

Meetings

The (re)discovery of ectomycorrhizal symbioses in Neotropical ecosystems sketched in Florianópolis

VIIIth Brazilian Mycological Congress, held in Florianópolis, Brazil, October 2016

The VIIIth Brazilian Mycological Congress, held in Florianópolis (Brazil) in October 2016, was organized by the Universidade Federal de Santa Catarina and brought together more than 1000 scientists of 20 nationalities, which illustrates the dynamism of South American mycology, in many fields. One of the major take-home messages, amongst many research talks and posters, was the rising interest in the ectomycorrhizal (EM) symbiosis, which was addressed by both a symposium and a 3-day workshop 'To the roots of trees: growing awareness of ectomycorrhizal symbioses in the Neotropics'. Talks on this symbiosis were given by taxonomists and ecologists, and focused on the Neotropics, the tropical realm that extends from the central plateau of Mexico and which includes South America. The inventories of ectomycorrhizal fungi (EMF), observations of EM roots, and metabarcoding studies presented revealed a hitherto unsuspected abundance of the EM symbiosis to all participants, including a number of South-American students. This meeting provided great opportunities to share points of view on the historical reasons behind gaps in knowledge on EMF associations in neotropical low-elevation areas. The meeting also highlighted recent discoveries and forthcoming challenges, based on three complementary approaches: studies on fruitbodies, EM roots, and the metabarcoding of soil samples.

Fruitbodies and an increasing number of new species

Historically, observations of fruitbodies that belong to EMF lineages were the first clues to detect EM symbiosis in the Neotropics. The very first step dates back to the description, *c.* 150 years ago, of *Cantharellus guyanensis* and *Scleroderma sinnamariense* in French Guiana (Montagne, 1855). The work of Singer & Araújo (1979) was probably the first well-known major contribution, together with Singer's inventories of EMF in Amazonian white sand forests (Singer *et al.*, 1983). Singer speculated that EMF provided the host with the ability to acquire more nutrients than other plants, and thus would make these plants more successful in areas with poor soils (Singer & Araújo, 1979). Later, the intense and long-term studies by Henkel and coworkers revealed a hot spot of diversity of EMF in the Guiana Shield with at least 70 new

species (see Smith *et al.* (2011, 2013) and Henkel *et al.* (2012) for reviews, a list can also be found via the website <http://tropicalfungi.org>). Elsewhere, the low number of fungal taxonomists in South America has been a major limiting factor in the generation of knowledge on EMF, and EM symbiosis remained, for decades, an overlooked issue in the tropics (Alexander & Selosse, 2009). For example, in Brazil, from 1906 to date, just 1006 specimens of EMF have been deposited in herbaria, but only 548 have been identified to species level, and only 175 specimens have been described and published (for details, see Roy *et al.*, 2016), essentially species growing on white sands, which fitted Singer & Araújo's (1979) hypothesis. As field mycologists attending the workshop recognized, the frequent formation of few and inconspicuous fruitbodies, including sequestrate or corticioid ones, are an impediment to representative sampling and formal description by taxonomists. Recently, taxonomists investigated white-sand forests along the Amazon, but also *tabuleiro* in north-eastern Brazil (savanna-type forest), *restinga* (open forest growing on sandy soil localized near the ocean; Pontes & Barbosa, 2008), the Mata Atlântica (coastal forest), upland wet forest enclaves ('*brejo de altitude*'), and cloud forest (between 1650 and 1800 m above sea level (asl) of the *Caatinga* region (northeast Brazil)). Two symposia illustrated the diversity of habitats where EMF were recently observed: the symposium on EMF and a parallel one on the 'Diversity and ecological function of hypogeous fungi' (organized by Iuri G. Baseia, Universidade Federal de Rio Grande do Norte, Natal, Brazil). Together, these symposia permitted us to draw a first sketch of EM fungal distribution based on recent observations. Marcelo Sulzbacher (Universidade Federal de Santa Maria, Brazil) presented his recent discoveries of hypogeous EMF in the semi-arid vegetation from Brazil, Felipe Wartchow (Universidade Federal da Paraíba, Brazil) made a synthesis on the recent descriptions of EMF from northeast Brazil, and Aida Vasco-Palacios (Universidade Federal da Santa Catarina, Brazil) pointed out new EM mentions in Colombian white sands. The presentations made it more and more obvious that EMF occur in many habitats scattered in Neotropical lowlands (see Roy *et al.* (2016) for a review on Brazil; Sulzbacher *et al.* (2017) for a review on neotropical hypogeous fungi; Wartchow *et al.* (2015), Baseia *et al.* (2016), Sá & Wartchow (2016) and Wartchow (2016) for further data for Brazil; Grupe *et al.* (2016), Vasco-Palacios *et al.* (2014) and Vasco-Palacios (2016) for Colombia); they expanded the range of soil conditions relevant for looking for EM symbioses. Despite an explosion of checklists and new species descriptions, species accumulation curves remain barely saturated (Roy *et al.*, 2016). Today, however, the known distribution of EMF remains patchy and biased towards accessible sites (see maps in Roy *et al.* (2016) and Sulzbacher *et al.* (2017)). Moreover, one-third of EMF specimens in Brazilian herbaria belong to introduced species recorded from plantations (Roy *et al.*, 2016), such as the widespread *Rhizopogon verii*, which is

