

## Letter

# Are true multihost fungi the exception or the rule? Dominant ectomycorrhizal fungi on *Pinus sabiniana* differ from those on co-occurring *Quercus* species

Most ectomycorrhizal (EM) plants associate with many unrelated ectomycorrhizal fungi (EMF), and many EMF associate with several different plant hosts (e.g. 'multihost' or 'generalist' fungi; Bruns *et al.*, 2002; Kennedy *et al.*, 2003). This generalist approach may enhance plant success, because seedlings dispersing into diverse habitats may find compatible EMF and may therefore have a competitive advantage (Bruns *et al.*, 2002; Nara & Hogetsu, 2004). Association with many EMF may also enhance a plant's access to nutrients, particularly if certain EMF are adapted to unique microhabitats or have access to different nutrients (Baxter & Dighton, 2001). Roy *et al.* (2008) estimated that multihost EMF comprise between 12% and 90% of all species, and suggested that multihost EMF increase the chance of carbon transfer between different hosts, even when present in low frequencies. Although multihost EMF dominate many ecosystems (Horton & Bruns, 2001; Selosse *et al.*, 2006), there are also important specialist taxa restricted to distinct host plant groups. EMF host specificity has been well documented in several genera, including *Leccinum* (den Bakker *et al.*, 2004), *Strobilomyces* (Sato *et al.*, 2007), *Alnicola* (Moreau *et al.*, 2006), *Alpova* (Nouhra *et al.*, 2005), *Chondrogaster* (Montecchi & Sarasini, 2001), *Terfezia* and *Tirmania* (Díez *et al.*, 2002), and many Suillineae (*Suillus*, *Rhizopogon*, *Truncocolumella* and *Gomphidius*) (Bruns *et al.*, 2002). It is also well established that some individual EMF species have strong host preferences (e.g. *Lactarius obscuratus* – Molina, 1979; *Tuber melanosporum* – Murat *et al.*, 2004; *Tricholoma matsutake* – Lian *et al.*, 2006), although these taxa may or may not be truly host specific.

To better understand host effects on EMF communities, we have previously documented the EMF as sporocarps and on root tips of *Quercus douglasii* Hook & Arn. and *Quercus wislizeni* A. DC. (Smith *et al.*, 2007; Morris *et al.*, 2008). These *Quercus* species are dominant, endemic EM trees throughout a large area of interior, low-elevation woodlands in California (Pavlik *et al.*, 1991). *Quercus douglasii* is deciduous and usually has a sparse litter layer, whereas *Q. wislizeni*

is evergreen and generally has deep litter. We hypothesized that these differences in physiology and litter deposition between the two oaks would influence their EMF communities. The same dominant EMF species occurred on both *Quercus* hosts, yet, paradoxically, the overall communities were distinct. *Quercus wislizeni* showed a greater diversity and frequency of EMF with epigeous sporocarps, whereas Ascomycota were more frequent on *Q. douglasii* (Morris *et al.*, 2008). Thus, despite the close phylogenetic relationship between these plants, each hosted a unique EMF community. Multihost EMF were detected on both hosts, but some EMF taxa or functional groups apparently 'preferred' one host over the other.

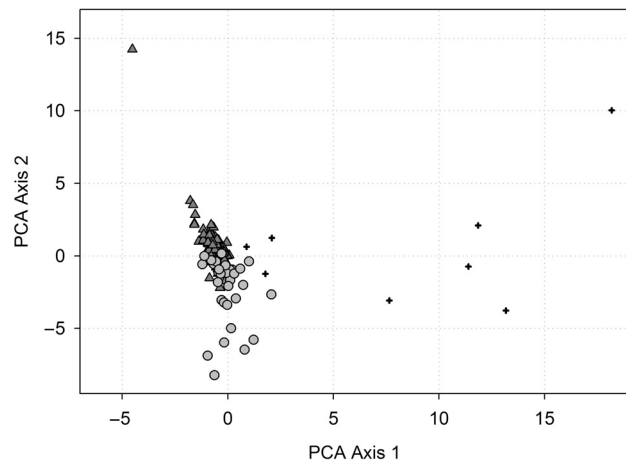
Across most of their range, these *Quercus* species co-occur with another widespread endemic, *Pinus sabiniana* Douglas (Graves, 1932). These three species are the dominant EM hosts across a geographically large area, but no studies have yet examined the EMF of *P. sabiniana*. The objective of this study was to determine the dominant EMF on *P. sabiniana* roots and to compare them with the extensively documented EMF on the co-occurring *Quercus* species. We wanted to examine whether multihost EMF would be frequently shared among the three hosts, or whether pine-preferring EMF would be dominant on *P. sabiniana*. Several recent studies have shown that plant host identity strongly influences EMF communities and that this effect is exacerbated with increasing phylogenetic distance of the hosts (Ishida *et al.*, 2007; Tedersoo *et al.*, 2008). As the closely related *Q. douglasii* and *Q. wislizeni* had unique EMF communities, we hypothesized that the EMF community on the distantly related *P. sabiniana* would be even more divergent.

