Commentary

Stepping forward from relevance in mycorrhizal ecology

Over the past decade, categorizing plants by the mycorrhizal fungi on their roots has allowed us to collapse the complexity of plant life's hidden, belowground half into a simple, sometimes even binary variable. Most plants are now being classified as associating primarily with ectomycorrhizal or arbuscular mycorrhizal fungi to facilitate soil nutrient uptake (Brundrett & Tedersoo, 2018; but see Bueno *et al.*, 2019). A plant's mycorrhizal 'type' predicts its soil environment's carbon (C) and nitrogen (N) stocks (Averill *et al.*, 2014; Cotrufo *et al.*, 2019), its response to global change pressures (Terrer *et al.*, 2016; Averill *et al.*, 2018), and even its global biogeography (Steidinger *et al.*, 2019). Mycorrhizal fungi are no longer journeying towards relevance to broader ecosystem science and biogeochemistry, as once suggested (Read & Perez-Moreno, 2003) – they have arrived.

> *'... the coming era of mycorrhizal ecology and its path forward from relevance ought to be built not upon plant and fungal binaries, but upon continua and communities.'*

Biogeochemical differences between ectomycorrhizal- and arbuscular mycorrhizal-associated plants and ecosystems, for example that the former have higher soil C : N ratios (Averill *et al.*, 2014) and a stronger carbon dioxide (CO_2) fertilization response (Terrer *et al.*, 2016) than the latter, are often attributed to physiological differences between ectomycorrhizal and arbuscular mycorrhizal fungi. Indeed, ectomycorrhizal fungi generally take up organic nutrients from soil more effectively than arbuscular mycorrhizal fungi do, which can affect whole-ecosystem elemental cycling (Orwin *et al.*, 2011; Phillips *et al.*, 2013). But if trait differences between ectomycorrhizal and arbuscular mycorrhizal plants and fungi can cause ecosystem function to diverge, then the scale at which meaningful variation occurs, whether between or within groups, could affect the scale at which such patterns emerge. A reasonable simplification has brought us relevance, but refinement thereof might thus offer even greater utility.

In this issue of *New Phytologist*, Fernandez *et al.* (2020; pp. 569–582) invite us to expand our thinking. The Gadgil effect, where resource uptake, especially of organic N, by ectomycorrhizal fungi slows litter decomposition by starving free-living saprotrophs (Fernandez & Kennedy, 2016), is hypothesized to drive soil C accumulation in ectomycorrhizal ecosystems (Orwin *et al.*, 2011; Averill *et al.*, 2014). However, theory predicts its occurrence only where ectomycorrhizal N mining abilities are strong and litter N is hard to access (Smith & Wan, 2019). Testing this prediction, Fernandez *et al.* performed a reciprocal litter decomposition and mycorrhizal exclusion experiment in two ectomycorrhizal forests, each with different leaf litter chemistry and a different ectomycorrhizal fungal community.

Excluding roots and mycorrhizal fungi in a pine forest accelerated the decomposition of pine litter but not of oak litter, while the same treatment in an oak forest had no effect on the decomposition of either litter. Only where recalcitrant litter and an ectomycorrhizal community adapted to it co-occurred could ectomycorrhizal N uptake slow decomposition. Fernandez *et al.* thus show that the same divergence in ecosystem function we expect to see across plant communities of different mycorrhizal type can also be found where mycorrhizal type does not differ, because the traits of the resident plants and fungi may nevertheless vary. In doing so, they demonstrate that the coming era of mycorrhizal ecology and its path forward from relevance ought to be built not upon plant and fungal binaries, but upon continua and communities.

In addition to expanding our basic knowledge about mycorrhizal functioning, these findings also allow us to take a step towards more detailed spatial predictions of ectomycorrhizal effects on nutrient cycling. To illustrate this point visually, we combined forest inventory data from the US Forest Service, tree leaf litter trait measurements drawn from the literature, and occurrence records of *Tomentella*, the dominant ectomycorrhizal genus in the pine forest studied by Fernandez *et al.*, from the Global Biodiversity Information Facility (GBIF.org, 2019). Then, we generated a map of the contiguous United States depicting the average litter lignin : N ratio of measured forest plots, their primary mycorrhizal type, and the locations where *Tomentella* has been reported (Fig. 1).

