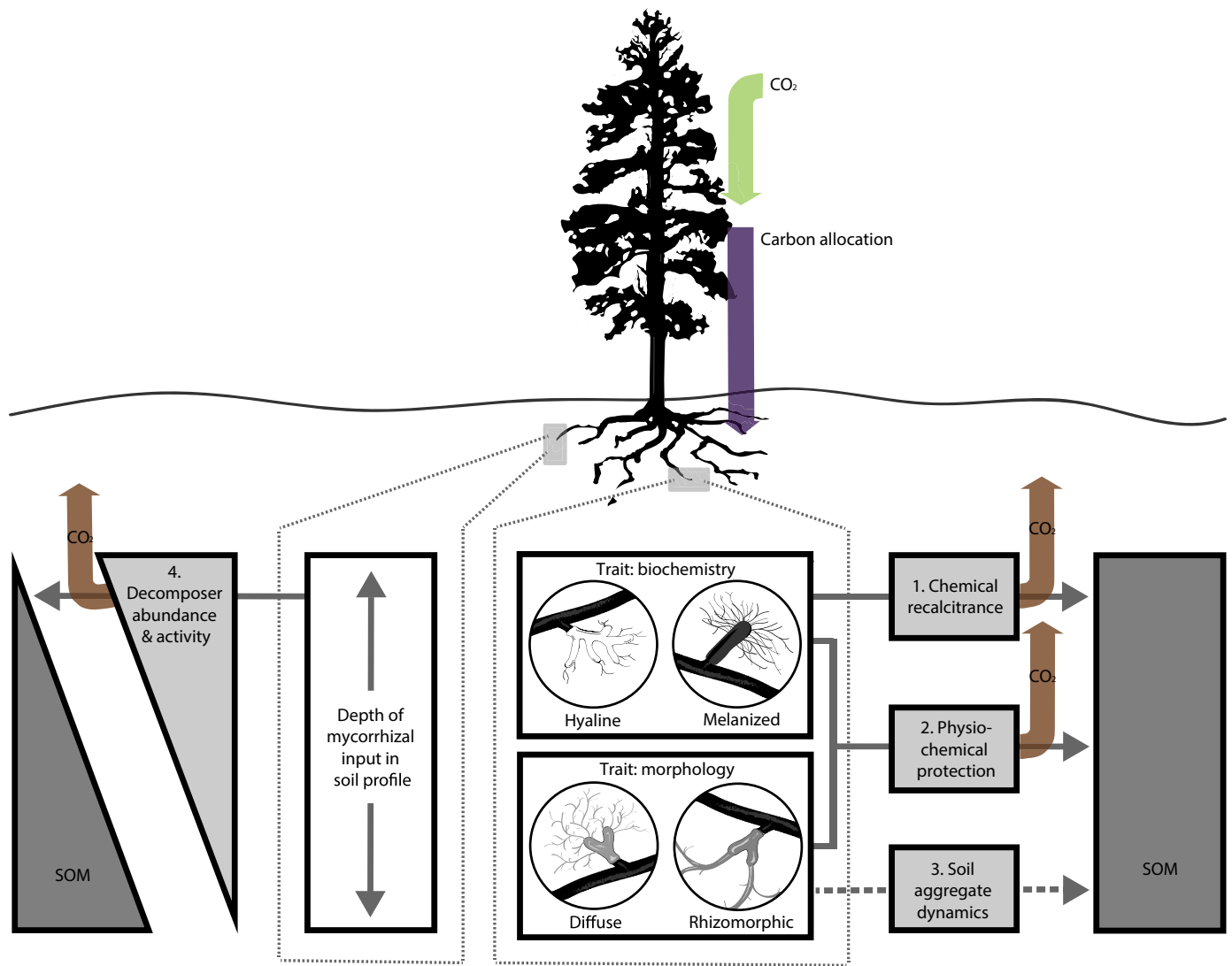
*‘... shifts in species traits, both within and among fungal guilds, may be key determinants of carbon sequestration in forest soils.’*

