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What processes shape the specialization of plant-fungi mutualisms? An investigation across scales and ecosystems

Mélanie Roy

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Mémoire
Présenté à l'Université de Toulouse 3 – Paul Sabatier

Ecole doctorale SEVAB, section 67

Par **Mélanie ROY**

Pour obtenir l'Habilitation à Diriger des Recherches

What processes shape the specialization of plant-fungi mutualisms? An investigation across scales and ecosystems

Jury
Doyle McKey (rapporteur), CEFE CNRS, Montpellier
Corinne Vacher (rapporteur), INRA BIOGECO, Pierroton
Marc Buée (rapporteur), INRA Champenoux
Christophe Thébaud (examinateur), EDB UPS, Toulouse
Nathalie Sejalon-Delmas (examinateur), LRSV UPS, Toulouse
Marc Ducousso (examinateur), CIRAD LSTM, Montpellier
……

Table Of Contents

ACKNOWLEDGMENTS 5

PHD AND ANTERIOR RESEARCH TOPICS 6

INTRODUCTION: SETTING THE QUESTIONS 9

A FOCUS ON PLANT-FUNGI MUTUALISMS 9
SPECIALIZATION IN PLANT-FUNGI MUTUALISMS: PUZZLING CASES AND NEW QUESTIONS? 11
CHANGING SCALES TO STUDY COMMUNITY ECOLOGY OF COMPLEX MUTUALISMS 15

PAST/PRESENT RESEARCH 19

AXIS 1 : DIVERSITY AND DISTRIBUTION OF EMF FUNGI IN THE NEOTROPICS 19
AXIS 2 : DRIVERS OF EMF SPECIALIZATION 33
A. REVISITING *ALNUS*-EMF SPECIALIZATION 33
B. SPECIALIZATION OF EMF IN NEOTROPICAL FORESTS 37
AXIS 3 : BIOTIC INTERACTIONS 43
A. INTERACTIONS ON ALDER ROOTS AND POPULATIONS 43
B. INTERACTIONS MEDIATED BY EMF IN THE BOREAL FOREST 45
C. INTERACTIONS WITHIN ENDOPHYTES COMMUNITIES 47

PRESENT/FUTURE DIRECTIONS 51

FROM COMMUNITY TO LANDSCAPE ECOLOGY 51
USING LANDSCAPE TO RECONNECT STUDENTS IN ECOLOGY 59
HOW TO INTEGRATE ECOLOGICAL NETWORKS TO STUDY ECOSYSTEM RESILIENCE? 61
BACK TO ROOTS: TOWARDS EXPERIMENTS TO LINK ECOLOGICAL AND COMMON MYCORRHIZAL NETWORKS IN A BIOGEOGRAPHIC CONTEXT 63
A PARALLEL WITH MYCORRHIZAL FUNGI AND VINEYARDS HISTORY: A PROJECT WITH STUDENTS? 69

CONCLUSIONS 69

LITERATURE CITED 70

CURRICULUM VITAE 84

TEACHING AND TRANSFER OF KNOWLEDGE 85

SUMMARY 85
INNOVATIVE TEACHINGS 85
INTERNATIONAL COURSES 86

RESEARCH ACTIVITIES : PUBLICATION LIST AND STRATEGY 87

SUMMARY AND STRATEGY 87
PEER-REVIEWED JOURNALS 87
SOCIETY JOURNALS 90
BOOK CHAPTERS 91
SUBMITTED MANUSCRIPTS 91
SUBMITTED BOOK CHAPTER 91
MANUSCRIPTS IN PREPARATION 92
ORAL COMMUNICATIONS AT CONGRESSES 92
INVITED CONFERENCES IN LABS 94
POSTERS 95
CONFERENCE FOR SOCIETIES 95

SUPERVISING EXPERIENCE 96

LICENCE 96
MASTER 1 96
MASTER 2 97
PHD 99
POST-DOCTORAL CONTRACTS 100

COUNCILS AND COMMITTEES 101

PHD COMMITTEE 101
JURY 101
PHD 101
HDR 101
COUNCILS AND EVALUATIONS 101
REVIEWING ACTIVITIES 102

INTERNATIONAL EXCHANGES AND SCIENTIFIC ANIMATION 102

VISITING STUDENTS 102
VISITING SCIENTISTS 103
INVITED VISITS 103
CONGRESS AND SYMPOSIA ORGANIZATION ..... ERREUR ! SIGNET NON DEFINI.

FUNDED RESEARCH PROJECTS 105

LIST OF PROJECTS 105
FIELD EXPERIENCE AND EXPERTISE 110

FIVE SELECTED ARTICLES 111

SUPPLEMENTARY MATERIAL 112
CURRICULUM VITAE (IN FRENCH, SIGNED)
LAB ORGANIZATION
PHD DIPLOMA
CERTIFICAT DE NON-DOUBLE INSCRIPTION

Acknowledgments

"How would you transmit your passion" was a question from a colleague, during my application for the *Maître de conference* position in Toulouse. At that time, I replied that bringing students to the field was the key. I would perhaps answer differently today, and mention that meeting passionate people can be contagious too. Through this synthesis, I have tried to tell how interactions, through scientific collaborations with great colleagues – often crazy about the field and dispersed all around the world- have built my research. However, my research has also evolved through coffee-breaks, mushroom, or salad-picking walks, creative dinners, wine tasting, gliding, with many other friends, scientific or not, and I already apologize for not naming all of you.

Today, I feel deeply lucky, to teach ecology and evolution, to enthuse students about symbioses, fungi and wine making, and share my interest for forests all around the world. I must thank my parents first, for letting me grow so close to the forest and discover the taste for freedom, travels and passions. I cannot thank Marc-André Selosse enough for his education during my PhD, his constant support and his friendship. His methods still inspire my creative teachings. The lab wouldn't work on fungi if Monique Gardes, Hervé Gryta and Patricia Jargeat were not there before, I joined the group and learned a lot about fungi and mycology from them and with Pierre-Arthur Moreau. The help and the enthusiasm of Sophie Manzi were also precious, to simplify the steps of metabarcoding and train the students in the lab. From my colleagues at EDB, I have learned a great deal about other models – such as tropical tree communities, plant-pollinator interactions, and host-parasite coevolution – and I deeply thank Jérôme Chave for suggesting a first trip to French Guiana. There, I have also met passionate researchers, Heidy Schimann and Philippe Gaucher, who encouraged me to stay and mushroom for years in this remote paradise. Thanks to my fieldwork in French Guiana, I also met passionate mycologists and "bougamoa", Régis Courtecuisse, Jacques Fournier, Christian Lechat, Gérald Gruhn, Stephane Welti, Cony Decock, Terry Henkel, Maria-Alice Neves, who have deeply changed my look on tropical *funga*. In France, I won't forget the wisdom of Maria Fernandez, about team work and student supervision. Meeting Antoine Brin and discovering the world of the DYNAFOR team also opened my eyes, on landscape ecology and on the way to enjoy science in the lab. Finally, I have learned a lot from my numerous students, and deeply thank them for their curiosity, enthusiasm, and creativity.

As a last word, I would have never found the time to write this synthesis without the encouragements of Jean-Louis Hemptinne, Emmanuelle Cam, Christophe Thébaud, Elisabeth Jamet, the precious feed-back of my father, Alain, and of my former post-doc, Julian Donald, the excitement of my "mothers": my mum, Véronique, her friends, Françoise and Catherine, and Maryse, my brilliant neighbour, and of course, the every-day support of my favorite symbiont, François, and our will to write a new page of travel, science, and tasty love in Argentina.

PhD and anterior research topics

Articles during my PhD	Consiglio et al., 2007 ; Roy et al., 2008 ; Roy et al., 2009a ; 2009b ; Selosse and Roy, 2009 ; Pedersen et al., 2009
Between PhD and MCF position	Selosse et al., 2010 ; Tranchida-Lombardo et al., 2010 ; Richard et al., 2011
On PhD topic during my MCF position	Hynson et al., 2013 ; Kohout et al., 2013a ; 2013b ; Roy et al., 2013b ; Tesitelova et al., 2013 ; Gonneau et al., 2014 ; Roy et al., 2014 ; Shefferson et al., 2016 ; 2018.

Before my recruitment at UPS in 2010, I was already familiar with plant-fungi symbioses. I was fascinated by symbioses early in my scholarship, thanks to naturalist books and observations. My first practical stage in Erasmus at La Sapienza (Roma, Italy) focused on lichens, and I worked in Master 1 (Magistère ENS Lyon) on *Medicago truncatula* and its bacteria. Marc-André Selosse supervised my M2 (DEA Ressources Phytogénétiques et Interactions Biologiques) at CEFE (Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier) on a very generalist symbiosis, between *Laccaria bicolor* and its diverse hosts, such as oaks, beech and pines (**Roy et al., 2008**). I discovered fungal taxonomy at CEFE, and began using my skills in molecular biology to help taxonomists and describe new fungi species (**Consiglio et al., 2007**). Marc-André Selosse also supervised my PhD at CEFE, on the evolution of mycoheterotrophy in orchids, and more specifically in the tribe Neottieae.

Orchids produce the smallest seeds among plants, and rely on fungi for their germination. Circa 200 species of orchids look parasitic, as they have lost their photosynthetic pigments or capacity (Leake, 1994). Thanks to the development of barcoding and the use of isotope labelling, studies in the 2000's identified the organic carbon source of these non-photosynthetic orchids, and in temperate regions, specific fungi were identified in orchids' roots (Selosse et al., 2002). Interestingly, those fungi were also associated with trees, and the organic carbon was indeed produced by trees, transferred to their symbiotic fungi and later received by the orchids. The tribe Neottieae is well represented in temperate forests and in tropical South-East Asia. Previous data have revealed specific but diverse fungi associated with Neottieae species and my PhD aimed at understanding the evolution of these interactions, and how orchids could become heterotrophic on fungi, i.e. mycoheterotrophic.

At the beginning of my PhD, my hypothesis was that specific interactions with fungi were acquired before the loss of photosynthetic ability. I expected convergent evolution in temperate and tropical ecosystems, but coevolution with distinct fungi depending on the orchid species. I spent 4 months in South-East Asia searching for rare mycoheterotrophic orchids, and have revealed that *Aphyllorchis montana* and *A. caudata* are associated with very diverse fungi (**Roy et al. 2009a**), while *Cephalanthera exigua* is very specific (**Pedersen et al., 2009**). In temperate region, I confirmed that specificity was the rule, for another rare orchid, *Epipogium aphyllum* (**Roy et al., 2009b**). To study closely related species of Neottieae, I followed several populations of green orchids, among which albino individuals are rarely observed. Such albino are scattered in populations (**Tranchida-Lombardo et al., 2010**) and are able to survive and reproduce. By measuring functional and reproductive traits for three years on two main populations, I showed that albino suffer from drought stress, lower germination rate and low

seed viability, as compared to green individuals (Roy et al., 2013b). On the other hand, their ability to survive underground could explain the high number of albino individuals (maximum of 30% of albino individuals, Shefferson et al., 2016 ; 2018). In co-supervising the master 2 internship of Cédric Gonneau with Marc-André Selosse, we conducted experiments to test how *Epipactis* species could survive with less light, and if fungal resources could be limited. We confirmed that *Epipactis* are partly mycoheterotrophic and that photosynthesis is useful mainly for fruiting (Gonneau et al., 2014). All these clues on Neottieae show that mycoheterotrophy is widespread, among species and ecosystems, and reveal that full mycoheterotrophy could evolve from partial mycoheterotrophy, but that specific interactions are not necessary (Selosse and Roy, 2009).

I contributed to larger syntheses on this peculiar trophic mode (Hynson et al., 2013) and the need for molecular tools to study them, especially in the tropics (Selosse et al., 2010). Moreover, I spent part of my time, during my PhD, working with "amateurs" and local societies, and sharing the results of my PhD in French journals such as Pour la Science (Roy and Selosse, 2010 ; Selosse and Roy, 2012). After my PhD, I maintained collaborations on orchids for example with colleagues in Czech Republic (Kohout et al., 2013a ; 2013b ; Tesitelova et al., 2013). Today, I still publish for a broad audience in France (Roy et al., 2014 ; Roy, 2018) and abroad (Roy and Kuyper, in prep), but I have developed my career on symbiotic fungi of trees and worked at community level.

After my PhD, I spent only 6 months in post-doc with Franck Richard (CEFE) and Alain Franc (INRA Pierroton), working on symbiotic fungi of oaks and their response to drought stress. I contributed to the DNA extractions, barcode sequencing and analysis, and community analyses. Fungal communities were highly variable but apparently resistant to drought stress (Richard et al., 2011). The contract was short (end of a European project) and I got my position at Université Paul Sabatier (UPS) right after. This short contract was a great opportunity to be trained with community level analysis on symbiotic fungi, and discover their below-ground diversity. Moreover, I still work with Franck Richard (Roy et al., submitted) and colleagues in CEFE, and have begun interacting with colleagues in forestry thanks to this post-doctoral experience.

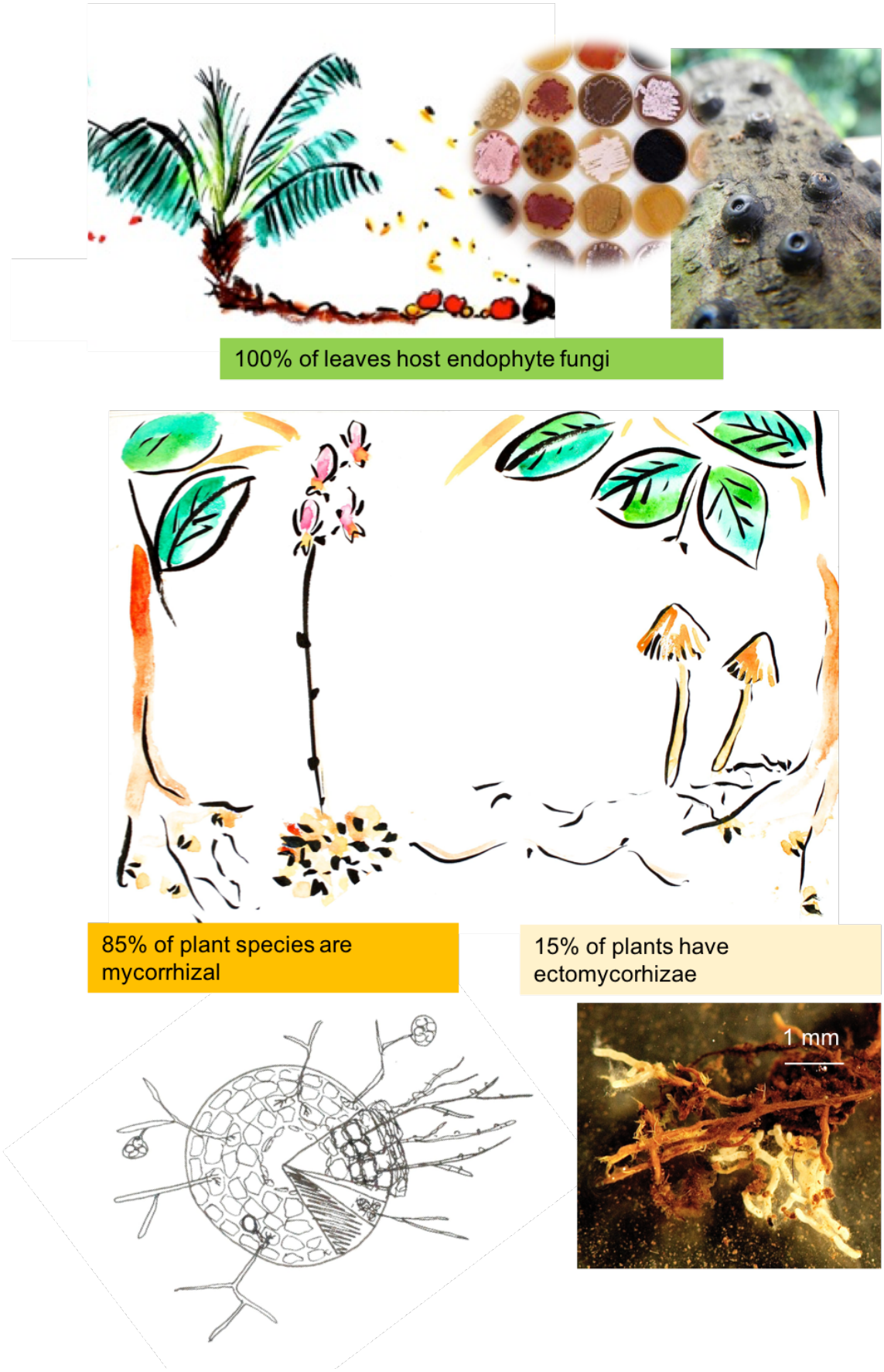


Figure 1: Plant-fungi mutualism, from roots to leaves. Images from A. Sagne and M. Roy

INTRODUCTION: setting the questions

A focus on plant-fungi mutualisms

As with all macro-organisms, plants are always surrounded by and associated with a diverse community of microorganisms, and indeed, it is hard to find a leaf which is not colonized by a fungus nor a root which is not associated with below-ground mycelium (Rodriguez et al., 2009). Plant-fungi interactions have even been detected in the first terrestrial plants of the Rhynia chert, 407 million years ago (Strullu-Derrien et al., 2018). As in all biotic interactions, the result of these interactions follows a continuum between positive and negative interactions, and vary depending on soil conditions and partner identities (Hoeksema et al., 2010). I am particularly fascinated by plant-fungal interactions, and have worked on two widespread interactions: mutualist fungi that colonize tree roots (ectomycorrhizal fungi, EMF) and fungi that grow within tree leaves and behave rather like commensals (endophytic fungi, EF; Fig 1).

Around 85% of plant species are documented as being associated with mycorrhizal fungi (Brundrett et al., 2009; Brundrett and Tedersoo, 2018). These fungi colonize their host plant roots, and form a relatively stable symbiosis in which the plant provides photosynthesis-derived sugars in return for water and nutrients (Smith and Read, 2010). Among fungi, Glomeromycota and Mucoromycotina were the first to interact with plant roots (Bidartondo et al., 2011; Strullu-Derrien et al., 2014; Rimington et al., 2015). Their interactions result in endomycorrhiza, which are observable on most herbaceous plants and tropical trees. Later during the course of fungal evolution, several linages acquired the ability to interact with plant roots and form a symbiosis materialized by an organ, made of both plant and fungi cells: the ectomycorrhiza (Fig 1). Ectomycorrhizal plants are documented in 335 genera and 8500 species, with recent articles suggesting that many more hosts await detection, especially in the tropics (Tedersoo and Brundrett, 2017). Ectomycorrhizal fungi have been assigned to 236 genera and circa 20.000-25.000 species (Comandini et al., 2012), which is relatively little compared to the 2.2 to 3.8 million species thought to exist (Hawksworth and Luecking, 2017). The ability to form EM mutualisms has been selected independently in several lineages, probably from saprophytic or endophytic ancestors (Shah et al., 2016). As a result, EMF consist of phylogenetically diverse fungi, that have undergone distinct evolutionary trajectories and phylogeographic events.

