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Still scratching the surface: how much of the “black box” of soil ectomycorrhizal communities remains in the dark?

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Symbiotic soil organisms such as ectomycorrhizal fungi (EMF) were long thought of as an
inscrutable “black-box”, yet the advent of molecular technologies has driven rapid advances in
identification and enumeration of their diversity (Horton & Bruns, 2001; Buée et al., 2009).
For instance, one 20 cm soil core can impressively yield 100’s of fungal OTUs (Taylor et al.,
2013). Importantly root symbionts play functional roles in sequestration or breakdown of soil
carbon pools (Trumbore & Czimczik, 2008; Harrison et al., 2011a,b; Clemmensen et al., 2013;
Kramer et al., 2013), nutrient and water cycling (Virginia et al., 1986; Read & Perez-Moreno,
2003), alteration of soil porosity (Perry et al., 1990), and provision of sustenance for different
trophic levels (Coleman & Whitman, 2005).
Yet root symbionts occur and contribute to function far deeper in the soil than is usually
sampled (Jenkins et al., 1988; Dalpé et al., 2000; Bornyasz et al., 2005). Soil properties vary
considerably among ecosystems (Schenk, 2005; Dickie et al., 2013), hence so too does rooting
depth (see below) – even within a single species (Stone & Kalisz, 1991; Canadell et al., 1996).
However, in practice, we are (understandably) encouraged to employ uniform sampling
strategies, even if these are known to only scratch the surface of potential symbiont habitat in
some ecosystems (see below). Although the issue of limited-depth sampling has been raised
before (Taylor, 2002), we are unaware of any efforts to quantify how much of the "black box"
typically remains out of reach of standard sampling techniques. Such information would be
extremely timely, due to the growing interest in accurately characterizing global patterns of
EMF diversity and distribution (Dickie & Moyerson 2008; Vellinga et al., 2009; Tedersoo et
al., 2012).
To begin addressing this question, we gathered sampling depth data from recent field studies
of EMF, and analysed these in relation to published data compiled by ecosystem ecologists
regarding (i) maximum rooting depths of trees and shrubs, including 137 EMF host species
distributed among 29 host genera, and (ii) estimates for 8 ecosystems of the mean depth above
which 95% of all roots are located. Rooting depth data were derived from the following
sources: (i) EMF host species/genera from Stone & Kalisz (1991) and Canadell et al. (1996),
(ii) ecosystem data from Schenk & Jackson (2002). Sampling depth data were obtained from
EMF studies published in the last 5 years of New Phytologist (Table S1). While the concepts
discussed here are equally applicable to all soil-borne root symbionts, for the sake of brevity
we focus our attention specifically on EMF and their hosts.

Based on 27 articles that reported sampling depth, the average was 13.4 cm (± 1.59 s.e.m.),
with a median value of 10 cm. This sampling depth was approximately doubled in boreal and
semi-arid ecosystems, and halved in semi-arid and tropical evergreen ecosystems. In
comparison, none of the 29 ectomycorrhizal host genera for which data was available exhibited
maximum rooting depths shallower than 50 cm (Fig. 1a), and on average maximum rooting
depth among the 137 host species is 530 cm (± 44 cm s.e.m.) (Fig. 1b). Correspondingly, the
average proportion of maximum rooting depth assessed is estimated to be 0.068 (± 0.0071
s.e.m.) across all host genera. If we consider maximum rooting depth as a proxy for the
amount of habitat available to symbionts, then an enormous amount of potential habitat
remains under-sampled, even within the Pinaceae (Fig. 1), which, according to a 2008
literature survey (Dickie & Moyerson, 2008), represented the focal family in 62% of all EMF
studies.

Although maximum rooting depth is a crucial variable in research examining ecosystem
function (Canadell et al., 1996; Jackson et al., 1996; Schenk, 2005), it could be argued that for
our purposes it provides an overly pessimistic outlook on the completeness of current sampling
efforts. We therefore also considered the EMF sampling depth data in relation to estimates of
ecosystem-specific mean rooting depths calculated using 16 to 59 observations per ecosystem
type, spanning all tree and shrub species for which rooting depth data existed (Schenk &
Jackson, 2002). Using an average sampling depth of 13.4 cm, the proportion of the mean
ecosystem rooting depth sampled varied from a high of 0.47 for tundra, to a low of 0.08 for
Mediterranean ecosystems (Fig. 2a), with a mean of 0.178 (+ 0.0442 s.e.m.). Thus, even in
tundra ecosystems where rooting depths are comparatively shallow (Fig. 2b), typical sampling
methods are likely to access less than 50% of the mean depth of host roots.

Although striking, our findings do not necessarily mean that standard sampling methods are
always doomed to miss an important or sizeable component of the symbiont assemblage
associated with any given host. Indeed, it is likely that some studies - especially those
occurring in shallow rooting regions (e.g. tundra ecosystems) - could yield reasonable
estimates of the actual number of symbiont species associated with the host (using appropriate
analytical techniques; cf. Gotelli & Colwell, 2001). Nevertheless, it has long been
acknowledged that important characteristics of EMF communities vary with depth, but only in
recent years have studies begun to clarify these details. For example, fungal hyphae show
vertical niche differentiation (Dickie et al., 2002), EMF community composition changes
between soil horizons (Rosling et al., 2003), ECM root tips and EMF extramatrical mycelium
differ in their vertical structure (Genney et al., 2006), and other depth-associated patterns
continue to emerge (e.g. Egerton-Warburton et al., 2003; Landeweert et al., 2003; Baier et al.,
2006; Lindahl et al., 2007; Courty et al., 2008; Scattolin et al., 2008; Beiler et al., 2010;
Clemmensen et al., 2013; Taylor et al., 2013). These observations, combined with our
findings, substantiate earlier statements that current sampling methods provide a limited view
of EMF assemblages (Taylor, 2002). Until more effort is spent sampling and characterising
symbiont diversity and function at depth, we cannot know the true extent of these limitations.