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The researchers use a natural island-based successional gradient to show that younger soils in the chronosequence (i.e. on larger islands) had a higher abundance of ectomycorrhizal (ECM) fungal species that produce rhizomorphic exploration types (Agerer, 2001) vs older soils (i.e. on smaller islands), which had more ECM fungi that produce diffuse mycelial exploration types. They also document shifts in fungal guild prevalence across islands, with a change from larger islands being dominated by ECM fungi to

smaller islands having a greater proportional abundance of ericoid mycorrhizal (ERM) fungi. Combining these results with the increased soil C accumulation observed on smaller islands (Clemmensen *et al.*, 2013), Clemmensen *et al.* (2015) suggest that the shifts in fungal community structure may in fact be driving the sequestration of C in SOM. Their argument is based on two aspects of the observed changes. First, they reason that ECM fungi with rhizomorphic exploration types, which dominate on larger islands, produce mycelia where the hyphae at the leading fronts are highly ephemeral and rapidly decompose after turnover. Furthermore, rhizomorphic ECM fungi may be particularly efficient in recycling their own biomass. Together, these traits would lead to fast turnover of ECM fungal tissues and reduced C input into SOM pools. Conversely, ECM fungi producing more diffuse exploration types have less efficient recycling of their tissues, resulting in a relatively larger contribution of necromass into soil C cycles after their death. Although there is evidence showing that rhizomorphic wood-rot fungi are quite efficient recyclers of their own biomass (Boddy, 1999), to our knowledge, trade-offs among exploration type, decomposition rate, and biomass recycling for ECM fungi have yet to be demonstrated. The second part of their logic is that ERM fungi, which dominate on smaller islands, frequently possess heavily melanized hyphae, a fungal trait that appears to be particularly important in determining the decomposability of fungal necromass. Research in other systems has shown that fungal necromass decomposition is strongly negatively affected by increasing melanin concentration (Fernandez *et al.*, 2013; Fernandez & Koide, 2014). Clemmensen *et al.* (2015) provide additional support to this pattern by showing significant correlations between the abundance of melanized fungi and C accumulation in SOM. While the authors correctly acknowledge that the correlative nature of their study does not allow causation to be inferred (i.e. whether fungal traits drive C sequestration or vice versa), taken together, the shifts in these key fungal traits provide intriguing evidence about the directionality of this relationship.

There are a number of possible explanations for why soil fungal community composition and soil C sequestration may be causally linked (Fig. 1). Clemmensen *et al.* (2015) focus on the potential effects of chemical recalcitrance of mycorrhizal fungal necromass on the accumulation of fungal derived carbon in SOM. With regard to melanized fungal necromass, the physiochemical properties of melanized hyphae have also been noted to have higher bonding interaction with soil mineral components compared to hyaline hyphae (Fomina & Gadd, 2003). This latter factor may result in physiochemical protection of this C, which would also result in increased incorporation into stable SOM. Along with these direct effects on C accumulation through mycorrhizal inputs, fungal hyphae are directly involved in the stabilization of soil C through soil aggregate formation and stabilization (Rillig *et al.*, 2015, this issue of *New Phytologist*, pp. 1385–1388). Soil particles are aggregated



**Fig. 1** Conceptual diagram of carbon (C) flow through plants and fungi in forest ecosystems. Carbon enters with CO<sub>2</sub> fixation (green arrow) followed by host plant C allocation to mycorrhizal fungi (purple arrow). These fungi vary in biochemical (hyaline vs melanized) and morphological (diffuse vs rhizomorphic) traits as well as distribution in the soil profile. Solid lines leaving the trait boxes represent the turnover of mycorrhizal biomass whereas the dashed lines indicate the biotic activity of mycorrhizal fungi. Light gray boxes represent four nonexclusive potential controls of C accumulation in soil organic matter (SOM). Brown arrows represent the CO<sub>2</sub> flux as a result of decomposition of the mycorrhizal necromass. The widths of the triangular boxes at a given depth in the soil profile indicate the magnitude of the pool or process.