Based on the results of Fernandez *et al.*, we speculate that the Gadgil effect should be most pronounced in ectomycorrhizal forests with high litter lignin : N ratios where *Tomentella* is common. In Fig. 1, regional gradients of litter lignin : N ratio appear nested within larger, continent-wide gradients, indicating that the strength of the Gadgil effect probably varies at multiple scales. Though *Tomentella* is widely distributed, ectomycorrhizal fungal community turnover, which also occurs at scales spanning several orders of magnitude (Smith *et al.*, 2018), is another likely source of variation. This suggests that coordinated, hierarchically structured research efforts, perhaps similar in design to prior studies of litter decomposition (e.g. Bradford *et al.*, 2017), could be useful for determining the relative contributions of aboveground and belowground trait variation to ecosystem biogeochemistry. Additionally, since it is not clear which specific traits enable *Tomentella*

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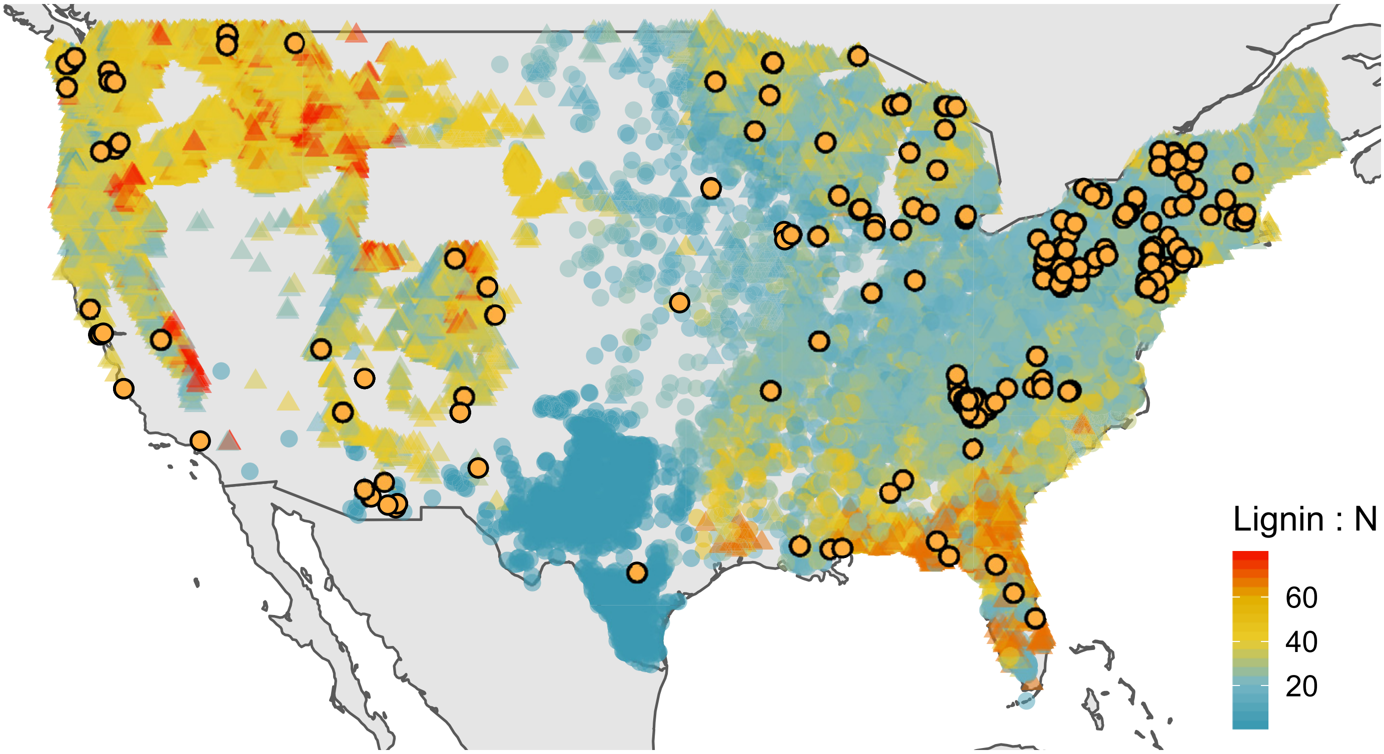

Fig. 1 Average litter lignin : nitrogen (N) ratios of trees in plots assessed by the US Forest Service Forest Inventory and Analysis program, weighted by basal area. Here, we show forest plots measured between 2005 and 2009 (inclusive) with no evidence of recent burning or silvicultural treatment and in which we had litter lignin : N values for the trees comprising at least 80% of the total basal area ($n = 33\,496$). Triangles represent plots with majority ectomycorrhizal tree species, while circles are majority arbuscular mycorrhizal; trees are categorized according to the classifications of Steidinger *et al.* (2019). Orange dots represent the coordinates of *Tomentella* records from the Global Biodiversity Information Facility ($n = 482$).

to compete effectively with saprotrophs, such projects could benefit from the application and development of trait databases like Fun$^{\text{Fun}}$ (Zanne *et al.*, 2019) to identify other important, functionally analogous taxa.

Our field's progress over the past 10 years has been remarkable, and we may be rightfully pleased with our achievements. The coming decade of mycorrhizal research will surely bring more fascinating discoveries, some lending support to long-held hypotheses and others defying our wildest expectations. However, the findings of Fernandez *et al.* demonstrate that answering the many remaining questions in mycorrhizal ecology will best be served by approaching them with an open mind rather than restricting our thinking to the same conceptual frameworks that have brought us here. Together, we have reached a notable height. As has long been emphasized (Wumen, 1228), we are confident that the greatest benefit will now be gained not by clinging to our perch or admiring the view, but by stepping forward.

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