Today, most temperate trees (Pinaceae, Fagaceae) and some tropical trees (Dipterocarpaceae, some tropical Fabaceae and Myrtaceae, and other families) are associated with EMF (Brundrett and Tedersoo, 2018), but this general rule has many exceptions. Soudzilovskaia et al. (2015; 2017) have shown that rare cases of EM plants are also reported in the tropics. Despite a significant sampling bias in the Neotropics (tropical region of American continent), Tedersoo et al. (2012; 2014; Fig 2) and Brundrett and Tedersoo (2018) have also shown that ectomycorrhizal symbiosis is more widespread in temperate regions and in tropical monodominant forests. Indeed, tree monodominance is partly explained by the ability of EMF to benefit mainly their hosts population and to limit the accessibility of inorganic N to other plants (McGuire, 2007; Corrales et al., 2016). Moreover, most EMF families probably emerged in temperate regions and dispersed later in the tropics (Tedersoo et al., 2014). Nevertheless, phylogenetic studies on widespread ectomycorrhizal lineages have suggested a tropical origin for some lineages such as Inocybaceae (Matheny et al., 2009), Russulaceae (Alexander, 2006) and Clavulinaceae (Kennedy et al., 2012).

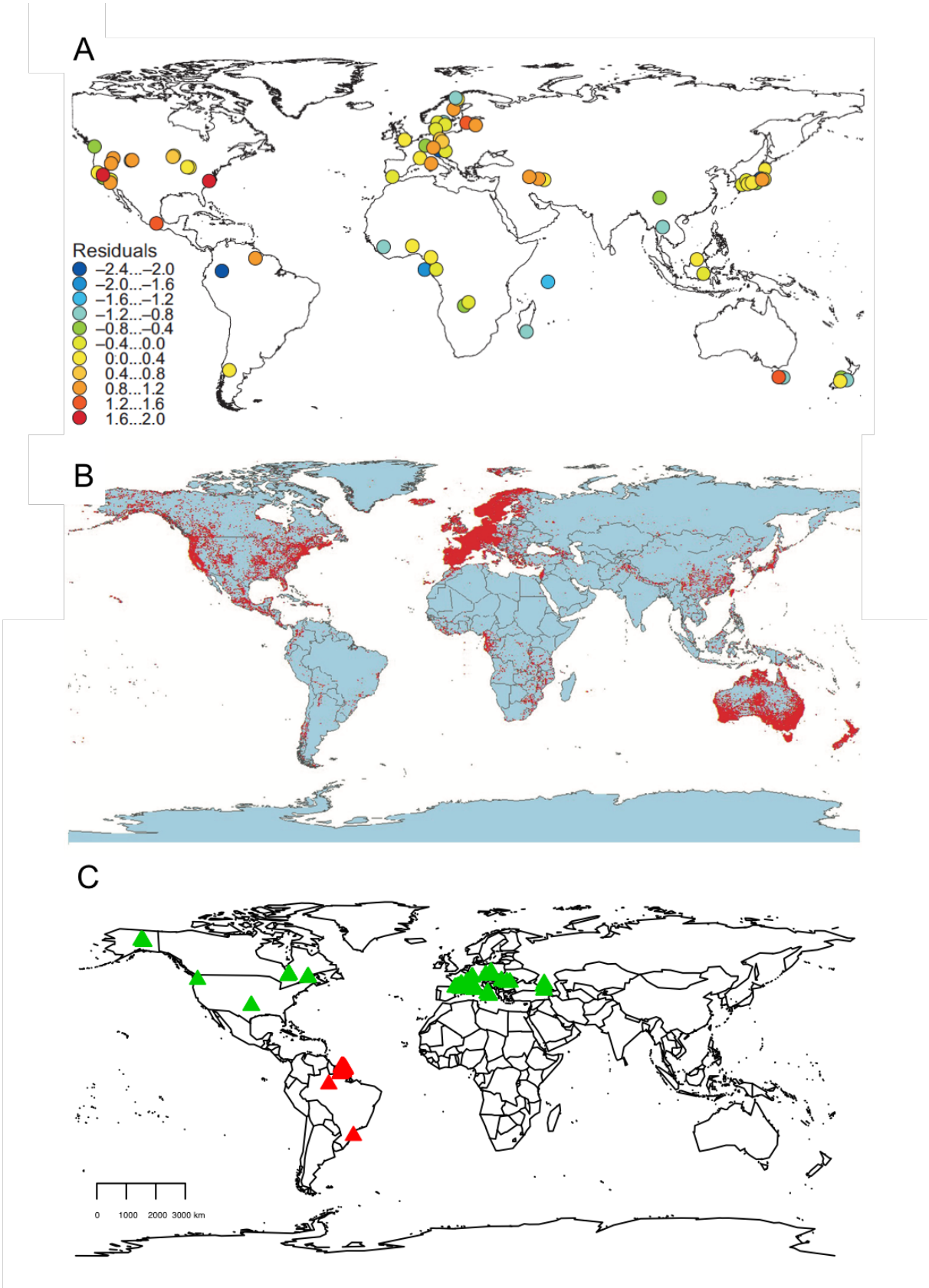


Figure 2: A, distribution of sampling plots of EMF communities (Tedersoo et al. 2012); B, distribution of confirmed EM hosts (Soudzilovskaia et al., 2017) and C, location of sampling sites for Alnus-EMF (green) and neotropical EMF (red).

Taxonomists regularly reveal new species of fungi in the tropics, including ectomycorrhizal species (Hawksworth et al., 2012; Truong et al. 2017) and more rarely, genera (Sánchez-García et al., 2016).

A fundamental question therefore emerges from these observations: **are EMF really so rare in non-monodominant forests of the Neotropics? And if so, what factors could explain their rarity and low density in Neotropical forests?** I have spent the past few years working with taxonomists to describe ectomycorrhizal species outside of monodominant forests in the Neotropics (Fig 2C), to fill this gap of knowledge on their diversity and distribution, and question their rarity (axis 1). This first axis led me to a second topic, focusing on a distinct trait amongst plant-fungi mutualisms: their specialization.

Specialization in plant-fungi mutualisms: puzzling cases and new questions?

Articles	Roy et al. 2013 ; Hynson et al., 2013 ; Kohout et al., 2013a ; Kohout et al., 2013b ; Těšitelová et al., 2013 ; Gonneau et al., 2014 ; Gladieux et al., 2015 ; Roy and Selosse, 2015

In most host-symbiont coevolutionary dynamics, specialization is often expected to occur, yet plant-fungi mutualism is on the contrary relatively generalist. Indeed, numerous studies have revealed a high proportion of fungi having multiple hosts in temperate ecosystems (Horton & Bruns, 1998; Cullings et al., 2000; Kennedy et al., 2003; Ishida et al., 2007; Twieg et al., 2007 ; **Roy et al., 2008**), and only exceptions have contradicted this rule (Bruns et al., 2002; Smith et al., 2009). This ability to associate with several hosts is expected to lead to positive interactions (so-called facilitation) between plant species (Molina and Horton, 2015), and eventually to the formation of a common mycorrhizal network (CMN, Newman, 1988; Simard et al., 1997). Indeed, shared mycorrhizal fungi have been shown to transfer organic carbon, nutrients or water between plants and the functioning of such networks can have deep consequences for plant-plant interactions (Simard et al., 1997; Simard et al., 2012 ; **Roy and Selosse, 2015**). For example, during my PhD, I studied orchids that were even dependent on such networks, the so-called mycoheterotrophic (**Hynson et al., 2013**) and mixotrophic orchids (**Selosse and Roy, 2009 ; Roy et al., 2013b ; Gonneau et al., 2014**). However, exceptions do exist, and most mycoheterotrophic orchids (Taylor et al., 2002 ; **Roy et al., 2009a**), trees of the genus *Alnus* (Molina, 1981) and Neotropical trees (Tedersoo et al., 2010) have often few, and specialized interactions (Fig 3).

Figure 3:Left, Alnus stand in Corsica, right, inselberg covered by a low canopy forest in French Guiana

Table 1: Two specialized EMF-host interactions and their characteristics

	Alnus	Neotropical trees : *Coccoloba, Neea, Guapira, Gnetum*
Host diversity	35 species distributed in the temperate zone and montane habitats in the Neotropics	60 species, belonging to Achatocarpaceae, Betulaceae, Cistaceae, Dipterocarpaceae, Fabaceae, Fagaceae, Gnetaceae* Juglandaceae, Nyctaginaceae* Pinaceae, Polygonaceae* and Salicaceae. In French Guiana only 3 families are represented (*), and occur mainly in low canopy forests
Specialized genera/lineages	*Alnicola, Alpova*	No
Specialized species	*Tomentella, Lactarius, Russula, Cortinarius*	*Cantharellus, Russula, Tomentella*
Diversity on host individuals	330 species of EMF worldwide, mean of 8 EMF species per tree and 13 species per population (**Roy et al., 2013a,** Polme et al., 2013)	38 species on 34 host individuals in Ecuador (Tedersoo et al., 2009)

Bruns et al. (2002) have already shown how exceptions are puzzling and raise questions, for example on the benefit of networks. Kennedy et al. (2015), focusing on the genus *Alnus*, have suggested several hypotheses to explain the specialization of its EMF, all linked with the ability of alders to associate with nitrogen-fixing bacteria of the genus *Frankia*. Indeed, Huggins et al. (2014) have experimentally demonstrated that specific EMF associated with alders are able to grow at a low pH, a consequence of *Frankia* presence and acidification in roots. As an association with specialized EMF might be advantageous to avoid losing nitrogen in a common mycorrhizal network, Kennedy et al. (2015) have suggested that plant to plant competition could also select for more specialized interactions. Another hypothesis instead relates to exchanges between *Alnus* and EMF: sanctions, adaptation to host metabolism or even nitrogen rewards which could select for more specialized and adapted EMF. From a more theoretical point of view, modelers are also interested in specialization, and show that isolation and environment or spatial heterogeneity, could play an important role in coevolutionary dynamics (Brown and Pavlovic 1992; Fussman et al., 2007; Mezquida et al., 2010). Geological events, such as glaciations, have also contributed to the isolation of several symbioses such as *Alnus*-EMF mutualism, and the question remains as to how far those past events have also shaped *Alnus* specialization. Through several projects in Europe, I have therefore tried to investigate **the extent to which biogeography could contribute to explain the actual pattern of diversity and specialization observed on *Alnus* EMF (axis 2a).**

Only a few EM hosts are mentioned in the Neotropics (Sulzbacher et al., 2012; Corrales et al., 2018), representing 0.004% of Neotropical tree species. Interestingly, there are numerous examples of non-monodominant trees and lianas associated with highly specialized EMF (Tedersoo et al. 2010), often among Caryophyllales. Like *Alnus* populations, these hosts are often isolated in Neotropical forests and occur at low density. In French Guiana, few EMF hosts are recorded according to botanists and root observations (Table 1; Béreau and Garbaye, 1994; Béreau et al., 1997).

Contrary to the case of *Alnus*-EMF interactions, fewer hypotheses have been formulated to explain their specialization. Moreover, as EM hosts are relatively rare, sampling bias can occur and may lead to an apparent specialization (Tedersoo et al., 2010). In French Guiana, EMF do occur, and EM hosts can locally co-occur in low canopy forests. Such a distribution raises questions as to the possible sharing of EMF between tree species in Neotropical forests, and the occurrence of a CMN. In monodominant EM forests, Corrales et al. (2016) recently showed that *Oreomunnea mexicana* (Juglandaceae) did not exchange or receive nutrients through a common mycorrhizal network, while Smith et al. (2011) detected a high proportion of multihost EMF in Guyana. Such contrasted results raise questions about EM habits in the tropics and I have therefore investigated **if specialization can be an artefact due to the low density of tree hosts, and if networks could occur between co-existing EM hosts in French Guiana (axis 2b).**

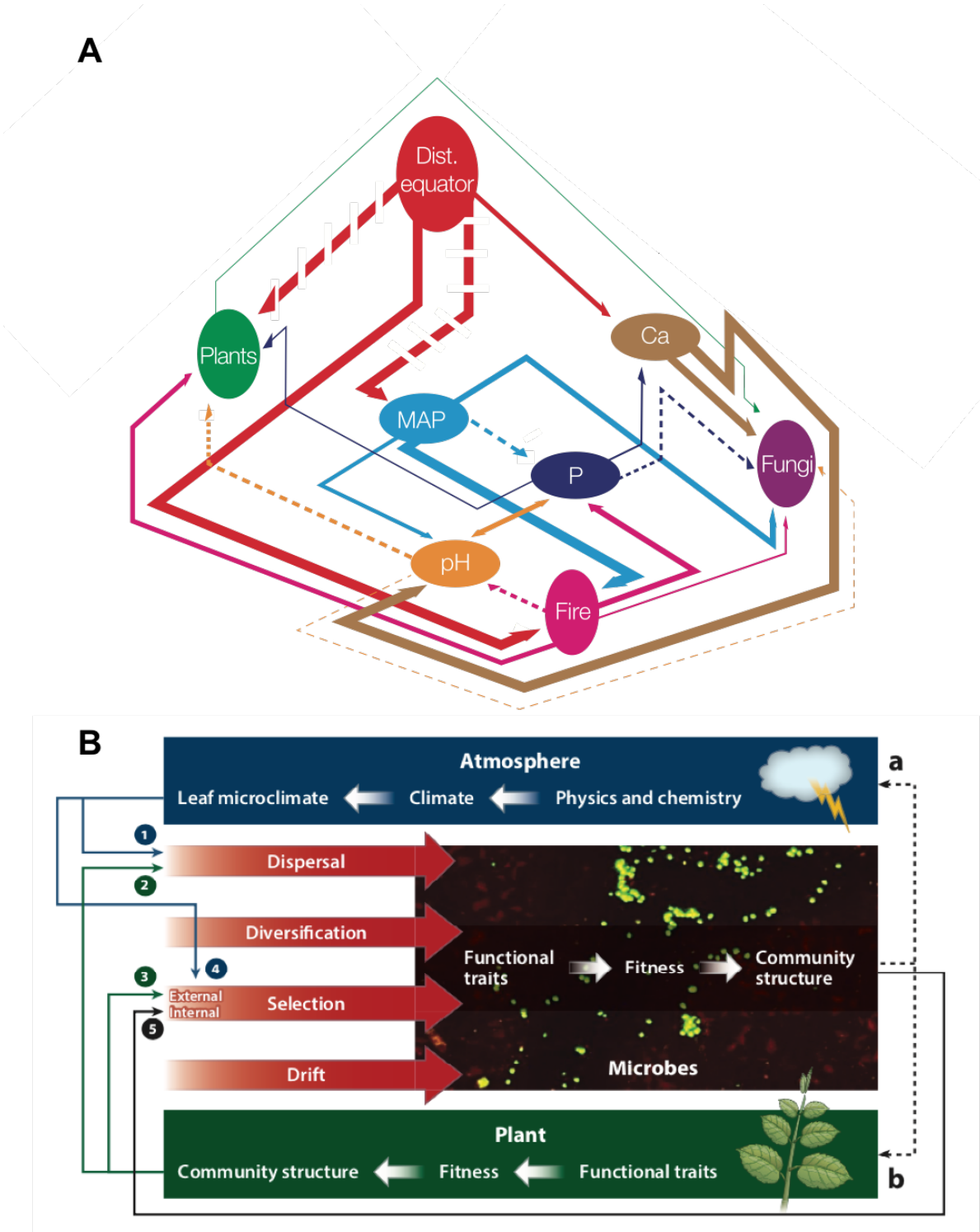


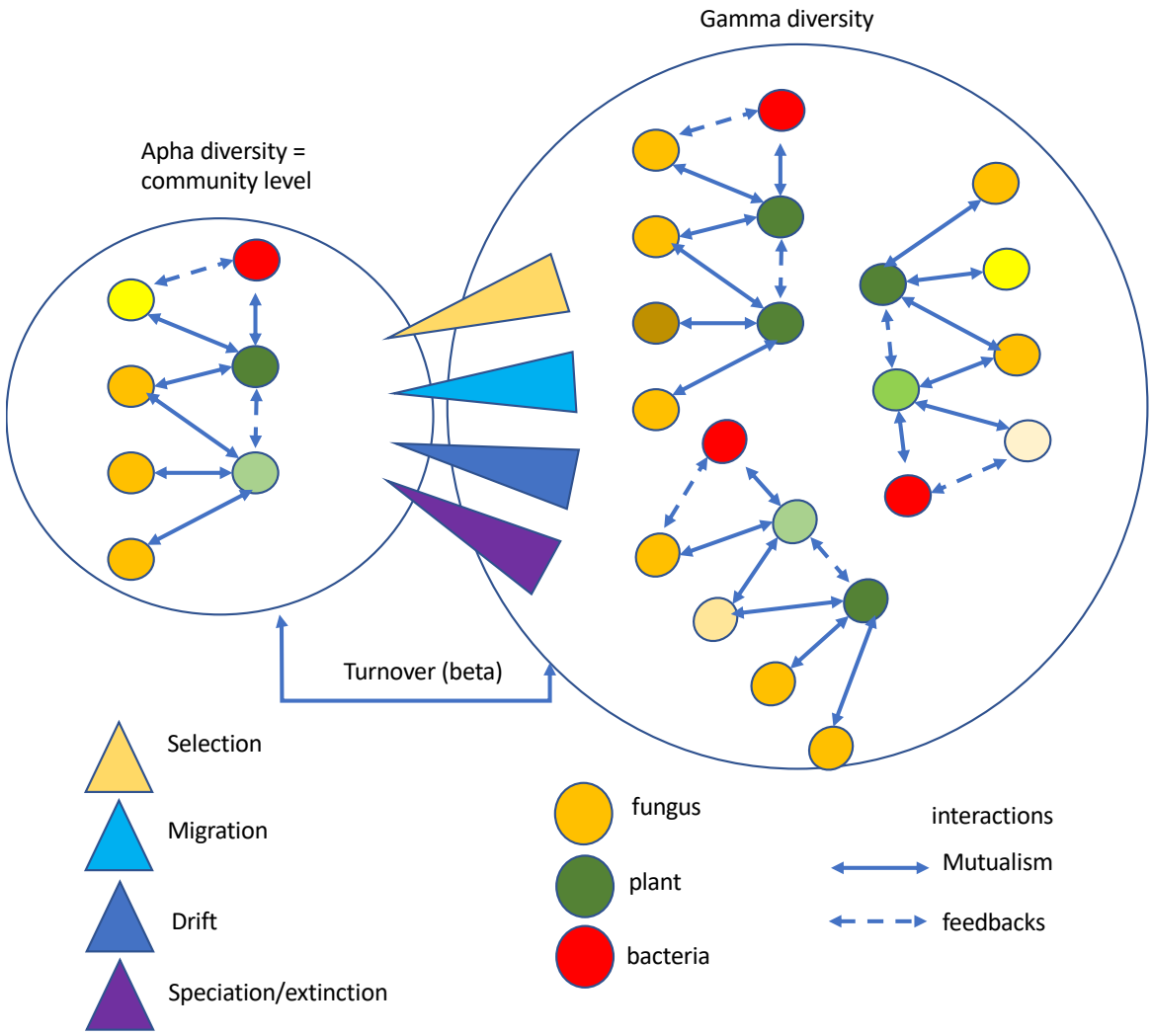
Figure 4: Processes shaping fungi (A, from Tedersoo et al., 2014) and endophyte community diversity (B, from Vacher et al., 2016a). MAP : Mean annual precipitation

Changing scales to study community ecology of complex mutualisms

Recent global analyses of soil fungal communities have highlighted the main factors shaping these complex systems (Tedersoo et al., 2014). Such analyses have been made possible by the rise of environmental DNA and next generation sequencing (NGS). Analyses based on these techniques have allowed demonstration of a strong correlation between fungal richness and numerous factors including a latitudinal gradient, mean annual precipitation, Ca concentration in soils and plant species richness, together with indirect effects of fire, soil pH and total P (Fig 4A). For EMF, the host plant remains a key parameter to explain their species richness, together with abiotic parameters such as pH and soil granulometry (Tedersoo et al., 2012). Moreover, the impact of climate can be detected not only on EMF richness, but also on EMF colonization rate (Soudzilovskaia et al., 2017). More local studies have revealed other important drivers, such as the host plant's genetic variability (Těšitelová et al., 2013).