associated with pines (Sulzbacher *et al.*, 2016). Unfortunately, comparisons between inventories are still limited because molecular data are often missing. The lack of publicly available DNA sequences partly explains why large-scale studies on EMF biogeography still undersample Neotropical taxa (Matheny *et al.*, 2009; Looney *et al.*, 2015), although this can deeply affect distribution patterns and phylogenies, as suggested for Clavulinaceae (Kennedy *et al.*, 2012). Finally, without reference sequences produced from fruitbodies, EMF cannot be identified on roots nor in soil. Since new lineages of EMF could still be discovered in the tropics (Tedersoo & Smith, 2013), as recently illustrated by the discovery of a new lineage, *Guyanagarika* (Sánchez-García *et al.*, 2016) and the first mention of *Tuber-Helvella* lineage in Africa (Ebenye *et al.*, 2017), and because total EM status is not obvious in some families such as Amanitaceae, Hymenochaetaceae, Entolomataceae or Sebacinaceae, EM roots should still be searched for, and sequenced, in the Neotropics. Finally, as emphasized by Marc-André Selosse (National Museum of Natural History, France), isotopic composition of fruitbodies also provides relevant criteria to assess the EM vs saprotrophic status of new fungal species (Rinaldi *et al.*, 2008).

Ectomycorrhizal (EM) roots remain largely unexplored

Indeed, observations on roots are scarce and observations have been made only recently, compared with fruitbodies. Tracing roots and identifying hosts are very difficult in hyperdiverse forests, and neotropical ectomycorrhizas often lack a well-developed mantle (Becerra & Zak, 2011). It is, therefore, even more challenging to recognize EM root tips without adequate methods and expertise, and during a practical session of the workshop, Masters and PhD students were trained to sample and recognize EM roots in the Lagoa do Peri State Park near Florianópolis. Beyond well-developed, typical EM colonizations, experts from different areas widened their scope, together with students, to recognize less conspicuous EM roots as well. During the symposium, Bart Buyck (Museum National d'Histoire Naturelle, France) illustrated how useful EM root-tip morphology can be to study Russulaceae evolution, and Andrea Rinaldi (University of Cagliari, Italy) presented detailed studies on EM root tips and their use in taxonomy. They both pointed out the lack of detailed descriptions in the Neotropics. Indeed, observations are not that rare in the literature, but cuttings and conclusions on EM status are often missing, pointing out the lack of appropriate methods.

In many checklists, the link with hosts is simply derived from the literature, while direct observations of EM roots are still missing for many potential hosts (as in Sulzbacher *et al.*, 2013). Indeed, several observations have been awaiting confirmation for some decades. Singer & Araújo (1979) sampled roots without confirming the link with plant hosts: beyond EM roots on *Aldina*, *Neea*, *Coccoloba* and *Gnetum*, which are all confirmed EM hosts, they also suspected *Glycoxylon inophyllum* (Sapotaceae), *Swartzia* sp., *Eperua falcata*, *Macrolobium* and *Sclerolobium* (Fabaceae) and *Psychotria* (Rubiaceae) to be EM, but this was never reinvestigated. Singer (1988) also described 'cicatrizing mycorrhiza', i.e. EMF that colonize nonobligate hosts by contact, a hitherto undemonstrated concept.

We point out the lack of expertise on roots, but this gap of knowledge can also be attributed to the choice of hosts investigated. In French Guiana, Béreau & Garbaye (1994), who were very experienced with European EM roots, did not detect any EM roots on timber trees on *terra-firme* (clay-rich soil typical in Amazonian lowland forests). Even in forests dominated by EM Fabaceae, McGuire *et al.* (2008) did not detect any additional EM tree families. These two studies confirmed that EM symbiosis was restricted to a few dominant hosts (Fabaceae and Dipterocarpaceae), and very few nondominant ones such as lianas belonging to *Gnetum* (Gnetaceae), *Coccoloba* (Polygonaceae) and shrubs belonging to *Guapira*, *Pisonia*, and *Neea* (Nyctaginaceae). Recently, new EM associations have been detected, for example *Craterellus atratoides*, *Craterellus cinereofimbriatus* and *Clavulina tropenbosii* (Dipterocarpaceae), suggesting a low specificity of these EMF (Vasco-Palacios, 2016), while Buyck *et al.* (2016) reported on a very strict association between *Cantharellus coccolobae* and various *Coccoloba* species. Nevertheless, no study has recently reported new putative EM host genera in the lowland Neotropics. Host-indiscriminate EM root sampling and metabarcoding, mainly in habitats harboring fruitbodies of EMF, have the potential to substantially increase our knowledge of EM hosts in the future.

