Editorial: Forest Rhizosphere Interactions: Cascading Consequences for Ecosystem-Level Carbon and Nutrient Cycling

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Editorial on the Research Topic

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Mycorrhizal fungi mine organic matter and subsequently transfer plant-available nutrients to roots. While there is disagreement considering the role of mycorrhizal fungi in ecosystem carbon (C) and nutrient cycling relative to factors such as climate (Cotton, 2018; Bennett and Classen, 2020), soil nutrient availability (Brzostek et al., 2015; Frey, 2019), or host plant community composition (Read and Perez-Moreno, 2003), it is now clear that mycorrhizal fungal symbionts control a substantial proportion of C and nutrient flow belowground (Steidinger et al., 2019). Yet, determining the relative importance of arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi to these processes is still an open field of inquiry in ecosystem ecology (Averill et al., 2019a) and earth system modeling (Sulman et al., 2019). At large scales, ecosystems dominated by EM fungi are thought to store more soil C per unit nitrogen (N) (Averill et al., 2014), have slower N cycles (Phillips et al., 2013), and respond more strongly to global change drivers such as N-deposition (Jo et al., 2019). However, it is unclear how generalizable these patterns are across sites, and plant and mycorrhizal taxa. If site or species-dependent relationships exist between mycorrhizal plants, fungi, and soil biogeochemical cycles, forecasting hot spots and hot moments of mycorrhizal fungal activities and their consistency across space and time would be even more challenging (Averill et al., 2019b; Kivlin and Hawkes, 2020).

Mycorrhizal contributions to ecosystem biogeochemical cycles are especially difficult to understand and predict in the context of environmental disturbances, such as land use and land cover change (e.g., mining, clear cut logging, forest fire, and exotic plant species invasion). If the disturbance is strong or persistent enough, mycorrhizal fungi may experience negative outcomes (Rudgers et al., 2020). Indeed, the legacy of prior environmental conditions may be too much to overcome, especially when climate and resource regimes are drastically altered (Hawkes et al., 2020). Yet, understanding when mycorrhizal fungi can withstand or are altered by disturbance is important because these fungi can potentially jump-start ecosystem recovery processes following a perturbation (Koziol et al., 2018; Vahter et al., 2020).

In this Research Topic we highlight six studies that examine the roles of mycorrhizal fungi on ecosystem resource dynamics in both undisturbed and disturbed terrestrial ecosystems.

Across a range of mycorrhizal-dominated forests in northeastern United States, Fitch et al. found that both the fungal-bacterial ratio (a marker of microbial community composition) and carbon to nitrogen ratio (an indicator of substrate quality) increased across an EM gradient (from no EM trees to 79% EM tree cover). Carbon use efficiency (CUE) increased with increasing relative abundance of EM fungi. Enzyme activities were correlated with metrics of community composition, but not with indicators of substrate quality. These results show a promising way forward for predicting ecosystem function and microbial composition from overstory tree composition and represent a step toward disentangling the effects of microbial community composition and substrate quality on biogeochemical cycling across gradients of mycorrhizal associations. Congruently, in midwestern United States forests, Midgley and Sims identified that EM-dominated forests had higher C:N ratios compared to AM-dominated forests. Here, EM forests also had faster rates of C and N cycling, reflected by rates of mineralization and enzyme activities. Biogeochemical cycling was better predicted by mycorrhizal association than by leaf quality, adding to the evidence that differences in biogeochemical cycling between AM and EM associations are driven by microbial community traits, not just by leaf litter properties. These two studies provide a contrast to other work demonstrating that EM-dominated forests slow N mineralization and enzyme activity rates (Averill et al., 2014). Therefore, there is still much to learn about site- or tree species-dependent effects of mycorrhizal associations on biogeochemical cycling.

Furthermore, within-guild mycorrhizal functional representations may not be ubiquitous. In this issue, Keller and Phillips found large variation in plant allocation of C belowground within and among mycorrhizal fungal guilds in a greenhouse experiment. In general, AM plants and fungi functioned as mutualists with positively associated acquisition of N per unit belowground C allocation. EM fungus—plant relationships were not beneficial resulting in a negative relationship between C allocation and N acquisition. There was also considerable variation in this relationship across tree species. These results confirm that the utility of predicting and modeling ecosystem biogeochemical cycling based on mycorrhizal association may be useful for some parameters (soil C:N). However, the influence of mycorrhizal association on narrower biogeochemical pathways, such as enzyme degradation and plant nutrient uptake, is subject to significant uncertainties given the high functional diversity of plants and fungi.

Because biogeochemical cycles can take decades to centuries to develop, the effects of mycorrhizal fungi on ecosystem biogeochemical cycles remains largely observational, or is measured in manipulated monodominant stands of trees with known mycorrhizal associations (Midgley and Sims). However, natural manipulations may provide the large-scale experimental designs necessary to test the mycorrhizal impact on ecosystems across environmental conditions. In their review article, Hoeksema et al. take advantage of natural co-invasions of EM fungi and EM hosts to evaluate how mycorrhizal traits alter ecosystem function. Their analysis determined that introduced and invasive forest species, namely *Pinus* sp., dominated by EM associations stored more soil C than adjacent native AM forests, but invaded grasslands lose soil carbon, and that carbon storage and loss is ultimately linked to differences in N availability between native and invaded ecosystems. Coupling natural experiments with controlled laboratory manipulations provides the opportunity to test hypotheses and improve our ability to predict how mycorrhizal fungi alter biogeochemical cycling with implications at the landscape scale, and across biomes. Overall, Midgley and Sims and Hoeksema et al. provide valuable contributions that incorporate mycorrhizal and microbial function to inform and test emerging biogeochemical models.

At the same time, mycorrhizal associations can also contribute to ecosystem restoration. In a qualitative review of mycorrhizal inoculum restoration studies, Policelli et al. identified promising success stories of EM fungal remediation of degraded ecosystems. Across multiple studies, EM fungi enhanced plant recovery from heavy metal contamination and soil erosion after mining, clear-felling, fire and in one case study during restoration after exotic plant invasion. While these results incentivize further inquiry, especially into ecosystem biogeochemical responses to inoculation, they also should be interpreted with caution as a 13-year survey of soil fungal recovery following mining in Australia revealed few signs of successful fungal recovery to undisturbed conditions (Hart et al.). Therefore, remediation techniques may also have long-lasting effects on fungal communities for decades to come and must proceed with caution.

Overall, this Research Topic highlighted how mycorrhizal fungi can control some common ecosystem biogeochemical parameters (e.g., soil C:N) fairly consistently, but many others (e.g., nutrient cycling, enzyme activities) remain context-dependent, based on site conditions and plant species. Further inquiry using natural experiments of invading exotic EM forests surrounded by native AM forests or planned restoration with mycorrhizal fungal inoculation is certain to provide much-needed landscape-scale evidence of such plant-mycorrhizal fungal-soil interactions across biomes.

AUTHOR CONTRIBUTIONS

SK led the writing of this editorial with comments from the other authors. All authors contributed to the article and approved the submitted version.

ACKNOWLEDGMENTS

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