Since deep roots are features of most ecosystems worldwide (Schenk & Jackson, 2005), the
discoveries that could come with deeper sampling have the potential to profoundly change our
outlook on patterns of EMF diversity and function. To illustrate, consider a recent and
enlightening global-extent meta-analysis of local EMF diversity (Tedersee et al., 2012). Based
on data from 55 published studies, total species richness (representing site-level species
richness) was significantly associated with a number of climate-based predictor variables (e.g.
mean annual temperature, mean annual precipitation), and not surprisingly, number of samples
and total sample volume. However, the meta-analysis included data gathered from a variety of
host genera and ecosystem types, meaning that the rooting depths of hosts also varied
substantially (see above). It would be interesting to determine if and how their findings would
change if sampling was deeper, or was adjusted to account for site-specific rooting depths.
Because different communities arise with increasing depth, we predict that deeper sampling
will increase estimates of total richness and reveal significant changes in community
composition. Perhaps every additional 50 cm of depth explored could provide as much
richness again as that found in the organic horizon (as per Rosling et al., 2003 & Landeweert et
al., 2003)? Based upon our findings, we speculate that the magnitude of this total increase will
vary significantly with ecosystem type due to the differences in host rooting depth and density.
Variation in the rooting depth of a given host species is related to multiple factors including
age, depth to bedrock, mean annual precipitation, mean annual potential evapotranspiration,
and depth to the water table (Schenk 2005), all co-varying with ecosystem type. Thus, a
Douglas-fir growing in seasonally dry evergreen forest is more likely to develop deep roots
than one growing in a cool-temperate to sub-boreal region (cf. Schenk & Jackson, 2002). This
has implications for sampling strategies (see below), and suggests that host species distributed
across multiple ecosystem types, like Douglas-fir, may be associated with a much more diverse
pool of EMF symbionts than current estimates indicate. This combination of varied rooting
depths and soil environments provides a greater diversity of habitat to symbionts than do hosts
whose distributions are predominantly restricted to a single ecosystem type (e.g. black spruce).
Another important finding concerns the thoroughness with which sampling methods are
described in published articles. Of the 30 EMF studies published in the past 5 years in New
Phytologist, 3 (10%) failed to report details about sampling depth. More generally, whereas
some authors give detailed descriptions of the soil environment in relation to sampling strategy
(e.g. Smith et al., 2005; Ryberg et al., 2009), depth information occasionally has to be derived
or is missing entirely. We suggest that where possible, details about sampling should be
accompanied by estimates of average rooting depths at the site, for the host species of interest,
even if these estimates are speculative. This would provide for better and more consistent
estimates of realized sampling effort across studies.

Lastly, future research may not only require deeper sampling to minimise bias (depending
upon the research objectives), but may also need to stratify sampling geographically according
to potential rooting depth. Combining global estimates of soil depth
(http://www.fao.org/nr/land/soils/harmonized-world-soil-database/en/) with global estimates of
deep root distributions (Schenk & Jackson, 2005) and species’ ranges (e.g.
http://esp.cr.usgs.gov/data/little/) could help hone in on potential sampling regions, and ground
penetrating radar technology (Sucre et al., 2011) could be used to identify final sample
locations. The logistical impediments associated with deep soil sampling (including cost;
Harrison et al., 2011) are daunting, but other research areas point to possible solutions, such as
using drilling equipment to acquire ice or sediment cores (Nogué et al., 2013), or using
excavation machinery such as a backhoe (Bornyasz et al., 2005). These challenges are worth
tackling given the potentially crucial roles that symbionts at depth may play in ecosystem
function (e.g. Clemmensen et al. 2013; Kramer et al. 2013).

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**Figure legends**

**Figure 1.** a. Proportion of maximum recorded rooting depth examined (± s.e.m.) across genera using mean sampling depth derived from values reported in the literature (Table S1). Note maximum y-axis value is a proportion of 0.15. b. Maximum rooting depths of selected host species, with multiple bars (records) per species. Dashed red line represents average sampling depth of EMF studies. In both panels, green bars indicate genera or species in the Pinaceae.

**Figure 2.** a. Sampled proportion of the mean depth at which 95% of ecosystem roots are located, calculated using mean of sampling values reported in literature (Table S1). b. Estimated mean depth (± s.e.m.) at which 95% of ecosystem roots are located using the interpolated values of Schenk & Jackson (2002).

**Supporting Information**

**Table S1.** Citation, sample depth and host species for all ectomycorrhizal articles from the last 5 years of *New Phytologist* in which sampling depth was provided.
Proportion of mean rooting depth sampled

Mean ecosystem rooting depth (m)

a. Mediterranean
b. Warm Temperate
b. Semi-arid
b. Cool Temperate
b. Tropical Deciduous
b. Tropical Evergreen
b. Boreal
b. Tundra

Mean ecosystem rooting depth (m)

0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
1.6
1.7
1.8
1.9
2