While literature is rich with regards to niche-based processes shaping fungal communities, neutral processes are often overlooked, and a large part of community variability remains unexplained. Following the scheme of Vellend (2010), Vacher et al. (2016a) have investigated how speciation, drift, selection and dispersal shape endophytic communities (Fig 4B). Selection has been particularly studied on endophyte communities, notably the role of climatic condition (Galès et al., 2014) and plant traits (Kembel & Mueller 2014). This framework is rarely applied to EMF communities, and is of particular interest to understand EMF specialization. Indeed, such interactions could also be selected by drift in case of isolation, by a low migration rate or by local speciation (Fig 5). Migrations of EMF are particularly limited over large distance, as illustrated by their low number of invasive species (**Gladieux et al., 2015**). Following this framework, through axes 1 and 2, I have investigated if a limited regional diversity may explain the high specialization of Neotropical EMF. Through axis 2, I have investigated how past migrations could shape the high specialisation of alder EMF. Therefore, two missing factors remain to be tested to understand those cases of specialisation: neutral processes and biotic interactions between fungi and eventually other micro-organisms.

Biotic interactions may prove important in shaping fungal communities and species distributions, but most studies only consider interactions with plants, not with other organisms (Fig 4A). Koide et al. (2005) were the first to reveal negative interactions between EMF, modulated by soil chemistry. Kennedy et al. (2009) have detected priority effects between fungi, suggesting again negative interactions. Kennedy (2010) produced a synthesis on the importance of competition between EMF and highlighted the priority effect. While experimental tests on interactions are rarely done, one option is to consider putative interactions based on co-occurrence, and study ecological networks. Bahram et al. (2014) reviewed our knowledge of EM ecological networks and concluded that their topology is often non-nested and variable across ecosystems. Taudière et al. (2015) were perhaps the first to study ecological networks between plants mediated by fungi, and to integrate neutral processes in their tests. Their study of Corsican trees also showed that *Alnus* species were less connected to other trees (i.e. associated with more specialized fungi) than neutral processes would predict. The analysis of ecological networks allows a comparison with null predictions and brings quantitative measures to describe EMF specialization and fungi to fungi interactions. I have begun using ecological networks to investigate **variations of *Alnus*-EMF specialization, at both local and global scales (axis 3a)**.



Scale/model	Processes	Axis	How could we explain the high specialization of EMF/endophytes?
Gamma EMF pool	All	1	What is the pool of EMF in Neotropical forests and why are EMF so rare?
Beta Host-EMF interactions	Migration	2a	How far host migrations and isolation could have shaped the low diversity and high specialization of alders EMF?
	Selection by host+migration	2b	Is specialization an artifact due to host tree isolation and do co-existing host share more EMF in neotropical forests?
Alpha Host-EMF-Bacteria Or bacteria-fungi interactions in leaves	Interactions/selection	3a	How far selection by *Frankia* or competition between trees could shape the low diversity and high specialization of alders EMF?
	Interactions/feedback	3b	How far sharing EMF or not can affect fir growth in boreal forests?
	Interactions/Selection by host	3c	How neutral processes, and host diversity, could shape endophyte fungi diversity and their interactions within leaves

Figure 5 : What are the processes shaping interactions and their specialization within a community? Evolutionary processes can be involved (triangles), and direct and indirect interactions can reinforce selection (arrows). Moreover, a low alpha and gamma diversity may reduce the number of possible interactions.

To investigate all factors shaping this specialized association, I also tested **how interaction with *Frankia* could shape *Alnus*-EMF interaction**.

These questions on fungi-fungi interactions are intimately linked to forest dynamics and plant-plant interactions. Bever et al. (2010) discussed how plant-fungi interactions may shape plant-plant interactions, and concluded that changes in abundance and contrasted feedbacks may contribute to explain facilitation processes in ecosystems. The role of EMF in facilitation processes is often assumed and has been well illustrated through the nurse plant effect (Dickie et al., 2004; Nara, 2006; Richard et al., 2009).

In boreal forests, where EMF are diverse and abundant (Taylor et al., 2014), climate change is extending tree distributions northwards (Woodall et al. 2009) and changing ecosystem dynamics. Specifically, at the ecotone between spruce-dominated forest to the north and mixed boreal forest to the south, firs are extending their northern distribution (Messaoud et al. 2007). In the spruce forest, patches of aspen are scattered, and firs are mainly growing under this broad-leaf tree, while regeneration seems limited under black spruce (Arbour and Bergeron 2011). Both forest types grow on the same substrate, under the same climatic conditions, and all these trees are also associated with EMF. **Through the PhD of Mélissande Nagati, co-supervised with Monique Gardes at UPS and Yves Bergeron and Annie Desrochers at University of Quebec in Abitibi Temiscamingue (UQAT), we have investigated the role of EMF in plant-plant interactions through field and *ex situ* experiments to test if shared EMF could contribute to facilitation of fir by aspen in boreal forest (axis 3b).**

Nevertheless, these questions of community ecology are difficult to answer with EMF fungi. Studying interactions in root or soil cores is possible but requires a reduced study scale, as suggested by Bogar and Peay (2017). Within roots, EMF and mycorrhizal fungi often live with diverse endophyte fungi (e.g. in orchid roots, Kohout et al., 2013a, 2013b). Within leaves, endophytic fungi can also co-occur, and colonize spaces between plant cell walls (Rodriguez et al., 2009). Their effect on plant can be neutral, positive or negative, depending often on host plant fitness and environmental conditions (Lindow and Brandl, 2003). Interestingly, because these diverse interactions all occur at a very small scale, the leaf, and this organ can therefore be sampled to study interactions, not only with the plants, but also between fungi within the leaf. In a study of endophyte global distribution, Arnold and Lutzoni (2009) have showed that their diversity was higher in tropical tree leaves, suggesting a hot spot for such fungi. Among the hypotheses proposed to explain this, the diversity of hosts, and the higher levels of photosynthetic activity in tropical leaves over a year as compared with temperate leaves, have been suggested. However, neutral processes have been neglected in explanation of the diversity of endophytic communities, despite the fact that tropical forests and their host diversity have been the key stone of the neutral theory of biodiversity (Hubbell, 2001; Chave, 2004). Through projects with chemists interested in interactions between micro-organisms within leaves, and **the post-doc project of J. Donald,** we have investigated **how neutral processes, and host diversity, could shape the diversity of endophyte fungi and their interactions within leaves (axis 3c).**

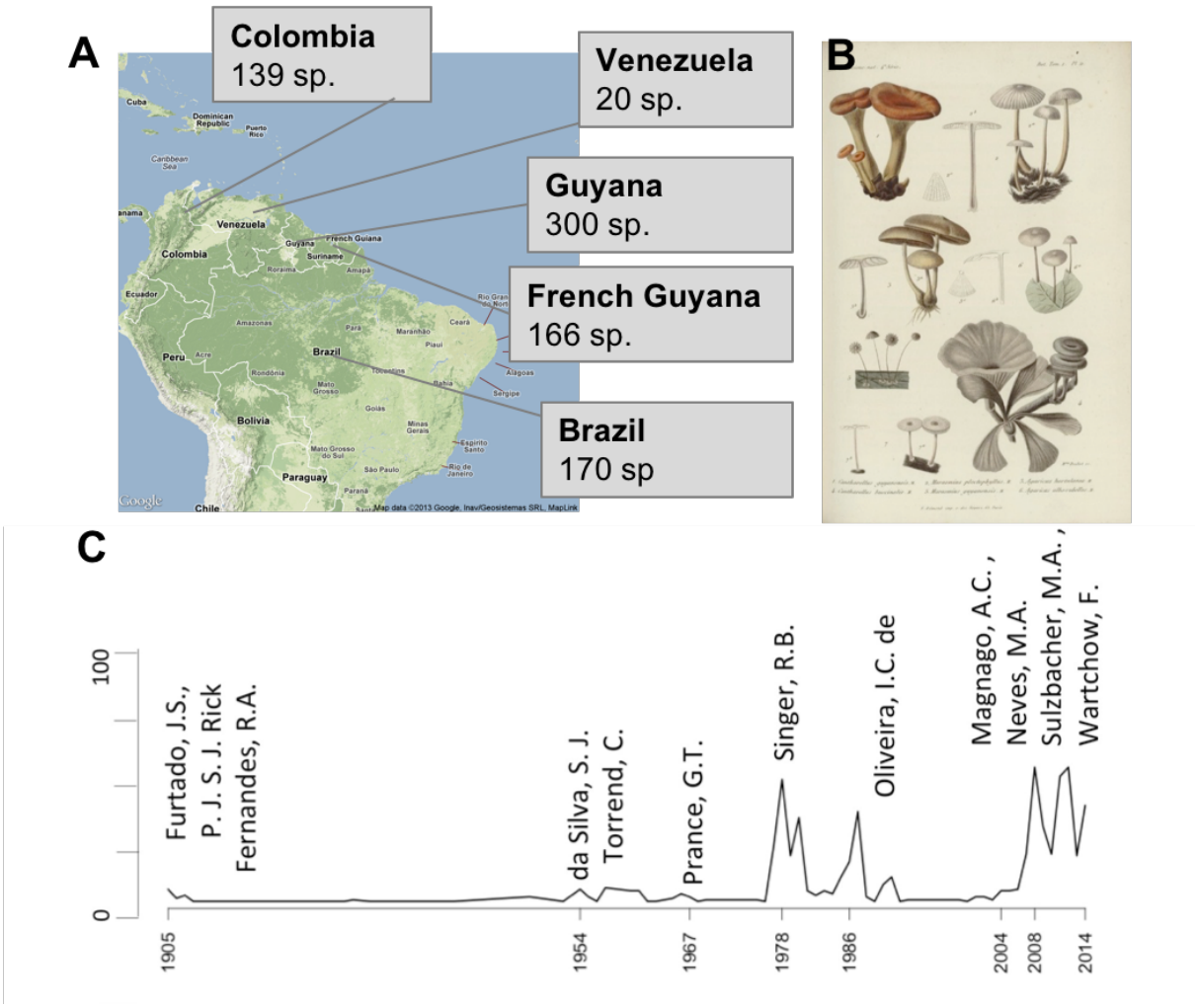


Figure 6: A, distribution of EMF species per country since 2010; B, first observation of Cantharellus guyanensis; C, number of EMF collections deposited in herbaria since 1905, Roy et al. 2016.

PAST/PRESENT RESEARCH

Axis 1 : Diversity and distribution of EMF fungi in the Neotropics

Projects	FUNGUY, DIADEMA, DIAMOND, LONGTIME
Articles	Henkel et al., 2013; Roy et al., 2016; Roy et al., 2017; Hoeksema et al., 2018; Buyck et al., 2017; De Crop et al. 2017; Barbosa-Silva et al., 2017; Crous et al., 2017; Gruhn et al., 2017, 2018, Roy et al., 2018 ; Accioly et al., 2019

The Neotropics refer to South and Central America, and include from tropical to temperate environments (Antonelli and San Martin, 2011). Neotropical forests at low elevation have several peculiarities, compared to other tropical forests, and show a higher tree diversity, and less mono-dominance (Ter Steege et al., 2013). Moreover, EMF hosts are rare and occur at low density, except in the Guyana highlands (Henkel et al., 2002; Henkel, 2003). Soil and root sampling in Neotropical forests have confirmed this trend and have allowed detection of only few EM hosts (McGuire, 2007, Bâ et al., 2016). All these data have contributed to shape our understanding of the actual diversity pattern of EMF symbiosis in the Neotropics (Soudzilovskaia et al., 2017), beside a strong sampling bias in the Amazon (Fig 2, Table 1).

Nevertheless, during my first visit to French Guiana I found an unexpected diversity of EMF, including *Cantharellus guyanensis* (**Henkel et al., 2013**). This first visit was fundamental in my career. By interacting with taxonomists, and by digging through local herbaria collections, I realised that many cases of EMF had already been reported (Fig 6A). *Cantharellus guyanensis* was not a newly described species, as it had been collected between 1835 and 1849 by Montagne and Leprieur (Montagne, 1850; Fig 6B). Interestingly, this species had been undetected for more than a century, while our research with taxonomists revealed its wide distribution, from South of Brazil to North of Colombia (**Henkel et al., 2013**). Thanks to a visit to Manaus herbarium, I had access to Rolf Singer's herbarium, and realised that boxes of specimens were still waiting for a further description. With Ricardo Braga-Neto (PhD, INPA, Brazil), we investigated **if genus-level records could provide more records of species for EMF and allow for expanded outlines of distribution for EMF in Brazil**. By searching in records of herbarium samples collected over the last century in Brazil, we detected 2268 records (search on species link project, http://splink.cria.org.br/). With the help of taxonomists, we were able to sort duplicates and incorrect assignments, and rejected half of the records. We revealed that EMF fungi could occur all over Brazil, but remain rarely and only recently observed (Fig 6C). Indeed, only 1066 observations were recorded over a century, and each species was observed on average 2.33 times (**Roy et al. 2016**).

There is a gap between the distribution of EMF outlined by ecologists and taxonomists, with taxonomists rapidly increasing the number of described EMF species (Fig 6A), and also the number of habitats where EMF could be detected, such as the *restinga* (dry forests) in Brazil (Sulzbacher et al., 2017). To increase communication between fields, sequencing specimens is key: it allows detecting EMF sequences in soil and reciprocally permits taxonomists to extend species distributions and describe fungal ecology (Truong et al., 2017, Box 1). Since 2016, I have contributed to this end by organizing symposia, linking taxonomists and ecologists, and building an integrative discussion on EMF distribution (**Roy et al., 2017b**). Colleagues working on EMF in the Neotropics are now organized in a network (Fig 7A, Bueno et al., 2017), and all agree that taxonomists are leading the way to find more habitats and better understand EMF distribution and ecology.