The rise of metabarcoding approaches

Talks at VIIIth Brazilian Mycological Congress included unpublished metabarcoding studies: the use of high-throughput sequencing is rising, especially in the study of EM fungal communities. Aida Vasco-Palacios presented a talk on EM communities on Colombian white sands and *terra-firme*, and Mélanie Roy (Université Paul Sabatier, Toulouse, France) presented her work on EM communities from inselbergs and their specificity, based on root-tip sampling and metabarcoding. There were also two related talks in the DNA-metabarcoding symposium (organized by Aristóteles Góes Neto, Universidade Federal de Minas Gerais, Brazil) on exploring soil fungal diversity, including EMF. Heidy Schimann (INRA, France) presented a case study from French Guiana to illustrate the use of next-generation sequencing (NGS) methods to improve fungal taxonomic identification and József Geml (Naturalis Biodiversity Center, the Netherlands) compared altitudinal distribution patterns of fungi in Borneo and in the Andes. All speakers noted the scarcity of identified reference sequences and emphasized the need for more taxonomic studies in the Neotropics. Ironically, the first studies on EM sequences in the Neotropics were carried out in very localized places, such as in dipterocarp and *Alnus* stands, or in Yasuni National Park (Ecuador) where previous studies reported the occurrence of EM hosts (Tedersoo *et al.*, 2012). Such 'phytcentric' studies have given support to the idea that EM symbiosis was very localized in the Neotropics (as suggested by Alexander, 2006), although a recent meta-analysis suggests that EMF are highly diverse at least in the Guiana Shield (Tedersoo *et al.*, 2012).

Thus, more sampling points are needed to better understand EMF distributional patterns in the Neotropics. Recently, studies not focused on EMF have revealed EM sequences in *terra-firme* and

white-sand forests in the Amazonian region (Vasco-Palacios, 2016), as well as along an elevation gradient in the Yungas at the southern limit of the Amazonian biogeographic domain (Geml *et al.*, 2014), extending the distribution of EMF in the Andes and also at mid- and low elevations. The metabarcoding approach in the Neotropics is still limited by the scarcity of reference EM sequences, as often only half of the generated sequences can be identified to the family level. The lack of reference sequences for EMF is extremely pronounced for hypogeous, resupinate and new EMF lineages. But things start to change in South America (see in this issue of *New Phytologist*, Truong *et al.*, pp. 913–919). The systematic build-up of reference sequence databases based on vouchered collections from herbaria, as recently carried out in Amazonian areas in Colombia (Vasco-Palacios, 2016), is crucial to make better use of the massive datasets generated from environmental samples.

Future steps

All three approaches, by way of fruitbodies, EM roots, and metabarcoding, are complementary: taxonomists can help build reference sequence databases based on vouchered specimens and encourage metabarcoding sampling in areas that potentially have new hosts. Ecologists working with roots can identify hosts and confirm symbioses, possibly with formerly unknown hosts. Finally, metabarcoding studies should investigate new habitats and better integrate sequences and distribution clues produced by mycologists. The EM symbiosis should be studied in the Neotropics to obtain a bigger scheme of this association (Tederloo *et al.*, 2012, 2014), to correct sampling bias, and to answer more specific questions and challenges. For example, our understanding of the ecological role played by EM symbiosis in the Neotropics is still in its infancy, and the peculiar features of EMF and EM roots in these ecosystems are key to solving the puzzle. Also, the relationship and possible interchange of EMF spores between lowland forests and those at higher elevation, where EM hosts like *Quercus* and *Alnus* are frequent, must be investigated. Sampling widespread EM hosts, such as *Salix humboldtiana* (Becerra *et al.*, 2009), and the diverse *Coccoloba* or *Gnetum* species might help in the study of the distribution of EMF across diverse Neotropical ecosystems and their biogeography. Furthermore, coupling metabarcoding with spatial information on host distributions can be used to model suitable habitats for EM symbioses, as has recently been done for Andean *Alnus*-associated EMF (Wicaksono *et al.*, 2016). The intense discussions held during the Florianópolis Congress and EMF workshop have trained a new generation of students, as well as experienced researchers, who learned in the field.

Based on the emerging awareness of EM symbiosis, future symposia are already planned, for example on 'Mycorrhizal symbiosis in the southern cone of South America' (6–9 March 2017; Valdivia, Chile) or sessions at the IXth Latin American Congress on Mycology (22–25 August 2017; Lima, Peru). To reinforce interactions, a Facebook group page was launched linking experienced researchers and students (called 'ECM connections'), to share published information, pictures of EM roots, specimens, questions and data that, taken alone, would not be sufficient for a publication. We hope that after the VIIIth Brazilian Mycological

Congress, this network and the future meeting will help in reinforcing scientific interactions, and raise a new generation to study the EM symbiosis in the Neotropics.

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