EMF sampling of *P. sabiniana* was conducted at the site studied by Smith *et al.* (2007) and Morris *et al.* (2008). The UC Sierra Foothill Research and Extension Center is located in a low-elevation woodland (400–600 m) with a strong Mediterranean climate in Yuba County, CA, USA (39°17'N, 121°17'W). We sampled EM roots on 1 April 2005 from eight randomly selected *P. sabiniana* < 50 m from previously sampled *Quercus* plots (Smith *et al.*, 2007; Morris *et al.*, 2008; 'plot 2'). *Pinus* were small to large trees found c. 2–15 m from *Quercus* within the contiguous mosaic of woodland–savanna. We intended to sample *P. sabiniana* as in Smith *et al.* (2007) because we assumed that *Pinus* roots would be easily distinguished on the basis of size and color. However, these differences were not obvious and preliminary sampling yielded many roots that could not be unambiguously assigned to host genus. Therefore, one lateral root system per tree (main root > 3 cm in diameter) was randomly selected and cut at the base. We then excavated the root system and extracted several

50–200-cm root sections. Each extracted root system was placed in a plastic bag, stored at 4°C and processed within 5 d following the protocols of Smith *et al.* (2007) with minor amendments. We were unable to gather 100 EM roots for two trees, and so we used all root tips for these samples (pines 1 and 6 had 82 and 32 EM tips, respectively). Tuberculate EM roots formed by *Rhizopogon* were large relative to other EM tips, and so several EM tips per tubercule were added to the pooled root tips from that sample. Taxon naming and molecular analyses of roots followed Smith *et al.* (2007), except that 94 instead of 48 clones were restriction fragment length polymorphism (RFLP) screened from each sample.

Morris *et al.* (2008) collected samples based on focal trees, whereas Smith *et al.* (2007) collected samples from a plot with many trees. In this study, we used the individual samples; although some autocorrelation may be present for samples taken around focal trees, this should not affect the host preference aspects of the data. EMF species' composition data were analyzed using principal component analysis (PCA) and multiple-response permutation procedures (MRPP) to collapse the large EMF dataset into groups and illustrate the separation of EMF communities by host. PCA depicts differences in species' composition in relation to host, whereas MRPP is a nonparametric procedure that uses randomization to test the significance of pre-assigned variables (e.g. tree species). PC-ORD v. 4.20 was used to calculate the PCA axes based on correlation coefficients with the Sørensen distance measure, because it performs well with presence–absence data (McCune & Mefford, 1999).