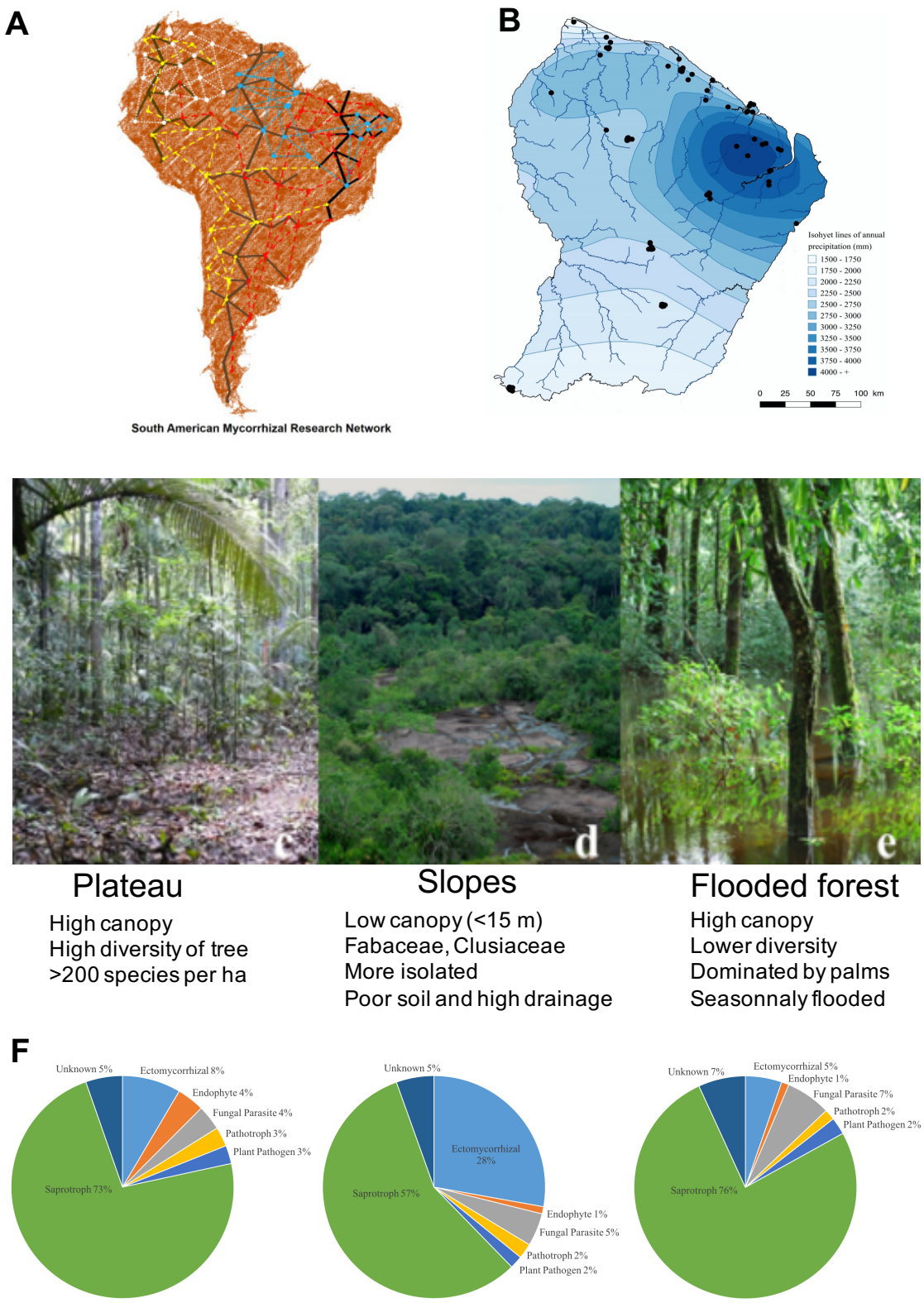


*Figure 7: A, network of colleagues working on mycorrhizal symbiosis in South America (Bueno et al., 2017); B, sites where fruiting bodies were inventoried in French Guiana (**Jaouen et al., submitted**), blue lines represent the precipitation gradient, C to E, habitats studied in French Guiana and F, proportion of observations (number of specimens) per trophic mode, including EMF (**Schimann et al., submitted**).*

In French Guiana, mycology has a long history, with Montagne and Leprieur collecting and describing 255 species as far back as 1850, among of which two were EMF (Montagne, 1850). Up until recently, the checklist of fungi in French Guiana (Courtecuisse et al., 1996) included more taxa (625) and 7 additional EMF (*Fistulinella venezuelae* and *Fistulinella* spp., *Lactarius epitheliosus, Russula hygrophytica, R. moyersoni, R. violaceotunicata* and *Tricholoma crissum*). To advance knowledge about EMF, but also on French Guiana fungi in general, with my colleague Heidy Schimann at ECOFOG (Kourou), we have hosted mycologists from abroad, deposited fungi in herbaria, and exchanged specimens. This work has led to several new descriptions (**Barbosa-Silva et al., 2017; Crous et al., 2017; Gruhn et al., 2017, 2018, Accioly et al., 2019**), projects funded by the LABEX CEBA and more recently by the *Atlas de la Biodiversité Communale de Saül* (ABC). Most specimens are already deposited at Paris national herbarium and a database has been built, now containing 9115 records, of which 5219 are already in the GBIF database (https://www.gbif.org/dataset/ca0dfc4e-6a98-4b1b-b010-c6ce894a72f1, **Jaouen et al., submitted**). Moreover, the checklist of fungi in French Guiana is now updated by the INPN and reports 2798 species (Taxref v12.0, Gargominy et al., 2018).

Since my research questions have also been centred on community ecology, together with Heidy Schimann I have set up a protocol to replicate our inventories and study, not only for the species distribution but also for fungal diversity across all French Guiana habitats (Fig 7B to 7E, **Schimann et al., submitted**). Indeed, Neotropical forests in French Guiana follow a pedo-hydrological (Epron et al., 2006; Quesada et al., 2011) and topographical gradient (Guitet et al., 2013), from seasonally flooded forests to hilltop forests (so-called "plateau"). Slopes also host typical low-canopy forests. The soil is also particularly important, as *terra-firme* forests – which represent 97% Amazonian soils – show a higher diversity and biomass than white-sand forests (Baraloto et al., 2011). Rolf Singer has spent part of his career studying white sand forests and has suggested that EM symbioses might be an adaptation to survive on these extremely poor soils (Singer and Araujo, 1979). During a teaching trip to the Amazon, we revisited his sites as well as 9 white-sand plots in French Guiana and Brazil, to show that **white sands are indeed generally colonized by EMF** (**Roy et al. 2016**). In French Guiana, through several projects of the LABEX CEBA, we have also visited plots on *terra-firme*, slopes and white sands, including some close to inselbergs (i.e. ancient granite outcrops) isolated in the forests (Porembski, 2007) to investigate **if, like tree communities, fungal communities would differ across those habitats**. These inventories revealed that forests on slopes were generally richer in EMF than other sites, even on *terra-firme* (Fig 7F, **Schimann et al., submitted**).

For fungi in general, our inventories showed a higher similarity between fungal communities on slopes and plateau compared to flooded forests, together with a strong coupling with plant communities (**Schimann et al., submitted**) and earthworm communities (**Vleminckx et al., submitted**). All the data collected in Brazil (Fig 8A) and French Guiana are now integrated with other records from the Neotropics to investigate, through spatial modelling, which factors (tree diversity, topography, climate) could explain their distribution (Fig 8B, **Braga-Neto et al., in prep**).

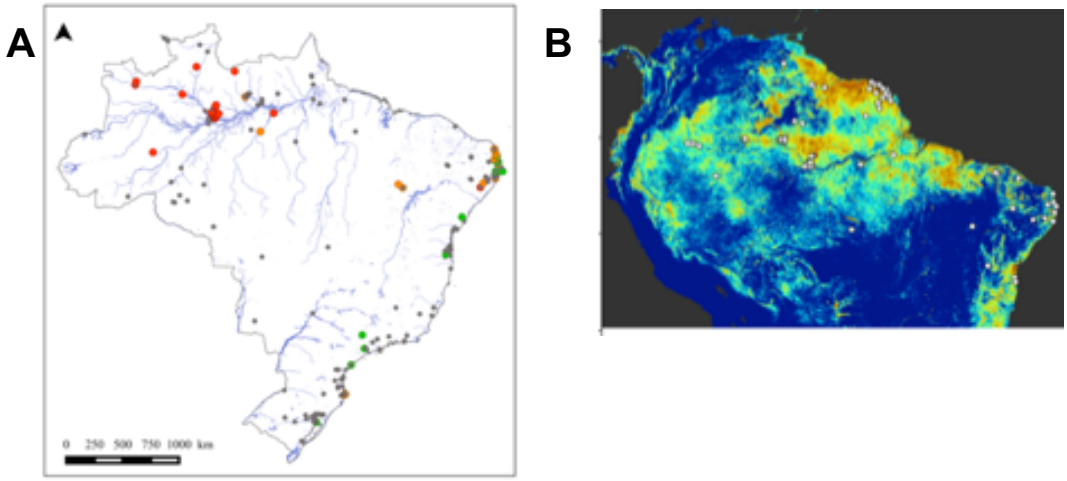


Figure 8: Map of EMF records in Brazil, based on genus-level identifications (Roy et al., 2016), B, modelling of EMF distribution, Braga-Neto et al. In prep

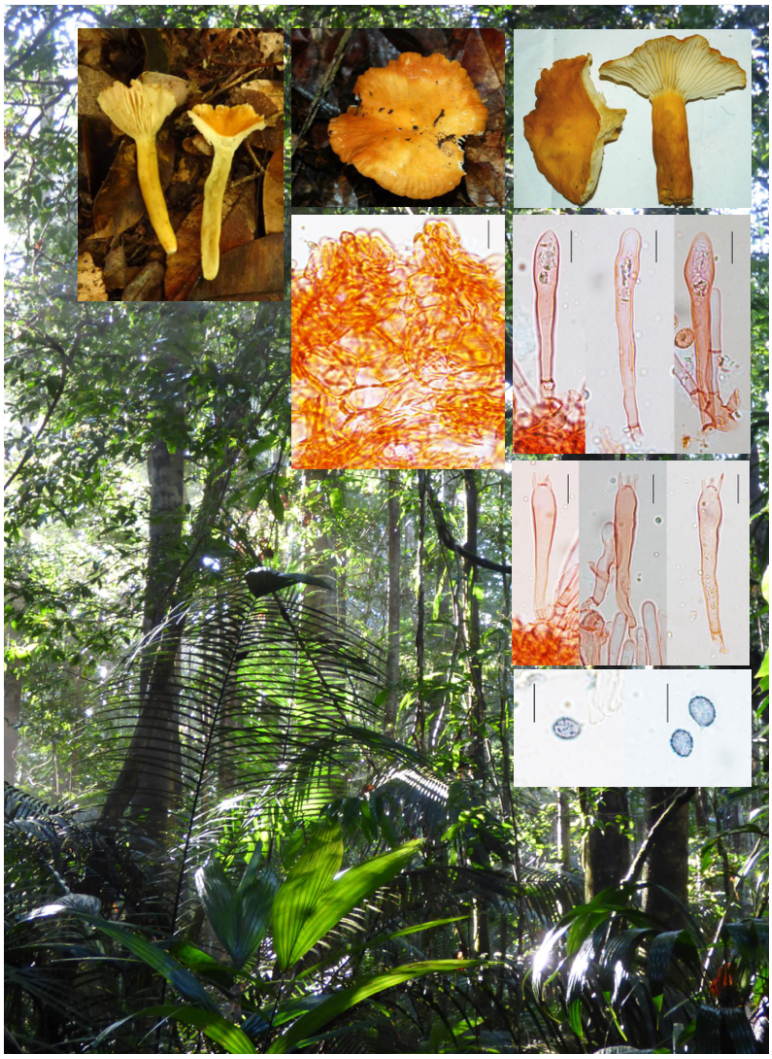
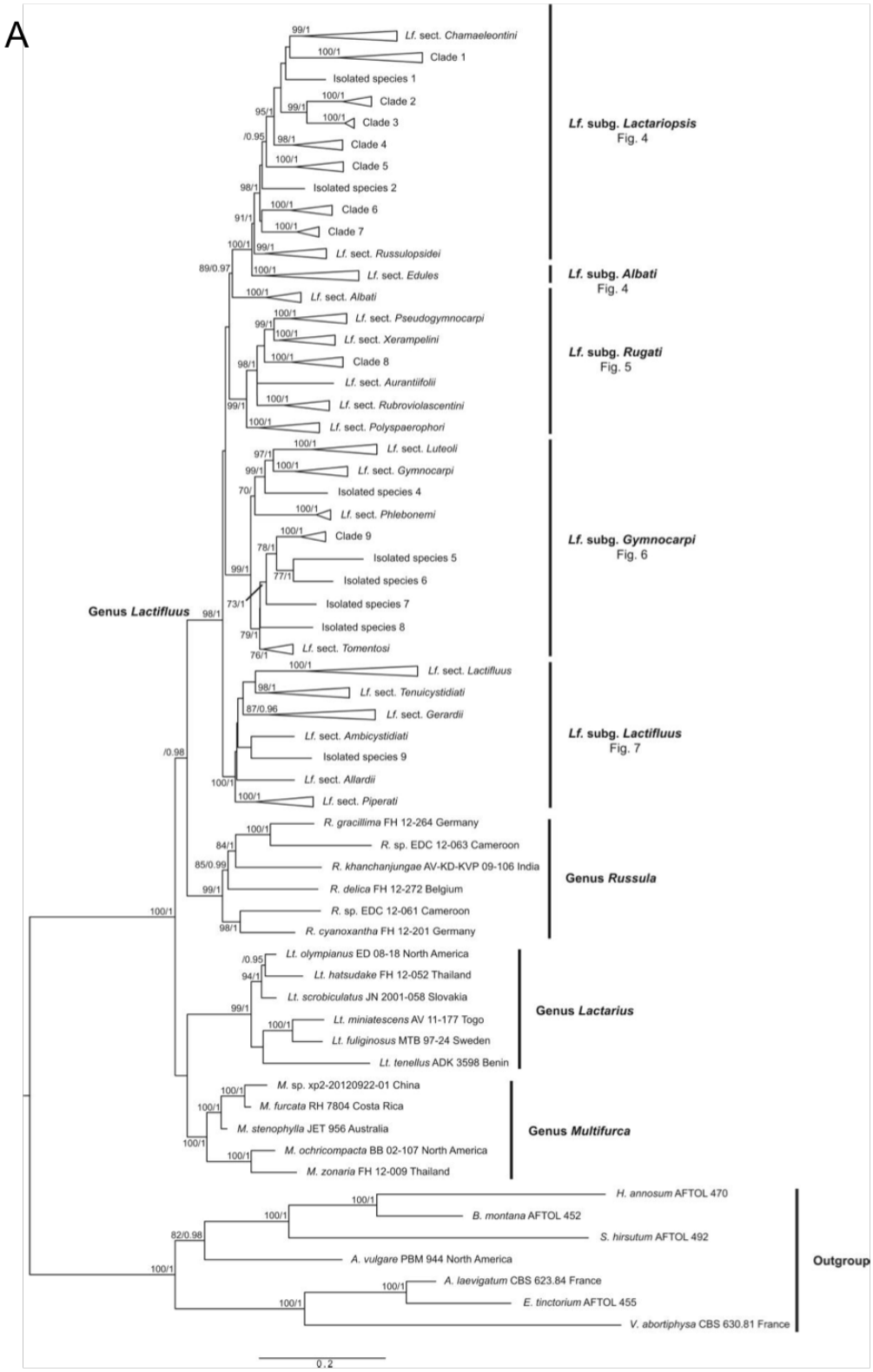


Figure 9: Description of a new Lactifluus *species (sect* Polysphaerophori*), from Trinité reserve (Crous et al., 2018)*

While my research has helped to record the distribution of EMF in the Neotropical lowlands, their rarity remains undeniable and is interesting *per se*. Indeed, each sampling has revealed new species to describe (Fig 9A, **Crous et al., 2018**), even in widely distributed families such as the Russulaceae. Such a pattern may signal **speciation events in the Neotropics**, and I have built collaborations to integrate Russulaceae sequences into large phylogenies in order to test this hypothesis. During Jan Hackel's master 2 internship and with colleagues from Ghent herbarium, we revealed new species and lineages within *Lactifluus* phylogeny (Fig 10, **De Crop et al., 2017**). In the lesser Antilles, we have revealed numerous endemic species and a recent diversification (**Delgat et al. submitted**). At a larger scale, Russulaceae have undergone a complex evolution, with possible long-distance dispersal from Africa, migration along the Andes, and possible vicariance for species associated with *Nothofagus* (**Hackel et al., in prep**). In another EMF family, the Cantharellaceae, together with T. Henkel and B. Buyck, I have detected both widespread species like *Cantharellus guyanensis* (**Henkel et al., 2013**), and endemic species in the lesser Antilles, such as *Cantharellus coccolobae* (**Buyck et al., 2016**). Moyersoen has suggested that dispersal could be an important mechanism of radiation of EMF in South America (Moyersoen, 2012). As favourable habitats are relatively isolated (such as the white sands), this hypothesis could be true, and would be investigated with phylogenomic tools (Looney et al., 2018). Moreover, for these mutualist lineages, coevolution with their host may also lead to speciation (Looney et al., 2016), as observed for the very specific lineages associated with *Alnus* (Rochet et al. 2011; **Hackel et al., in prep**).

If speciation has occurred, **why are EMF represented by so few species in the Neotropical lowlands today**, while plants, birds, mammals, insects are so diverse in this region (Antonelli and San Martin, 2011)? They occur at low densities nearly everywhere, and in lowland forests they could represent 11% of fruiting bodies (based on **Jaouen et al., submitted**) and a minor proportion of soil sequences (Tedersoo et al., 2014). Corrales et al. (2018) produced a synthesis on EMF distribution and ecology in the tropics, but focused on mono-dominant forests. Based on studies of French Guiana forests, we can now propose several hypotheses to explain their widespread distribution at low density, linked with EMF and EM host biogeography, and the constraints shaping EMF communities (**Roy and Verbruggen, in prep**).

Compared to the distribution of EMF worldwide, the Neotropics only host a subset of EMF lineages and only one genus is endemic to the Guyana, *Guyanagarika* (Sánchez-García et al., 2016). Molecular dating of divergences within the Russulaceae tree suggests several independent speciation events around 50 million years ago (**Hackel et al., in prep**), a relatively recent period as compared to the emergence of EMF lineages (Hibbett et al., 2009). During this period, the landscape was completely different, probably dryer, as the Amazonian basin formed more recently, ca. 23 million years ago (Hoorn et al., 2010). Radiations of palms, which characterise Amazonian forests and flooded habitats, were even more recent, dated 8 million years ago (Roncal et al., 2012), illustrating how young Amazonian landscapes are. Prior to this, 50 millions years ago, dry forests and savannas were probably more extensive and represented favourable EMF habitats, or at least represent similar conditions to white-sand forests and slopes. With the recent functioning of the Amazon, ECM-favourable habitats such as white-sand forests may have been isolated and or may have disappeared. They currently represent only 3% of Amazonian forests.