through the activity of fungi (and fine roots) and as a result the C contained in these aggregates is protected from decomposition processes (Schmidt *et al.*, 2011; Rillig *et al.*, 2014). Given the importance that morphological traits of fungal mycelia have on the likelihood of encountering and interacting with soil particles (Rillig *et al.*, 2014), shifts in community structure from mycorrhizal fungi with rhizomorphic to diffuse exploration strategies likely have strong effects on these processes as well. ECM fungi exhibiting a diffuse and medium distance exploration types have been shown to have greater coverage per area of soil occupied than long distance rhizomorphic exploration types (Weigt *et al.*, 2011). This greater coverage of a given volume of soil may increase C protected through aggregate formation and stabilization.

Along with differences in mycorrhizal fungal community structure, the fact that Clemmensen *et al.* (2015) also found a

higher abundance of fungi from decomposer guilds in the younger soils supports their claim that C cycling on larger islands may be relatively faster and result in lower soil C accumulation. Additionally, unlike aboveground inputs, root and soil fungal biomass is produced and subsequently decomposed at specific depths in the soil profile. The authors showed that both ERM fungi and diffuse exploration type ECM fungi generally increase in abundance with soil depth across the chronosequence. Because decomposer activity sharply declines with soil depth (Schmidt *et al.*, 2011), fungal necromass produced deeper in the soil profile may be spatially segregated from the majority of decomposers and result in a net accumulation of C, which may also explain the positive association between these guilds and C sequestration. Regardless of the specific mechanisms responsible (all of which are not mutually exclusive), the results

of their new study provide strong support to the conceptual framework put forth by Koide *et al.* (2013), which posited that traits of mycorrhizal fungi that are adaptive to environmental factors (response traits) may also be the drivers of ecosystem processes (effect traits). The results of Clemmensen *et al.* (2015) also reinforce the idea that a better understanding of the autecology of mycorrhizal fungal species will likely be crucial in improving our ability to explain and predict both fungal community shifts and the associated consequences on ecosystem processes (Peay, 2014).

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While this new study provides exciting insight into the influence of mycorrhizal fungi on C sequestration in soils, the generality of its findings remain to be tested. Plant C allocation to fungal symbionts may differ greatly across ecosystems (as has already been demonstrated for ECM fungi; Hobbie, 2006), which may alter the importance of root associated fungal C that enters into stable SOM fractions. Utilization of chronosequences like the one used in Clemmensen *et al.* (2013, 2015) is a powerful approach to understand processes that occur on longer timescales (Dickie *et al.*, 2013; Martínez-García *et al.*, 2015, this issue of *New Phytologist*, pp. 1565–1576) and comparing similar temperate and tropical chronosequences is one promising direction for assessing the robustness of their findings. In addition to correlative approaches, manipulative experiments involving long-term soil incubations of isotopically-labeled fungal necromass coupled with high-resolution analytical chemistry techniques will be key to providing a mechanistic understanding of sequestration of mycorrhizal fungal C in soils. In particular, experiments examining the relative roles of chemical, physical, and physiochemical protection of mycorrhizal fungal C from decomposition will greatly enhance our understanding of mycorrhizal influence on C sequestration in soils. Finally, the incorporation of fungal necromass inputs into global C cycle models will also be an important next step, given the large amount of C entering the soils as mycorrhizal fungal biomass (Clemmensen *et al.*, 2013) and the differences in the biochemical and morphological traits of these inputs depending on ecosystem age (Clemmensen *et al.* (2015).

## Acknowledgements

The authors thank L. Lofgren for the digital rendition of Figure 1 and M. Öpik for helpful input on an earlier version of this commentary.

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**Key words:** carbon cycle, microbial black-box, mycorrhizal fungi, soil organic matter, traits.