We have previously sampled EMF at this site by extensive surveys of sporocarps and EM roots (*Q. douglasii*, 110 root cores with *c.* 11 000 roots; *Q. wislizeni*, 32 root cores with *c.* 3200 roots) (Smith *et al.*, 2007; Morris *et al.*, 2008). In this study, we sampled eight *P. sabiniana* (717 EM roots and 752 clones; mean of 89.6 roots per tree). We detected 33 EMF species, with two to nine species per lateral root (mean of 6.1 species). Basidiomycota were dominant on *P. sabiniana*, with 25 species accounting for 77.6% of the relative frequency (Table S1, see Supporting Information). We detected eight Ascomycota, but these only accounted for 22.4% of the relative frequency, and only two Ascomycota were detected on more than one *Pinus*. By contrast, 37–39% of the EMF species on *Quercus* were Ascomycota, and they accounted for 31–49% of the relative frequency. Furthermore, many dominant *Quercus* EMF were Ascomycota (e.g. *Cenococcum*, *Tuber*, *Peziza*). Nineteen of the 33 EMF detected on *P. sabiniana* (*c.* 58% of the taxa, 65% of the relative frequency) had not been detected previously on *Quercus*, despite sampling > 140 root cores (14 000+ roots). This was true for seven of the 10 most common *Pinus* EMF, including all species that occurred on three or more *Pinus*. Five species in two lineages that associated only with *Pinus* (*Rhizopogon*, Atheliaceae) were major contributors to this pattern; together, these taxa accounted for 28% of the relative frequency on *Pinus*. PCA visually segregates the



**Fig. 1** Principal component analysis (PCA) of ectomycorrhizal (EM) fungal species composition relative to host tree species, showing axis 1 and axis 2. Each point on the graph represents an independent sample of EM roots from one of the three plant host species (triangles, *Quercus douglasii*; circles, *Quercus wislizeni*; crosses, *Pinus sabiniana*). (Root cores for *Quercus* spp., lateral roots for *Pinus sabiniana*.)

EMF communities by host plant, although there is significant overlap between *Quercus* species (Fig. 1). MRPP confirmed the separation (*t*-test;  $P < 0.0001$ ), indicating greater variance between than within groups. To ensure that these host preferences were not strongly affected by the small *P. sabiniana* sample size, we performed 10 additional MRPP tests with reduced *Quercus* datasets. For each MRPP test, we randomly selected data from 10 *Q. wislizeni* and 10 *Q. douglasii* cores, and analyzed them with the entire *P. sabiniana* dataset. In each of the reduced datasets, MRPP confirmed the separation between the *Quercus* and *Pinus* ECM communities ( $P < 0.001$ ), but the effect size remained low ( $R < 0.10$ ). These low effect values are not surprising considering the smaller sample size and the nature of community data, yet the statistical analysis still confirmed higher homogeneity within groups than between. This pattern of host structured ECM communities was detected regardless of whether or not species of the Pinaceae specialist genus *Rhizopogon* were included in the PCA.

Although the majority of *Pinus*-associated EMF were only detected on *Pinus*, 14 EMF co-occurred on the roots of at least one *Quercus* species (*c.* 42% of taxa, 35% of relative frequency); all EMF species shared by both *Pinus* and *Quercus* were Basidiomycota. Five 'generalist' EMF were found on all three hosts (*c.* 15% of taxa, 10% of relative frequency). *Pinus sabiniana* shared about the same number of EMF with *Q. douglasii* (nine) as with *Q. wislizeni* (10). However, most of the EMF detected on both *Pinus* and *Quercus* tended to have low relative frequency on *Quercus* (< 2% relative frequency). Two notable exceptions, *Laccaria bicolor* (4.3% relative frequency on *Q. wislizeni*) and Thelephoraceae (3.5% relative frequency on *Q. douglasii*), may be strong 'multihost' fungi.

Species of *Laccaria* may be preadapted as 'multihost' EMF because they are often pioneer species, regularly establish new genets from spores, are readily cultured in the laboratory and have great potential to become invasive (Gherbi *et al.*, 1999; Kropp & Mueller, 1999; Fiore-Donno & Martin, 2001; Díez, 2005; Roy *et al.*, 2008; Vellinga *et al.*, 2009).