A
Lf. sect. Chamaeleontini
Clade 1
Isolated species 1
Clade 2
Clade 3
Clade 4
Clade 5
Isolated species 2
Clade 6
Clade 7
Lf. sect. Russulopsidei
Lf. sect. Edules
Lf. sect. Albati
Lf. sect. Pseudogymnocarpi
Lf. sect. Xerampelini
Clade 8
Lf. sect. Aurantiifolii
Lf. sect. Rubroviolascentini
Lf. sect. Polyspaerophori
Lf. sect. Luteoli
Lf. sect. Gymnocarpi
Isolated species 4
Lf. sect. Phlebonemi
Clade 9
Isolated species 5
Isolated species 6
Isolated species 7
Isolated species 8
Lf. sect. Tomentosi
Lf. sect. Lactifluus
Lf. sect. Tenuicystidiati
Lf. sect. Gerardii
Lf. sect. Ambicystidiati
Isolated species 9
Lf. sect. Allardii
Lf. sect. Piperati
R. gracillima FH 12-264 Germany
R. sp. EDC 12-063 Cameroon
R. khanchanjungae AV-KD-KVP 09-106 India
R. delica FH 12-272 Belgium
R. sp. EDC 12-061 Cameroon
R. cyanoxantha FH 12-201 Germany
Lt. olympianus ED 08-18 North America
Lt. hatsudake FH 12-052 Thailand
Lt. scrobiculatus JN 2001-058 Slovakia
Lt. miniatescens AV 11-177 Togo
Lt. fuliginosus MTB 97-24 Sweden
Lt. tenellus ADK 3598 Benin
M. sp. xp2-20120922-01 China
M. furcata RH 7804 Costa Rica
M. stenophylla JET 956 Australia
M. ochricompacta BB 02-107 North America
M. zonaria FH 12-009 Thailand
H. annosum AFTOL 470
B. montana AFTOL 452
S. hirsutum AFTOL 492
A. vulgare PBM 944 North America
A. laevigatum CBS 623.84 France
E. tinctorium AFTOL 455
V. abortiphysa CBS 630.81 France
Genus Lactifluus
Lf. subg. Lactariopsis
Fig. 4
Lf. subg. Albati
Fig. 4
Lf. subg. Rugati
Fig. 5
Lf. subg. Gymnocarpi
Fig. 6
Lf. subg. Lactifluus
Fig. 7
Genus Russula
Genus Lactarius
Genus Multifurca
Outgroup
0.2

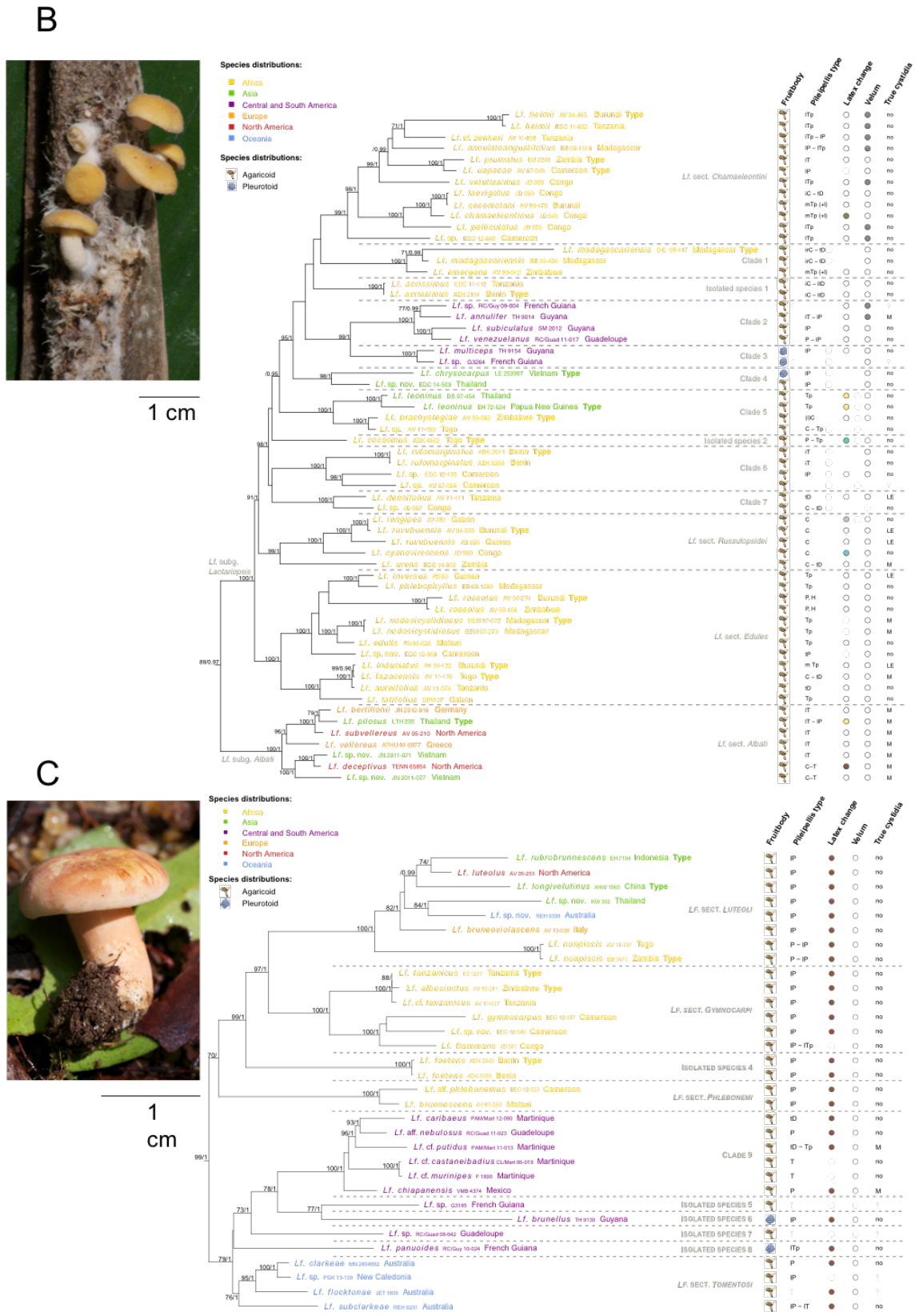


Figure 10: Multigene phylogeny of Lactifluus (A), highlighting species from the Neotropics and French Guiana (violet). Pictures illustrate representative species from French Guiana for Albati *(B) and* Gymnocarpi *(C) sections (**De Crop et al., 2017**).*

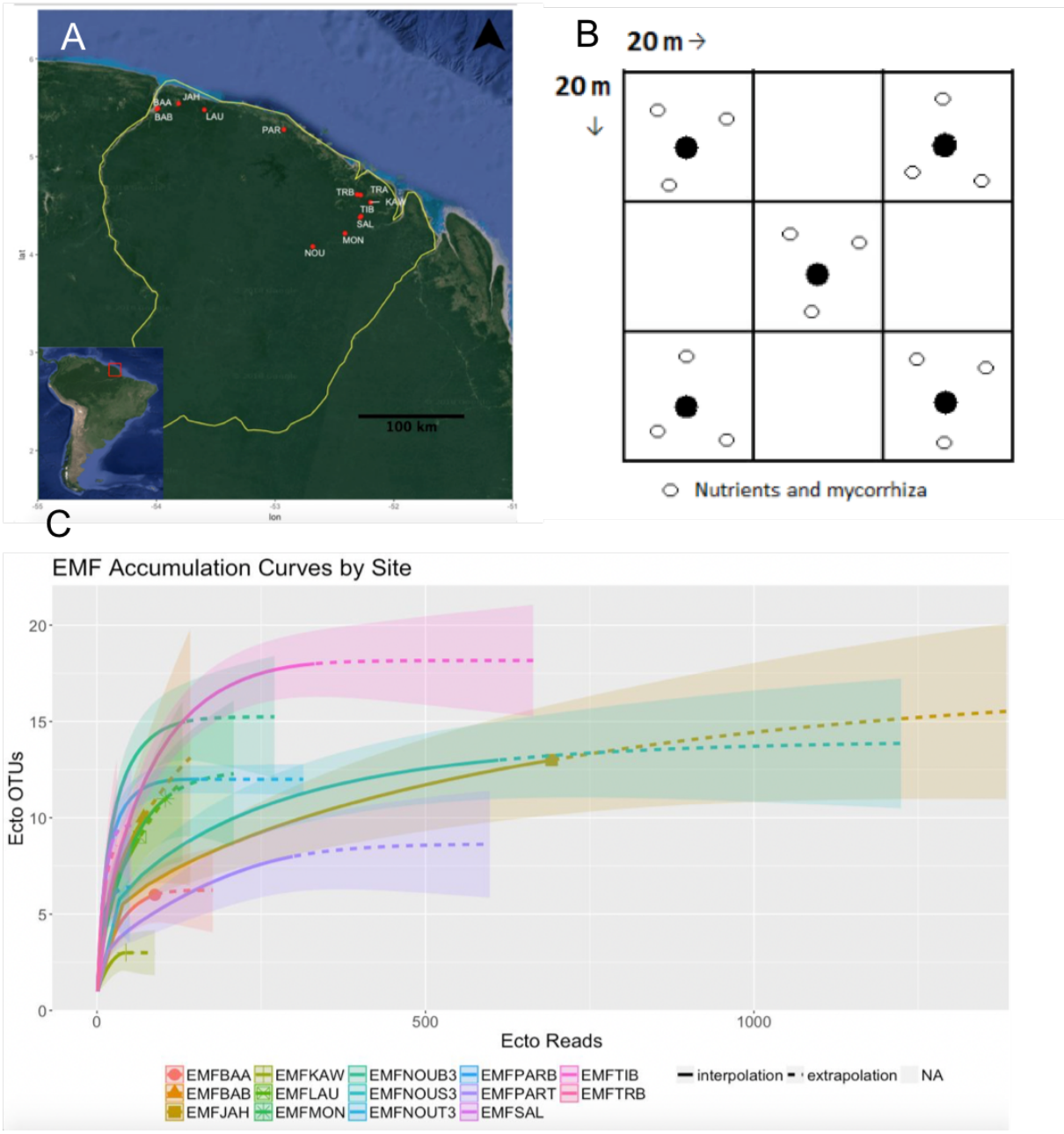


Figure 11: A, location of soil cores sampled along a phosphorus gradient in French Guiana, B, sampling scheme of soil cores and C, accumulation curves of EMF (Ecto) OTUs for each site.

Among the peculiarities of Amazonian forests, we note that EM hosts are neither mono-dominant nor do they systematically occur at low densities. Moreover, they do not belong to widely distributed families or lineages that are highly mycorrhizal. Among Polygonaceae, only *Coccoloba* and *Polygonum* are EM hosts, and not in all habitats. Moreover, Béreau and Garbaye (1994) and Béreau et al. (1997) showed a relatively low colonization of *Coccoloba* roots in French Guiana. Among Nyctaginaceae, only *Pisonia, Guiapira*, and *Neea* are EM, and despite recent clues, not all Caryophyllales nor Fabaceae are indeed EM hosts (Alvarez-Manjarrez et al., 2018). Those associations may have evolved in the Neotropics, potentially dispersed by seeds over long distances (**Sené et al., 2018**). The phylogenetic diversity of hosts, and their variable mycorrhization, may suggest a recent acquisition of EM interactions for plants in the Neotropics. There is therefore a need to date the emergence of EM interactions in the Neotropics, based on plant phylogenies. Radiations of *Coccoloba* are fairly recent and dated to between 17 and 27 million years ago (Schuster et al., 2013), which may support this hypothesis. Inversely, *Gnetum* are EM worldwide (Singer and Araujo, 1979; Onguene & Kuyper, 2001; Tedersoo and Polme, 2012; Bâ et al., 2012). Their distribution and EM habit might be more ancient than other EM associations in the Neotropics, as *Gnetum* belongs to gymnosperms.

The current distribution of EMF in low forests raises questions about their physiology and interactions with tree roots. Singer and Araujo (1979) have suggested that EMF may be advantageous for plants on white sands and poor soils, where phosphorus may be more limited. Corrales et al. (2018) have reviewed the importance of EMF in mono-dominant forests and have suggested that tannins and C/N ratios may also limit mineralization and favour EMF. During the master 2 of Benjamin Durrington, we worked on the distribution of EMF along natural gradients in French Guiana (Fig 11A). Roots had been previously collected from soil cores by E. Verbruggen and his team (Fig 11B), and we aimed to test **if phosphorus and nitrogen are key determinants of EMF distribution**. We hypothesized that **poor soils would favour EMF symbioses**. By using NGS sequencing of ITS1, we detected only a few EMF (89 Operational Taxonomic units out of 6224 OTUs) but in 14 plots out of 22 (Fig 11C). We showed that nitrogen had a negative effect on their diversity, and that sandy soils tended to have less EMF (**Durrington et al., in prep**). Interestingly, the number of EMF OTUs was positively correlated with the number of tree species known as endomycorrhizal, associated with endomycorrhizal fungi. These results partly support the hypothesis that poor soils would host more EMF, and confirm their wide distribution at low densities.

This pattern raises another question: **what if the low density observed for each EMF species was the result of processes shaping the low density of each tropical tree species**? Indeed, Neotropical forests are well-known for their high diversity and the low density of tree species. Janzen (1970) and Connell (1971) both observed that the low density of individual spcies resulted from a local and negative effect of density on seedling growth and survival. They hypothesized that natural enemies, host specific, may cause such an effect. This "Janzen-Connell" hypothesis has been tested through different approaches, and natural enemies could indeed be fungi (Bagchi et al., 2010; Mangan et al., 2010). More recently, Levi (2019) have highlighted how important enemies are for plant communities in the Neotropics, and Peay et al. (2013) illustrated the strong links between plant and fungi diversity. Thus, EMF may occur at low density in relationship with their host distribution, but on the other hand, interactions with other organisms and local fungi may also reduce their density.

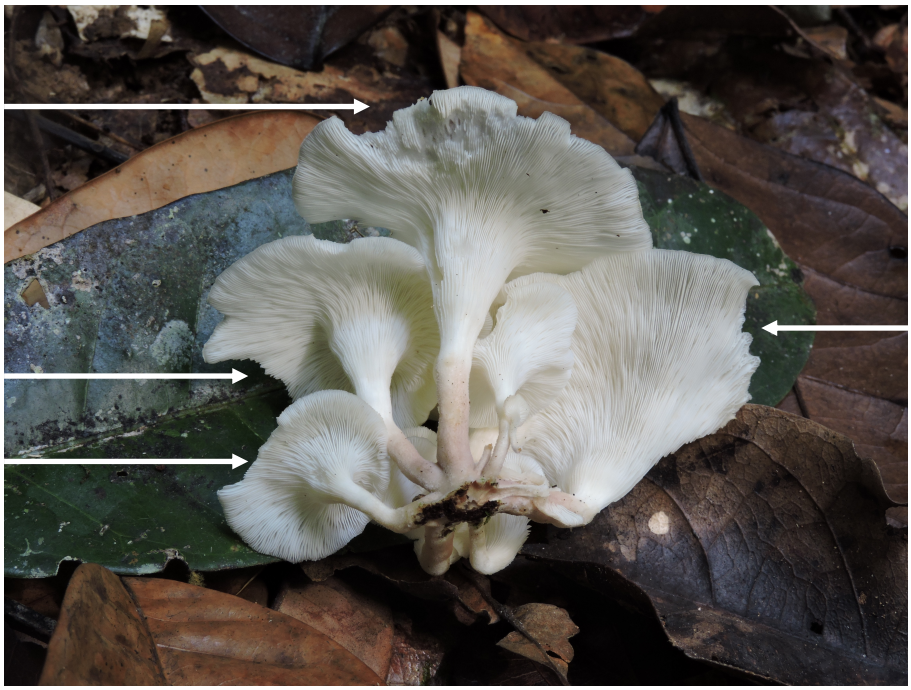


Figure 12: Observation of mycophagy clues (arrows) on a Pleurotus.

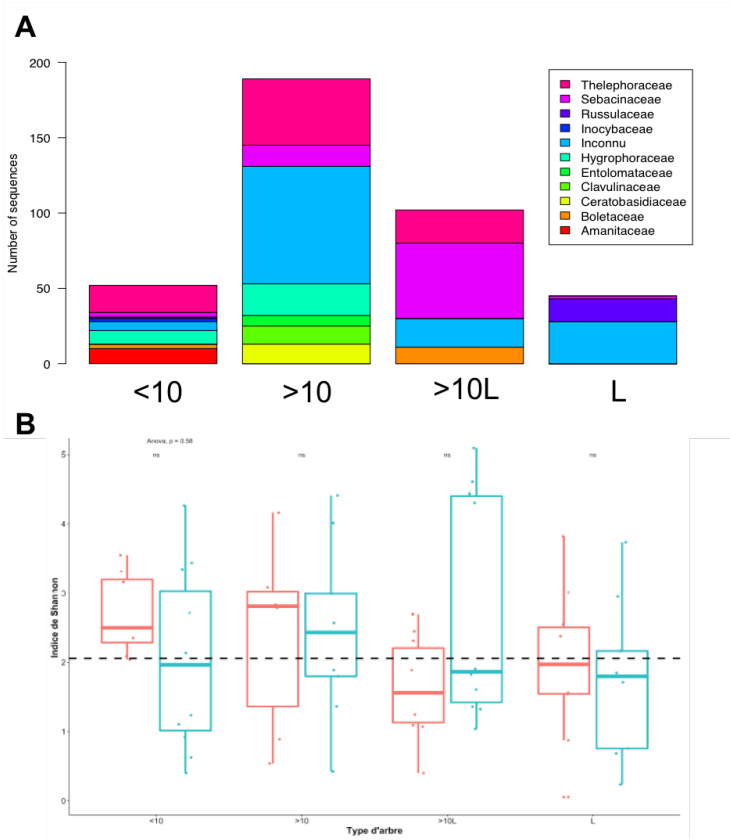


Figure 13 : A, number of EMF sequences per family and per host, and B, Shannon indices for EMF diversity on roots of liana roots (L), small trees (< 10 cm DBH), bigger trees (> 10 cm DBH) and bigger trees supporting a liana (> 10L) and on terra-firme soil (red) and white sands (blue).

Through repeated observations in the field, I have always been amazed by the poor state of fruiting bodies, and numerous traces of mycophagy. Though our inventories with Heidy Schimann, I have tried to systematically report those signs, and indeed 39.1% of the specimens showed signs of mycophagy (over 10514 specimens, Fig 12). Mycophagy is reported in the Neotropics to be caused by rodents (Mangan and Adler, 2002; Trierveiler et al., 2016) and tortoises (personal observations), potentially reducing fruiting-body lifespans, and possibly the local density of fruiting bodies.

Finally, the low density of fruiting bodies and possibly the low diversity of EMF can also be related to their host biomass. Indeed, most EM hosts outside of monodominant forests are lianas or shrubs. Unfortunately, hosts with a diameter at breast height (DBH) below 8 cm are not counted in most inventories. As a result, EM host distributions are highly likely to be underestimated. Through the LONGTIME project, I have had the opportunity to investigate soil communities in liana forest, pristine forests and "*cambrousses*" (vegetation dominated by herbs) in French Guiana (at Nouragues reserve). During Nina Gazal's master 2, we revealed that EMF were present in every habitat, especially in *cambrousses*, and in lianas forests (**Gazal et al., submitted**). Mycologists have under-explored those sites, but EMF specimens are recorded, such as a dense population of *Cantharellus guyanensis*. *Coccoloba* are frequent in liana forests and around *cambrousses* and can be potential hosts for these EMF.

As lianas are diverse and abundant in low-canopy forests, through Alexandre Ramon's master thesis and with Hans Verbeeck, I have investigated **if lianas and small hosts may host more EMF in liana forests**. Fine roots were collected from two sites on white sands, and two sites on *terra-firme* in French Guiana. Roots were harvested on small trees (< 10 cm DBH), big trees (> 10 cm DBH), lianas (L) and big trees surrounded by lianas (> 10L = > 10L+lianas), with 5 replicates per category on each site (80 samples in total). I extracted fungal DNA and amplified ITS1 barcode but detected only a few EM sequences (388), confirming that EM hosts are rare even in low-canopy forests. The distribution of EM families is moreover not homogeneous (Chi-square = 379.56, p-value < 0.0001, Fig 13A) and lianas tend to have even less EM sequences (Fig 13B). Therefore, small trees and lianas cannot be confirmed as EM hosts here (**Ramon et al., in prep**). The low number of EM sequences contradicts our hypothesis, and confirms that EM hosts are relatively rare in French Guiana forests, even in liana forests where EM fungi are observed.