Many of the higher level EMF lineages detected on *P. sabiniana* were the same as those on *Quercus* (e.g. Thelephoraceae, Pezizales), but, at the species level, many EMF were different on the two host genera. Although based on a small *Pinus* sample, these data suggest the possibility that some EMF groups may be more or less likely to exhibit host preferences. For example, Pezizales appeared to be strongly structured by host; they were common on *Pinus* and *Quercus*, but none of the seven *Pinus*-associated pezizalean EMF species were ever detected on *Quercus*. Interestingly, we detected a similar pattern of host structuring for pezizalean hyphae at the same site (M. M. Hynes *et al.*, unpublished). By contrast, other groups appeared to be less likely to exhibit host preference. For example, four of five Russulaceae were found on both *Pinus* and *Quercus*. This result for Russulaceae is similar to that presented by Ishida *et al.* (2007) where, of the 22 species that occurred more than once, 17 Russulaceae were found on more than one host plant species. These patterns of host preference may be system specific, however, as many studies have indicated that some Russulaceae exhibit strong host preferences and some Pezizales are host generalists (e.g. Hutchison, 1999; Kennedy *et al.*, 2003; Ishida *et al.*, 2007; Twieg *et al.*, 2007; Tedersoo *et al.*, 2008). Although it would be interesting if some EMF lineages tended to have stronger host affinity than others, this hypothesis requires further testing.

To date, we have detected 225 species of EMF from sporocarps and EM roots of three host species in this dry woodland habitat. This is closely comparable with the 205 EMF species reported by Ishida *et al.* (2007) from a mesic, closed-canopy forest containing 12 host species in six genera. In terms of community composition, however, the *Pinus* EMF community in this dry woodland was similar to other dry, inland *Pinus* EMF communities (Bidartondo *et al.*, 2001; Hubert & Gehring, 2008) and to the post-fire spore bank EMF community in coastal *Pinus muricata* (Taylor & Bruns, 1999). It was dominated by species with inconspicuous sporocarps, and the hypogeous genera *Rhizopogon* and *Tuber* were abundant and species rich. We only detected 10 species with epigeous sporocarps (29% of the relative frequency), and only two of these (*Hygrophorus* cf. *gliocyclus*, *Clavulina* cf. *crystata*) inhabited multiple trees. Dominant genera from mature coastal pines, such as *Suillus* and *Amanita* spp., were notably absent on *P. sabiniana*.

Unfortunately, because of the destructive techniques needed to complete this study, we were unable to sample large numbers of *Pinus* roots or individuals. With further sampling, we would probably have detected more EMF species that are occasionally shared between *Quercus* and *Pinus*. However, we believe that the overall pattern would remain; except for a

relatively small number of 'multihost' taxa, most of the dominant *Pinus* EMF rarely associate with or have a low frequency on *Quercus*, and most dominant *Quercus* EMF rarely associate with or have a low frequency on *Pinus*.

The prevailing ideas about EMF host preference may be changing. Early studies of Northern Hemisphere ecosystems, mostly dominated by Pinaceae and with routinely overlapping canopies, reported high diversity and abundance of shared EMF taxa between hosts, suggesting that 'multihost' fungi are dominant (Horton & Bruns, 2001; Horton *et al.*, 1999, 2005; Cullings *et al.*, 2000; Kennedy *et al.*, 2003; Richard *et al.*, 2005; Twieg *et al.*, 2007; Hubert & Gehring, 2008). However, on a global scale, most EM host plants and ecosystems remain unstudied or undersampled (Dickie & Moyersoen, 2008). Sampling EMF communities with different sets of host plants (Ishida *et al.*, 2007; Tedersoo *et al.*, 2008) and in different habitats (e.g. tropical forest – Tedersoo *et al.*, 2007; woodland-savanna – Morris *et al.*, 2008) might change our view of host preference and, consequently, the perceived importance of 'multihost' fungi. The emerging picture is one in which many EMF appear to display some level of host preference, and most EM plants host some fraction of the locally available EMF. These complex interactions appear to be governed by some combination of host plant relatedness (Ishida *et al.*, 2007; Tedersoo *et al.*, 2007), plant life-history traits and physiology (Morris *et al.*, 2008; Tedersoo *et al.*, 2008) and successional strategies of both hosts and fungi (Horton *et al.*, 2005; Twieg *et al.*, 2007; Roy *et al.*, 2008). The end result is that 'multihost' EMF fungi may be much less dominant than previously thought.

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**Key words:** ectomycorrhizal fungi, host preference, *Pinus*, *Quercus*, specificity.

### Supporting Information

Additional supporting information may be found in the online version of this article.

**Table S1** Ectomycorrhizal fungi detected on the roots of *Pinus sabiniana*

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