These studies on the distribution of EMF in the tropics are extremely descriptive, but necessary to guide future samplings, which should be more focused on soil and mycorrhiza than on fruiting bodies. One important aim of all those specimen collections and descriptions is the sequencing of barcodes, to better assign short sequences from metabarcoding. Metabarcoding refers to the next generation sequencing (NGS) of environmental DNA (Taberlet et al., 2018). The extraction of extracellular DNA and metabarcoding have permitted the production of millions of sequences from very diverse samples of materials such as water and soil. Such methods are "cheap, fast and reliable" (Zinger et al., 2016) and reduce the sampling time, as compared to methods based on fungal cultures or sequencing of EM root tips. However, various chimeras can occur, and methods are sensitive enough to amplify a high number of contaminants (Nguyen et al., 2015). As such, technical controls are included, PCRs are replicated, yet chimeras can still be sequenced, and may be difficult to remove from the datasets.

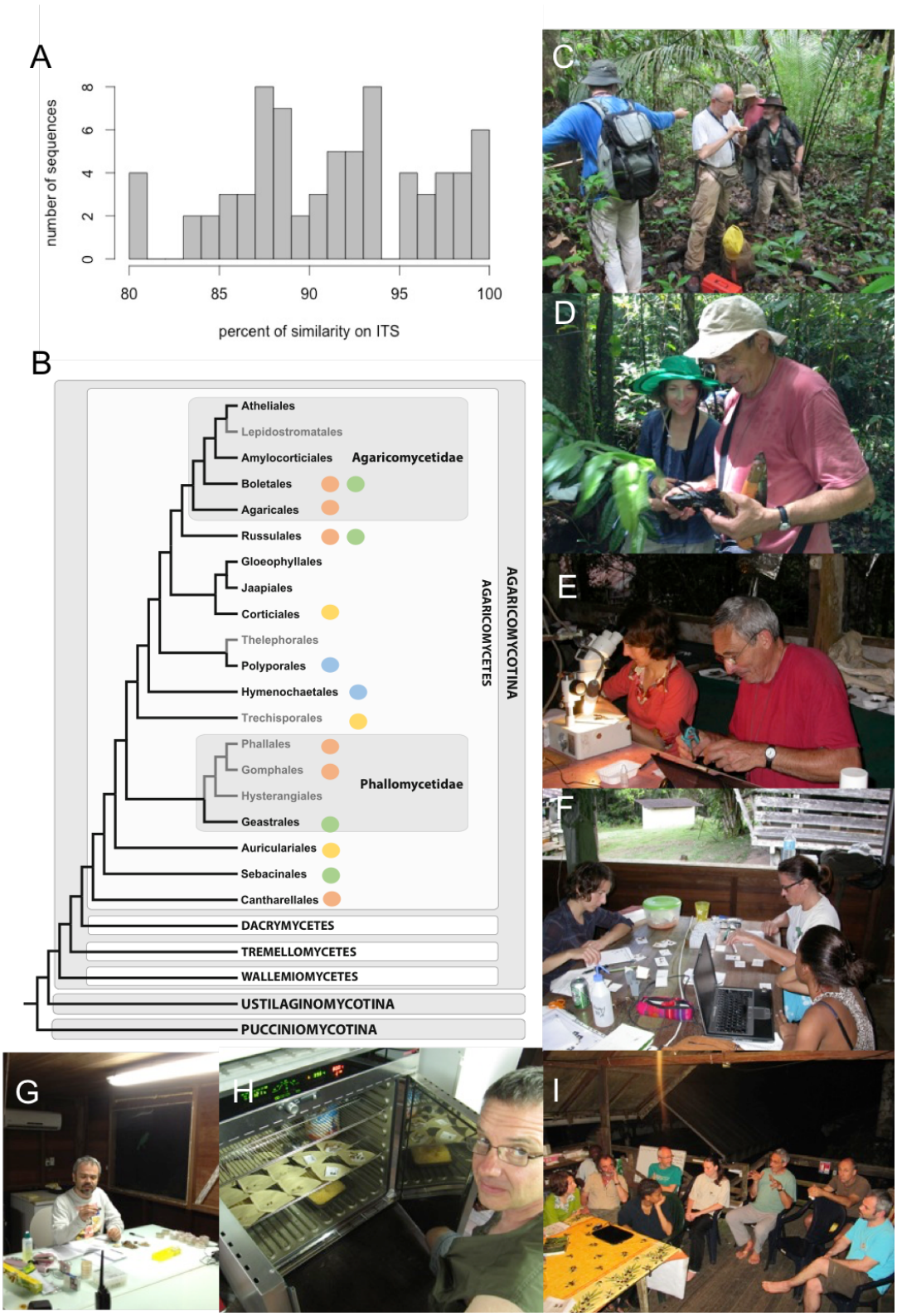


Figure 14: A, low similarity of EMF sequences to databases in 2013; B, groups targeted by my projects in French Guiana within the Agaricomycetes tree (Hibbett et al., 2016) and showing the expertise of R. Courtecuisse, P.-A. Moreau, B. Buyck, A.-M. Verbecken, J.L. Cheype and T. Henkel (orange), F. Wartchow and T. Accioly (green), G. Gruhn and H. Voiry (green), C. Decock and S. Welti (blue) ; and C to I, specimen collection from the field to the lab, during the first FUNGUY field trip in 2013 in French Guiana.

Assigning sequences to a given family or genus is a good way to eliminate dubious sequences and link biodiversity patterns to other studies or to functional traits. Several methods are available, from BLAST (Basic Local Alignment Search Tool, Altschul et al., 1990) to methods positioning sequences in classifications (ecotag, Boyer et al., 2016) and larger phylogenies (Berger et al., 2011 ; Berger and Stamatakis, 2012). All these methods try to compare short sequences with a database of barcodes, such as Genbank (http://www.ncbi.nlm.nih.gov/) or UNITE (http://unite.ut.ee/; Kõljalg et al., 2005).

Whatever the method, assignation may be strongly biased by gaps in the database (Nilsson et al., 2006) and this is particularly true for Neotropical fungi. When I began working with such techniques in French Guiana, only 8% of the fungal sequences (from soil) were assigned to a taxonomic level. This was a particularly low proportion, and probably linked to the low number of sequences deposited in public databases such as Genbank (in 2011, only 4 sequences of fungi were available). Moreover, the sequences of the internal transcribed spacer of the ribosomal DNA (ITS, Gardes and Bruns, 1993), a barcode for fungi, revealed very low similarity to databases (Fig 14A). As a result, BLAST may be of poor quality even for soil sequences, while they could belong to true fungi and not chimeras. Moreover, position in classifications may be basal (as for *Cantharellus guyanensis* within Cantharellaceae, **Henkel et al., 2013**), and such fungi may be assigned to the root of fungi, instead of being positioned within a fungal family.

The FUNGUY and FLAG projects have aimed at collecting specimens with the help of taxonomists and at sequencing ITS barcodes to improve the assignment of environmental sequences (Fig 14 B-I). Part of the DIADEMA and DIAMOND projects also aim at sequencing barcodes, using NGS on specimens to reduce the price of sequencing, and applying the same methods for both specimens and environmental DNA. Short barcodes were even easier to produce for old herbarium specimens, such as collections from R. Singer (**Hackel et al., in prep**). However, some specimens revealed several ITS that cannot be attributed only to contaminants, mainly in Xylariaceae, Geastraceae, Lepiotaceae, Gomphaceae, and Clavulinaceae. Within fungal genomes, ITS are already present in multiple copies (circa 50), but their polymorphism are usually low within an individual. Multiple and distinct copies could indicate a contaminant, or multiple genomes, for example in dikaryotic organisms. **Jaouen et al. (submitted)** analysed short sequences of ITS barcodes produced from specimens, and developed tests to investigate this polymorphism. Such barcodes are now beginning to be deposited in Genbank (771 barcodes, Jaouen et al. submitted), to fill the gap of public databases on fungi in French Guiana.

Sequencing all collected specimens and beginning to deposit sequences in public databases have greatly improved sequences assignation. Moreover, linking specimens with environmental sequences has enabled the opening of the black box (Horton and Bruns, 2001) to understand EMF ecology and specialization in the Neotropics.

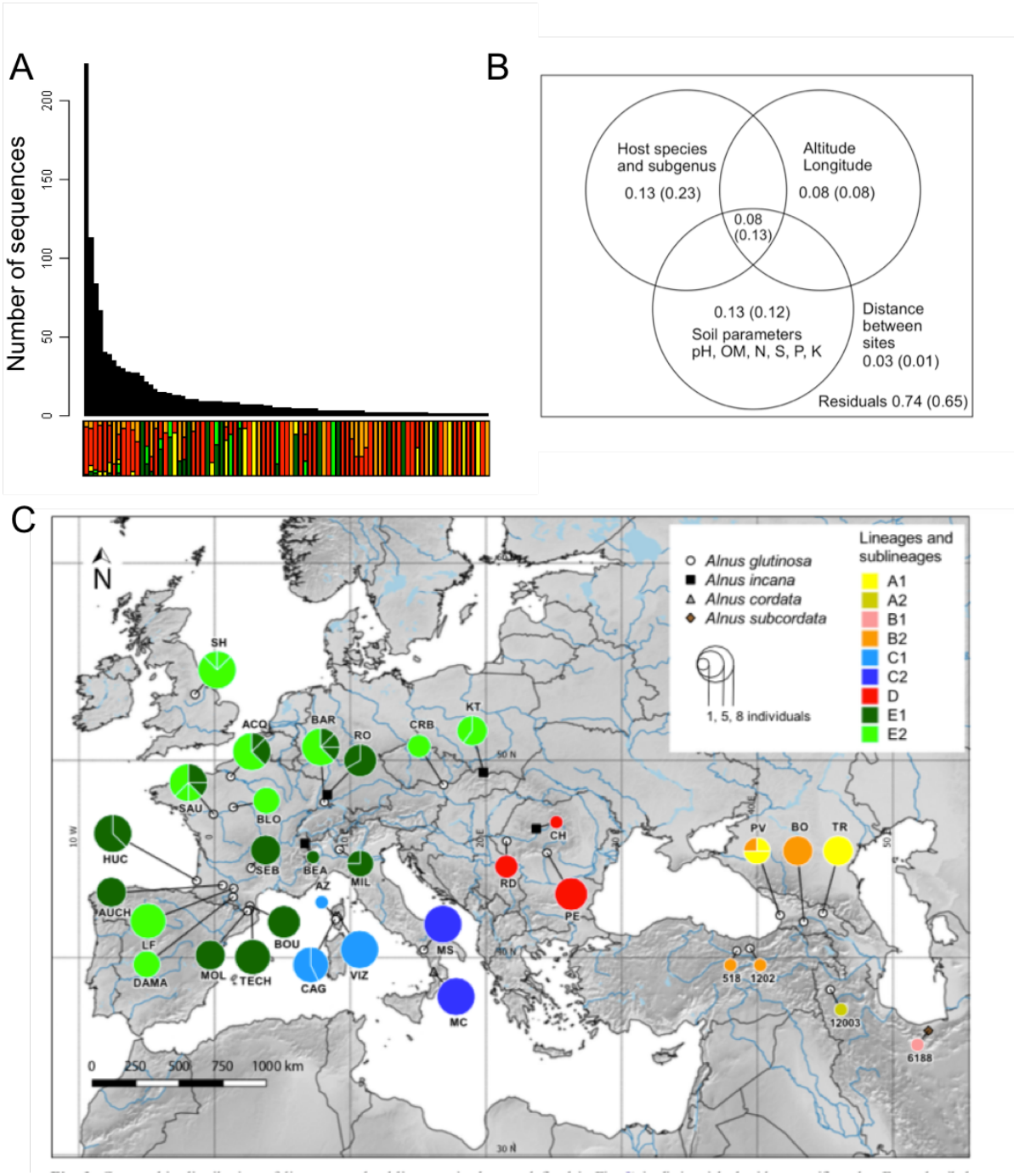


Figure 15 : A, distribution of EMF OTUs per host species in France, and B, factors shaping EMF community (beta diversity), from ***Roy et al. (2013****) and C, Distribution of chloroplast haplotypes in* Alnus *leaves, from* ***Gryta et al. (2017)****.*

Axis 2 : Drivers of EMF specialization

Projects	EC2CO, ARC, DROUGHT, MYCOTIN, NEBEDIV
Articles	Roy et al., 2013a; Roy et al., 2017; Schwob et al., 2017; Gryta et al., 2017; Sene et al., 2017; Buyck et al., 2017; Pozzi et al., 2018 ; Hoeksema et al., 2018.

Specialization is a common pattern observed in plant-parasite interactions, where partners are involved in an arm-race or a 'red queen' coevolutionary dynamic (Thompson, 1994; Kawecki, 1998). However, theoreticians have tried to find other models to understand the non-specialization observed in plant-EMF mutualism (such as the slow red King; Bergstrom and Lachmann, 2003). Indeed, even the most specialized fungi are associated with generalist hosts, and the term "preferences" is more realistic than "specialization" (Dickie et al., 2007; Molina and Horton, 2015). I have always been interested in the exceptions – i.e., the more specific associations among mycorrhizal symbioses – as they contribute to understanding the ecological advantages of more generalist strategies.

a. Revisiting *Alnus*-EMF specialization

Alnus-EMF fungi are well known for their specialization, initially demonstrated experimentally (Molina, 1981). When I began working on alders, investigations of their below-ground communities with molecular tools had already confirmed this high specificity, but only on a single host at a time. My first study intended to determine the base of this specificity, thanks to sampling already achieved by the team at EDB. We showed that the five species and subspecies of alders in France were associated mainly with specialized fungi, such as *Alnicola* spp. and *Tomentella* spp., often sharing their partners with other *Alnus* species (Fig 15A). The soil chemistry and climate contributed to explain the diversity of EMF recorded on *Alnus* roots (Fig15B, **Roy et al., 2013a**), and this trend was confirmed at larger scale (Põlme et al., 2013). This bloom of articles on *Alnus*-fungi mutualism also revealed interesting exceptions among mycorrhizal symbioses, particularly in locations where *Alnus* populations were isolated, as compared with the extended distribution of some species such as *Alnus glutinosa* (Chen et al., 2004). For example, on *A. subcordata* roots in Iran, the EMF diversity was higher than elsewhere, and included generalist fungi such as *Tuber* and *Inocybe* spp.

As *Alnus* pollen is easily recognizable in sediments, its phylogeography has been intensely studied in the temperate region and in Europe, revealing southern and northern glacial refugia (King & Ferris, 1998; Douda et al., 2014; Havrdová et al., 2015; Mandak et al., 2015; 2016). Corsica is recognized as a glacial refugium for several trees, including alders. While isolation could have selected for more intimate interactions, another hypothesis based on the distribution of alder's genetic diversity can also be proposed (Fig 15C, **Gryta et al. 2017**). Indeed, hypogeous fungi, which disperse at shorter scales than epigeous fungi (Douhan et al., 2011), may not have recolonized Europe after the last glaciation. If alder populations had been maintained in glacial refugia, they would have retained more diversity. I have therefore launched several projects **to test if glacial refugia can host a higher diversity of EMF associated with alders, and if isolation can lead to more specialized interactions**. I have also worked with colleagues on *Frankia* to understand if these hypotheses can apply to a more obligate symbiont.

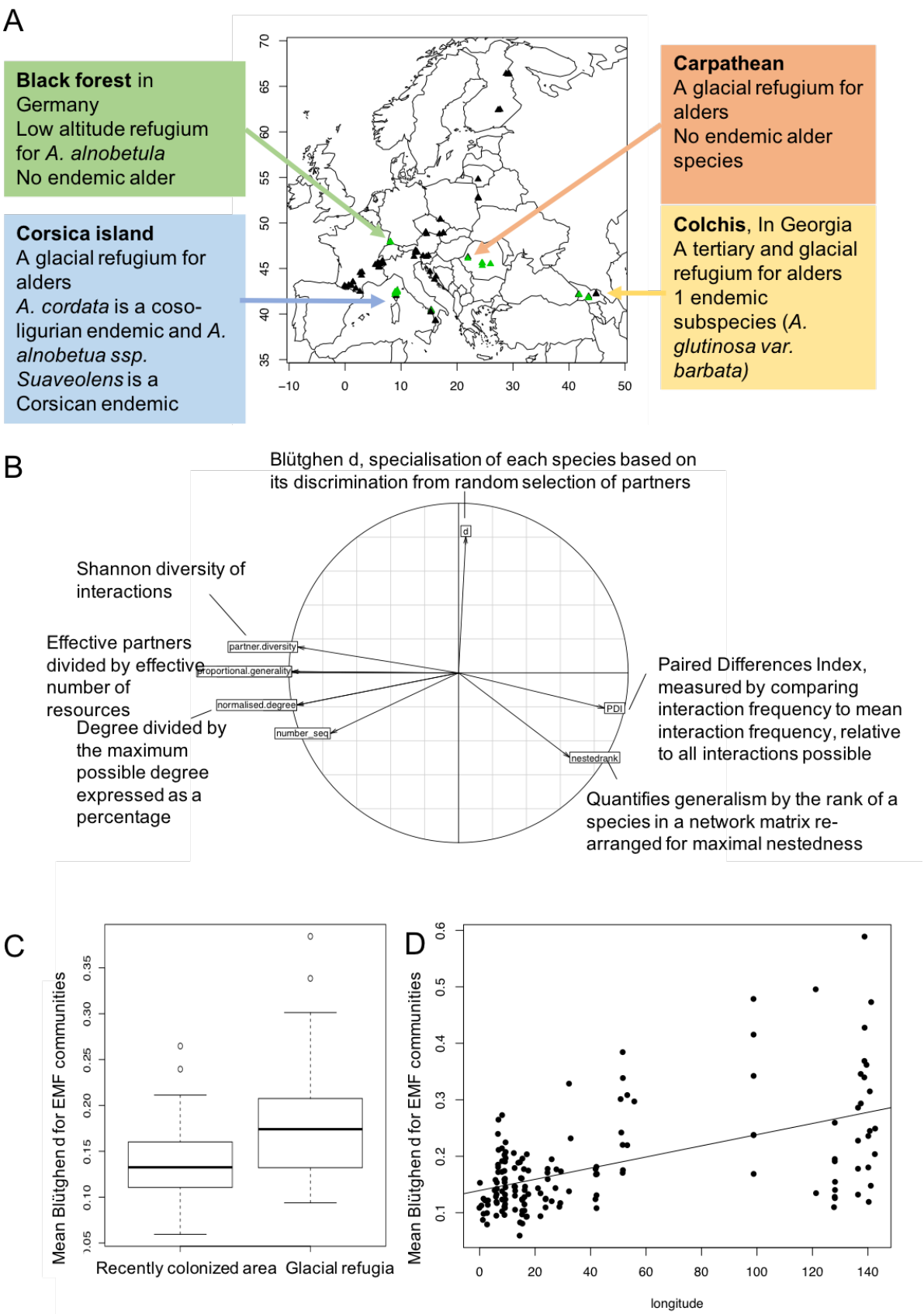


Figure 16: A, sampling in glacial and Tertiary refugia, B, Metrics reflecting EMF specialization, C, difference of specialization for alders EMF communities, reflected by the mean Blütghen *d, between sites in refugia and recently colonized areas, and along a longitudinal gradient (D).*

Perhaps because each glacial refugium has undergone a different history (Fig 16A), our results are distinct from one refugium to another. In Georgia, where the largest alder populations are found today, we have detected a high diversity of EMF, but rather in isolated populations than in the glacial refugium (**Roy et al., 2017**). In Corsica, the diversity is higher on *A. cordata* roots, but not on *A. glutinosa* ones (**Pozzi et al., 2018**). Moreover, very generalist fungi are detected as well. In the Carpathians, endemic hypogeous fungi are detected, but the global diversity is not higher than in recolonized areas. Finally, for *A. alnobetula* ssp. *alnobetula* in the Black Forest, a low elevation refugium in Germany (Kamruzzahan, 2003), EMF diversity is extremely low. Therefore, our analyses of EMF distribution do not support a consistent pattern of higher EMF diversity in refugia. Conversely, *Frankia* distribution is more intimately linked to the biogeography of alder, and shows a high endemism in Corsica and Georgia (**Roy et al., 2017; Pozzi et al., 2018**). Interestingly, Vercken et al. (2010) have also revealed that *Microbotryum caryophyllacearum*, an obligate pathogen of Caryophyllaceae, has probably followed its host along post-glacial migrations. It is probably easier to detect such trends at the species level, and the sampling done at the community level can now be used to investigate the distribution of specific lineages, such as the EMF genus *Alpova*.

Investigating specialization was initially done by identifying generalist or specialist species, well-described by taxonomists, and indeed, we had expected to detect endemic species within *Alnicola* or *Alpova* lineages. Our markers have probably not been variable enough to detect recent differences between populations, and microsatellites would be more useful. Nevertheless, the large amount of data for alder communities can be also used to describe EMF species specialization with metrics. By comparing all sequences available for alder symbionts (3816 on ITS) with Adrien Taudière, I have investigated EMF distribution among 29 alder species worldwide, measured their number of hosts (degree), and computed several specialization indices. I have searched for indices not biased by sequence number, and chose "Blüthgen d," which compares specialisation to a random distribution (Fig 16B; Blüthgen et al., 2008). By computing a mean Blüthgen d for EMF communities, I have revealed that EMF communities in European refugia were indeed characterized by a higher d, and therefore were more specialized than communities in recently colonized areas (Fig 16C; **Roy et al., submitted**). Interestingly, EMF communities in Asia, which is the postulated center of origin of alders, are also more specialized (Fig 16D), suggesting more links between alder phylogeography and EMF specialization at the community level.

Taken together, the results from refugia illustrate variations of EMF specialization at the community level. The spatially variable specialization has been a keystone of the geographic mosaic theory of coevolution (Thompson, 2005). Hoeksema and Thompson (2007) have detected geographic variations of EMF-*Pinus* interactions and Piculell et al. (2008) have suggested that interactions between abiotic and biotic factors may result in a selection mosaic. The specialization of alder-EMF interactions is definitely high, but probably follows the same pattern, as suggested by the importance of abiotic factors in the crossing experiment (**Schwob et al., 2018**). Several clues also suggest that geography could affect *Alnus*-EMF interaction, especially in isolated locations. For example, during M. Nagati's master 2, we were also able to sequence the EMF associated with isolated populations of *Alnus maritima* in the USA. Indeed this species shows disjunct populations (Schrader et al., 2000) and has a low regeneration rate, especially by seed (Rice and Gibson, 2009). The EMF communities are of low diversity (16 OTUs over 4 populations) and reveal numerous Helotiales.

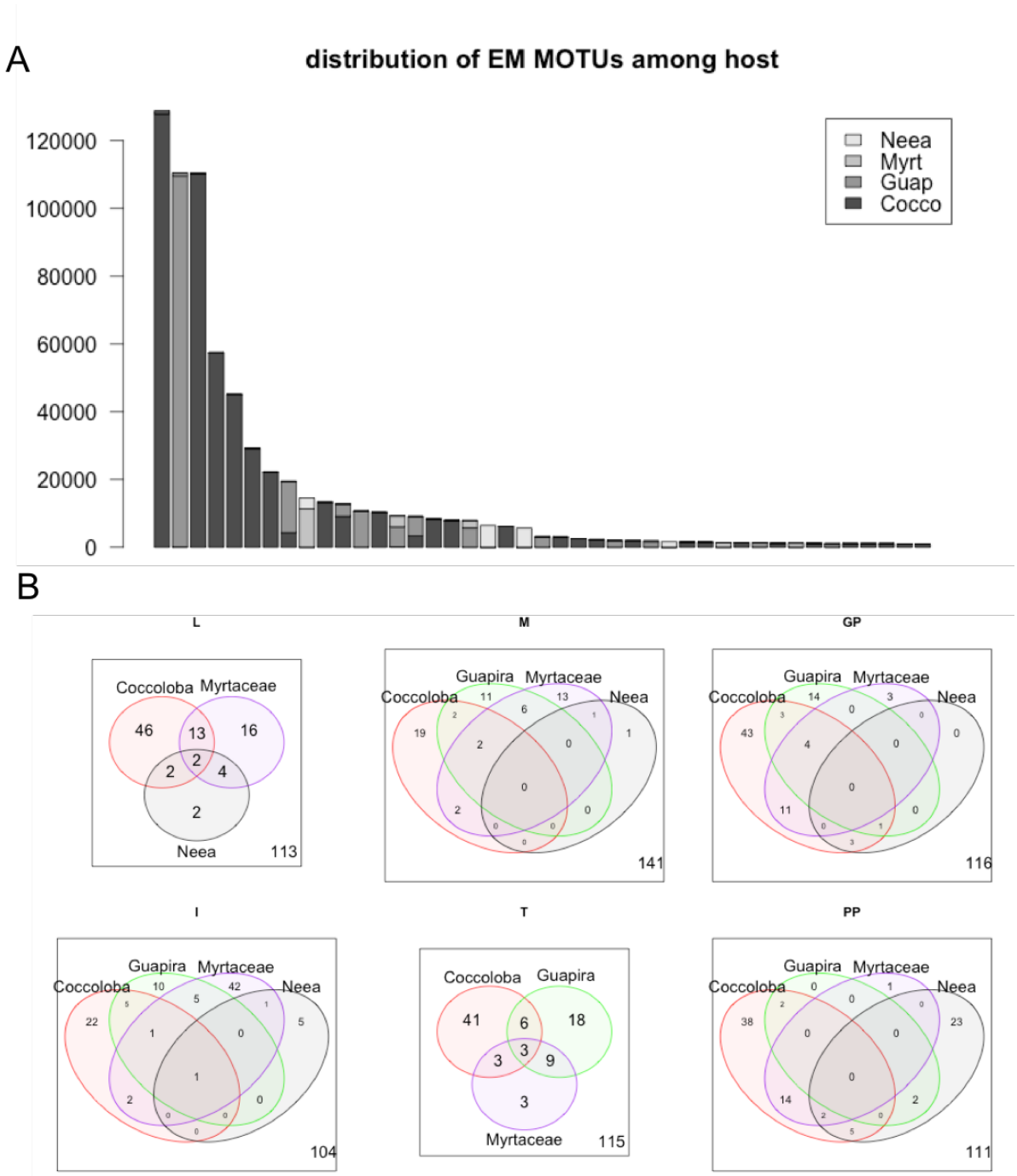


*Figure 17: A, number of sequences per OTU and per host, and B, sharing of OTUs on each plot between host genera represented by Venn Diagrams (**Fernandez et al., in prep**).*

Specialized lineages are represented only by one *Alnicola* and by *Lactarius omphaliformis*, which suggests a loss of several partners, as compared with other alders. Reciprocally, Bogar et al. (2015) have detected possible host shifts of *Alnicola* in New Zealand.

To summarize, alder-EMF interactions are definitely more specialized than other EM interactions (Taudière et al., 2015), but investigations in glacial and Tertiary refugia have revealed important variations of specialization. Thanks to the use of metrics to characterize EMF specialization at the community level, and the development of new genetic markers for alders (**Gryta et al., 2017**), it is now possible to investigate further the interactions between host biogeography and EMF specialization.

b. Specialization of EMF in Neotropical forests

While the isolation of *Alnus* populations remains an exception in the temperate zone, Neotropical trees and EMF are often isolated, and this distribution could also shape their specialization. In Yasuni National Park, Tedersoo et al. (2010) showed, for the first time, a comparison of EMF communities associated with Neotropical trees, and demonstrated their specificity. At that time, the sampling was relatively reduced, with 100 sequences produced over 26 trees. With an increased sampling of roots of co-occurring Fabaceae, Smith et al. (2011) have concluded that all fungi are shared between *Aldina* and *Dicymbe* (Fabaceae) in Guyana. In French Guiana, EM hosts occur at low densities, such as the genus *Coccoloba*, *Guapira* and *Neea*. Their abundance is higher on slopes and low-canopy forests as is the abundance of EMF based on fruiting-bodies. As these symbioses are relatively rare in non-monodominant forests, I hypothesise that **generalist association may be favoured, and that EMF could be shared between co-existing hosts**.

By searching for hosts with a team of mycologists and botanists, I have been able to sequence the EMF community associated with 110 individuals belonging to ten host species (the three above mentioned genera, and Myrtaceae, that include putative EMF host) over 8 plots. Two hundred and thirteen OTUs (Operational Taxonomic Units) were detected on 106 host individuals, which confirms the low diversity of EMF in these Neotropical forests. The more abundant OTUs are not shared between hosts (Fig 17A), and different genera are associated with very contrasted EMF communities and lineages. For example *Neea* individuals are associated mainly with Russulaceae, while the closely related genus *Guapira* is associated with Thelephoraceae. Locally, at the plot scale, the sharing of EMF is also extremely low (Fig 17B), and associations are highly specific and more specialized than a random sampling would predict (estimated by H2, **Fernandez et al., in prep**). Therefore, the specificity of Neotropical EMF is clear, and is very conservative at a large scale. Indeed, by gathering all data on *Coccoloba uvifer*a, **Sene et al. (2018)** were able to show how specific was this association, all along its migration routes. In the lesser Antilles, *Coccoloba* species notably associate with very specific *Cantharellus* spp. (**Buyck et al., 2016**). By comparing the EMF community of *Pisonia* species in Hawaï and Ecuador, Hayward and Horton (2014) showed that their association with the genus *Tomentella* is extremely phylogenetically-conserved. Our first study at the Nouragues station also reveals that Neotropical Myrtaceae can potentially associate with EMF. This result is particularly striking, and contrary to the literature on Myrtaceae, which assumes that only the lineage *Eucalyptus* is EM (Tedersoo and Brundrett, 2017).

*Table 2: Records of EM observed or EMF sequenced on saplings identified by Tim Paine (in 2013) and later sequenced on ITS1 by Miseq, and on roots collected along a phosphorus gradient in French Guiana, and later identified by short sequences of rbcL (**Durrington et al., in prep**)*

Family	genus	species	Obs 2013	Miseq 2013	Miseq 2018
Annonaceae	*Duguetia*	*yashinoi*	0/5	0	
Apocynaceae	*Aspidosperma*	sp.	0/1	15	1/2
Bignoniaceae		sp.	0/1	59	
Burseraceae	*Crepidospermum*	sp.	0/3	29	
	Protium	*aracouchini*	0/3	3	
		opacum	0/3	13	
		sagotianum	0/3	39	
	Tetragastris	*altissima*	0/1	37	
Chrysobalanaceae		sp.	0/1	8	
	Lycania	*alba*	0/2	11	
	Parinari				1/4
Clusiaceae	*Clusia*	sp.	0/2	4	
	Clusia	*nemorosa*	0/3	21	
Dilleniaceae		sp.	0/1	0	
Ebenaceae	*Diospyros*				1/3
Euphorbiaceae	*Mabea*	*piriri*	0/1	0	
Fabaceae	*Bauhinia*	*guianensis*	0/1	0	
		sp.	1/1	100	
		sp.	1/2	78	
	Dicorynia	*guyanensis*	1/5	8	0/2
	Eperua	*falcata*	0/1	0	
	Inga	*sp.*	1/1	94	
		alba	1/2	282	
		rubiginosa	2/2	651	
	Parkia	*nitida*	1/1	229	
		sp.	0/1	49	
	Swartzia	sp.	0/1	0	
Humiriaceae	*Humiria*		1/1	25	
Ixonanthaceae	*Cyrillopsis*	*paraensis*	0/2	2824	
Lauraceae	*Octotea*	*argyrophylla*	0/1	0	
Lecythidaceae	*Lecythis*	*persistens*	1/3	2027	
Malvaceae	*Eriotheca*	cf *surinamensis*	1/1	153	
Loganiaceae	*Quaribea*	*duckei*	1/1	240	
Loganiaceae	*Strychnos*	*erichsonii*	1/1	895	
Melastomataceae	*Miconia*	*egerensis*	2/2	226	
		guyanensis	1/3	223	
		suaveolens	0/2	0	
Sapotaceae	*Micropholis*	*melinoniana*	1/1	77	
Meliaceae	*Trichilia*	*emetica*	0/1	0	
Moraceae	*Helicostylis*	*pedunculata*	0/1	0	
	Trymatococcus				0/2
Myrtaceae	*Maarvelia*	*ferruginea*	1/1	88	
		sp.	10/26	31533	
Olacaceae	*Ptychopetalum*	*olacoides*	0/1	229	
Quiinaceae	*Touroulia*	*guianensis*	3/4	321	
Rhamnaceae	*Ziziphus*	*cinnamomea*	0/1	135	
Sapindaceae	*Paullinia*	*latifolia*	0/1	30	
Sapotaceae	*Manilkara*	*bidentata*	0/1	0	
	Micropholis	sp.	1/1	74	
	Pouteria	sp.	0/1	118	
	Pradosia	*ptychandra*	0/1	39	
Simaroubaceae	*Simarouba*	*mama*	0/1	11	
Siparunaceae	*Siparuna*				0/2
Urticaceae	*Pourouma*	sp.	0/1	25	
Vochysiaceae	*Qualea*	*rosea*	1/2	1407	

A quest for new EM hosts is ongoing in the tropics (Tedersoo and Brundrett, 2017) and in herbaceous plants in temperate forests (**Hoeksema et al., 2018**). For example, Alvarez-Manjarrez et al. (2018) tested if dominant Fabaceae were EM in Mexican dry forests and instead, have revealed a new EM host – *Achatocarpus (*Achatocarpaceae, order Caryophyllales*)* - and showed that Caryophyllales are the main EM hosts in this habitat. Considering the sampling gap for EMF in the Neotropics, we can expect to increase the number of EM hosts. As taxonomists are often going to the field, and describing new EM species in the Neotropics, I have co-organized three field trips to search for and observe EM root tips, twice in Brazil (Rio Negro, **Roy et al., 2016**; Florianopolis dunes, **Roy et al., 2017**) and more recently in Argentina (Buenos Aires, Faculty of Agronomy). We have always detected EM structures and interestingly, students and taxonomists have been disappointed with native EM root tips as compared to those of introduced *Eucalyptus* and *Pinus*. Indeed, the mantle is often reduced, and the abundance of EM root tips is lower on native trees. Becerra and Zak (2011) have already mentioned a reduced mantle for Neotropical EM root tips, which can make their detection more challenging.

Through repeated field trips to French Guiana, I have had the opportunity to observe in the field and sequence the roots of young trees identified by botanists, and therefore try **to detect new EMF hosts**. Observations have revealed possible root tips on nine families (Table 2), and sequencing has revealed EMF on 10 families (Table 2). By sequencing 250 bp of the plant barcode rbcL on roots sampled along a phosphorus gradient in French Guiana (axis 1), only a few plants are identified, and only three families are EM. The results are variable between observations and sequencing, and only seven species, belonging to Fabaceae, Malvaceae and Melastomataceae, are always observed associated with EMF. To demonstrate these associations, cuttings of EM roots have been inconclusively attempted. Moreover, among roots collected around EMF fruiting bodies and preserved in 50% alcohol, only 52% have shown a mantle or a Hartig net (188 samples, Master 1 Mike Hélion). Identifications by sequencing were successful only for Apocynaceae, Chrysobalanaceae and Ebenaceae, but not supported by morphological observations (Table2).

Those scattered and non-conclusive observations fit the hypothesis of Singer and Araujo (1979), who suggested that EMF can extend their mycelium and colonize other root trees and then form “contact mycorrhiza” with non-obligate EM hosts in Neotropical forests. Alexander (2006) had already wondered how far EM nutrition might be obligate in the tropics. As an example, together with M.-A. Neves (Santa Catarina, Brazil), we have recently observed EM-like root tips colonized by *Trechispora* mycelium (**Vanegas León et al. submitted**). I have also collected fruiting bodies of *Trechispora* in French Guiana, and their isotopic signature is close to EMF in some sites, but is variable (Fig 18). Indeed, isotopic signatures can help distinguish between EM and saprophytic habits (Mayor et al., 2009). Those root-associated *Trechispora* are probably more endophytic than EM, and do not obligatorily form an EM structure. Similarly, *Amanitopsis* are relatively widespread in the Neotropics, and are closer to saprophytic Amanitaceae (Redhead et al., 2016).

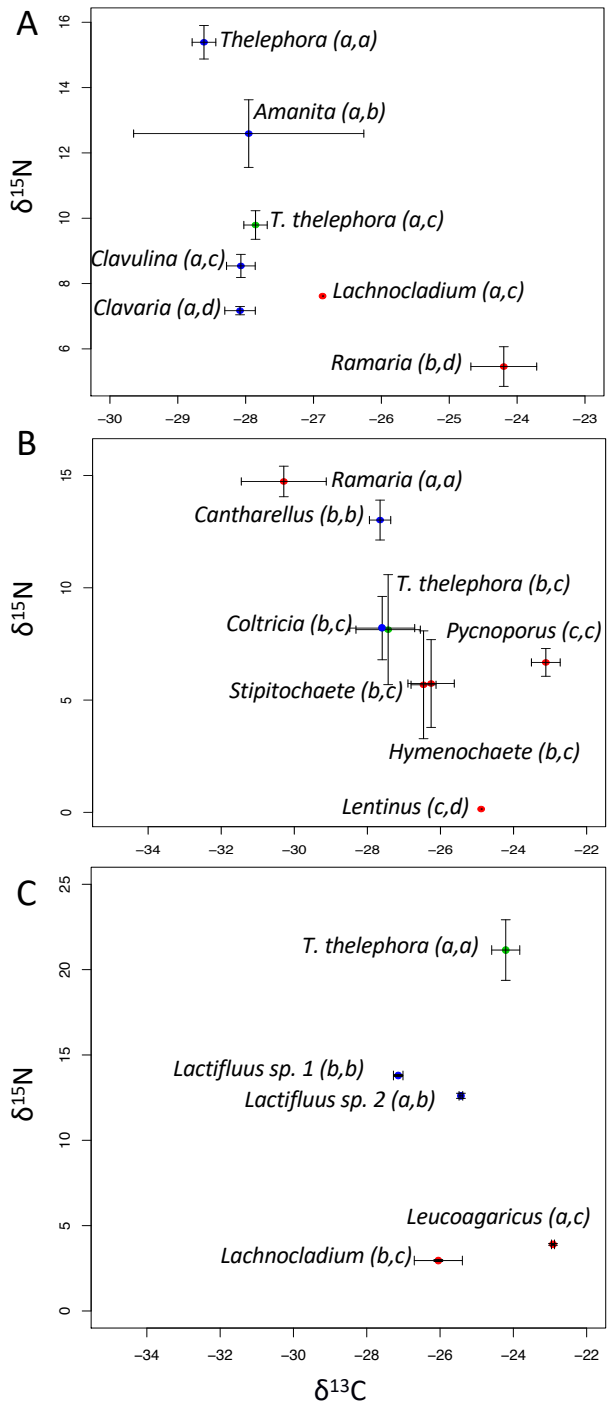


Figure 18: $\delta^{15}N$ and $\delta^{13}C$ isotope signature of Trechispora thelephora *(green) compared to surrounding fruiting bodies of saprophytic species (red) and EMF (blue). Small letters indicate groups of significance according to Wilcoxon tests. From* ***Vanegas-Léon et al****. (submitted in 2019).*

Compared to our delineation of EM symbioses (Rinaldi et al., 2008), Neotropical trees represent a continuum of associations with soil fungi, not obligatory and often superficial, considered as "wrong" observations by Tedersoo and Brundrett (2019). Experiments may be necessary to test if EMF are obligate symbionts and reciprocally how EMF could affect plant fitness. As plants are not water limited in Neotropical forests, and considering the abundance of fungal pathogens in tropical soils, the protective role of EMF (ZengPu et al., 1994; Mohan et al., 2015) may be more important than their benefits on plant nutrition. Moreover, if the association with EMF is more advantageous only in some habitats, like the white sands, then a variable association could represent an adaptation to the environmental gradients in the Amazon (e.g. soils and topography). To test this hypothesis, and more generally to test if habitats are drivers of specialization in plant-fungi (and also plant-insect) interactions, I am contributing to an ANR project where 11 lineages of plants are sampled in plateau, slopes and flooded forests, on *terra-firme* and white sands, in both French Guiana, Peru and Brazil. Within this ongoing and rather ambitious project, we hope to investigate the distribution of fungi (and possibly of EMF) among hosts and habitats, and test if host or habitat are key drivers of fungal specialization.

To summarize, my different projects have revealed and raised questions on different drivers of EMF specialization, for alders and tropical EMF. All these studies are based on field sampling and observations, and would require experimental tests to disentangle all the complex processes shaping EMF communities. The projects presented in the following sections focus on a smaller scale, and intend to target a missing link to understand specialization: the complex interactions of fungi with fungi.

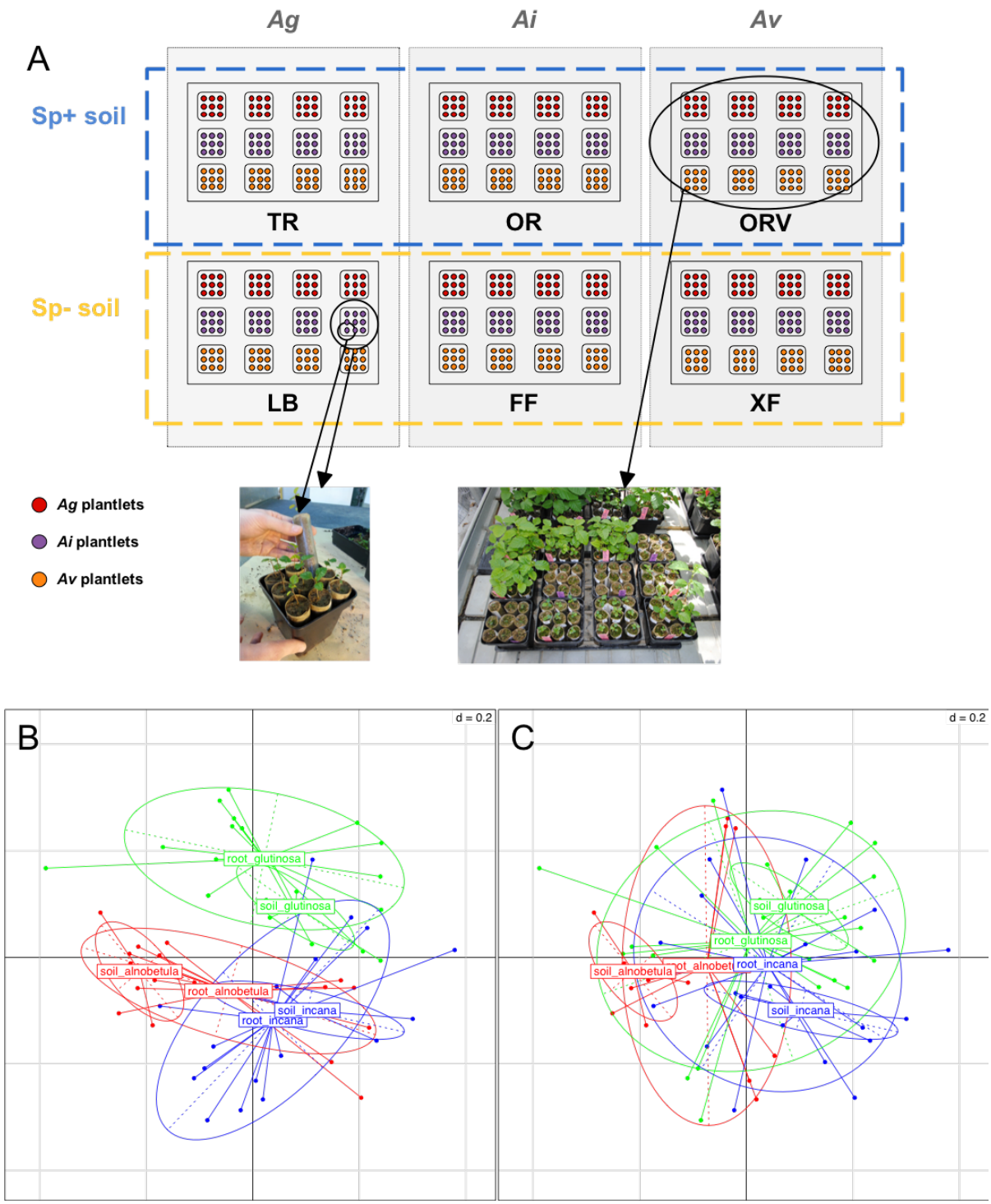


Figure 19: A, design for crossing experiments (Ag: A. glutinosa, Ai: A. incana, Av: Alnus alnobetula ssp. *alnobetula, Sp+: in planta-sporulating phenotype, TR, OR, ORV, LB, FF and XF are soil localities where respectively, Ag, Ai and Av are naturally growing) and NMDS showing the differences between communities colored by their soil origin (B) or by their host identity (C); from* ***Schwob et al., 2018****.*

Axis 3 : Biotic interactions

Projects	FUNCHEM, SECIL, RECO-RECO, DROUGHT
Articles	Kohout et al., 2011; Schwob et al., 2018; Lagarde et al., 2018 ; Roy et al., submitted; Gazal et al., submitted; Donald et al., submitted; Nagati et al., 2018; Nagati et al., submitted

Perhaps because NGS data allows for the sequencing of greater numbers of fungi in a community, we are now able to go beyond fungal diversity, and look at fungus-fungus interactions and more generally at ecological networks involving fungi (Vacher et al., 2016b). While ecological networks have been used to study plant-pollinator interactions and food webs for decades, their use to study fungi-plant interactions or fungi-fungi interactions is relatively recent (Bahram et al., 2014). Ecological networks represent interactions within a community, and the tools developed to study them allow for quantifying the interactions and testing hypotheses compared to random distribution of interactions. During my previous projects on EMF communities, I have always wondered if the specialization observed was not a sampling bias, especially in the tropics. In the case of alders, the occurrence of *Frankia* on roots also raised questions on *Frankia*-fungi interactions. More generally, the large part of unexplained variability in my previous analysis of EMF communities, and currently published in the literature on fungal communities pushed me to investigate interactions within communities.

a. Interactions within alder roots and populations

Interestingly, alders appear as an exception, not only because of their specific EMF, but also for their lack of interactions with other trees. Indeed, Kennedy et al. (2014) showed that interactions between alder's fungi are not competitive. This result contrasts with the competitive exclusion between other EMF detected in other ecosystems (Koide et al., 2005; Kennedy et al., 2009; Pickles et al., 2012). Moreover, Huggins et al. (2014) have highlighted the selective role of acidity and nitrate on alder fungi. Indeed, in the presence of *Frankia*, or under highly acidic conditions, only specific lineages of fungi are able to associate with alders. Kennedy et al. (2015) suggested that reward and sanctions of EMF could also contribute to select few and specialized fungi, dependent on nitrogen fixed by *Frankia* on alder roots.

There are several *Frankia* strains on alder roots worldwide and their traits can be variable. Pozzi et al. (2015) showed that *in-planta* sporulation phenotype was particularly abundant in montane habitats, or on some species of alders such as *A. alnobetula*, and can contribute to the resistance of *Frankia* to cold environments. To better understand **how *Frankia* strains could interact with EMF, and more generally, to investigate how interactions could shape alder specialization**, I have collaborated with G. Schwob (during his PhD at *Ecologie Microbienne*, Lyon) to establish a crossing experiment on young alders (3 alder species, 2 soil provenances with two different *Frankia* phenotypes, Fig 19A). We hypothesized that *in-planta* sporulating phenotypes would rapidly invade their host root and reduce possible interactions with EMF. We also hypothesized that such phenotypes would be more host-specific than others. After 6 months, the colonization by EMF was low, but some specific lineages were already present. The soil provenance explains 15% of the EMF community structure, while the host species explains only 6% (**Schwob et al., 2018**).

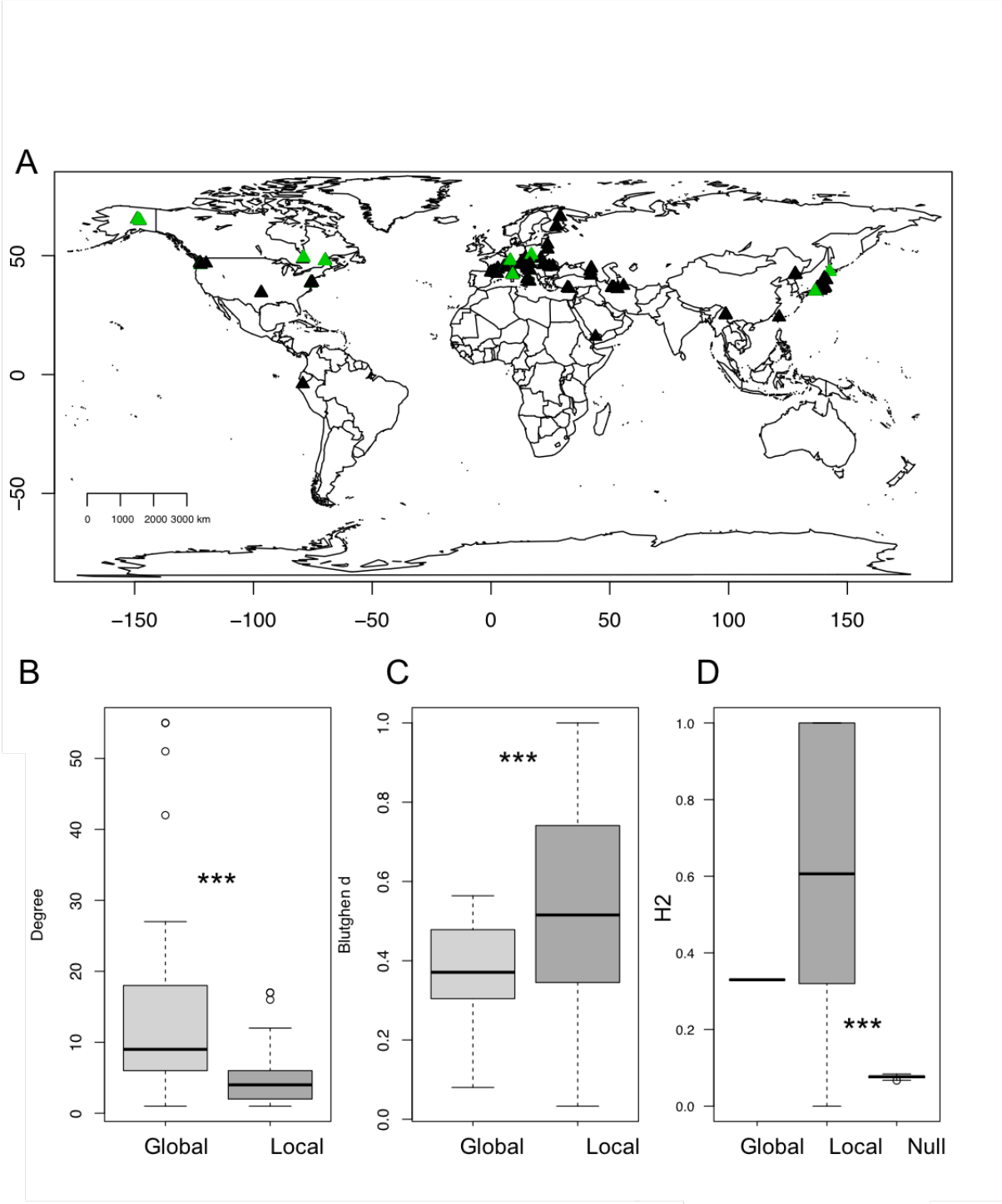


Figure 20: A, map of alder populations sampled to calculate network metrics (triangles) and sites where two alder species were sampled (green triangles); comparison of plant degree (B) and Blüthgen d (C) calculated from all interactions (Global) and local interactions (Local) and comparison of H2 (a network level of specialization) between cases of co-occurrence and predictions by null model (D).

Interestingly, the phenotype of *Frankia* contributes to shape EMF communities, and explains 8% of the EMF community structure as well as 10% in interaction with the habitat. This first experiment should be completed by measures of N-fixation activities to understand if benefits or sanctions can contribute to these interactions on alder roots, as suggested by Kennedy et al. (2015). These results already show how important habitat and microbial interactions are compared to host effects on alder roots (Fig 19B, C).

The similarity between EMF communities associated with different alder species was particularly puzzling in this experiment, and contrasts with the differences observed in the field (**Roy et al., 2013a**). Theoretically, closely related species that share a common niche (EMF partners) may compete locally, or avoid growing together. Interestingly, alder species rarely co-exist, except in some locations such as in Corsica. Using ecological networks and the metrics of specialization, I have therefore tested **if in case of co-occurrence, EMF could show competitive-exclusion patterns and plants could be more specialized**. Such cases are relatively rare and sites in USA, Québec and Europe were analysed by Circé Collongeon during her master 2 internship (Fig 20A). The specialization of alders, reflected by degree and Blüthgen d, is always higher locally than globally (Fig 20B,C), and at the network level, H2 is higher locally than predicted by null models (Fig 20D, **Roy et al., submitted**). The resulting networks are highly specialized, while theoretically, 31% of OTUs are potentially shared between alder species. This result fits the idea that closely related species that are associated with similar partners, compete more than species sharing fewer partners or species that are more distant phylogenetically. Moreover, this result confirms the hypothesis of Kennedy et al (2015), who suggested that alders are avoiding networks, even with co-existing alder species.

Interestingly, a few scattered cases have revealed shared partners between alders and other tree species. In New Zealand, where *Alnus* and *Salix* have been co-introduced, alders are able to share fungi with *Salix*, and partly lose their specificity. In Corsica, where *A. cordata* often grows in forest dominated by *Castanea sativa* (Gamisans, 1999), *Fagus sylvatica* and *Pinus halepensis*, very generalist and potentially shared EMF have been detected on *A. cordata* roots (**Pozzi et al., 2018**). Growing in mixed forest is not common among alders, and this habit could have favoured novel associations and also lowered their specialization. All these clues lead us to consider interactions with other trees to better understand geographic variations of EMF specialization.

b. Interactions mediated by EMF in the boreal forest

At the ecosystem level, root-associated fungi and microbes have a key role for plant-to-plant interactions (Van der Heijden and Horton, 2009; Bever et al., 2010). As EMF are often able to associate with multiple hosts and tree individuals, shared EMF can contribute to ecosystem dynamics and succession (Dickie et al., 2004; Nara, 2006; Richard et al., 2009; Diédhiou et al., 2010b; Simard et al., 2012). With climate change, tree migrations are observed, especially in boreal ecotones (Midgley et al., 2007 ; Leithead et al., 2010), modifying ecosystem dynamics and tree communities. As dominant trees in boreal ecosystems are EM, changes in distribution may be correlated with below-ground changes in EM communities, and reciprocally.

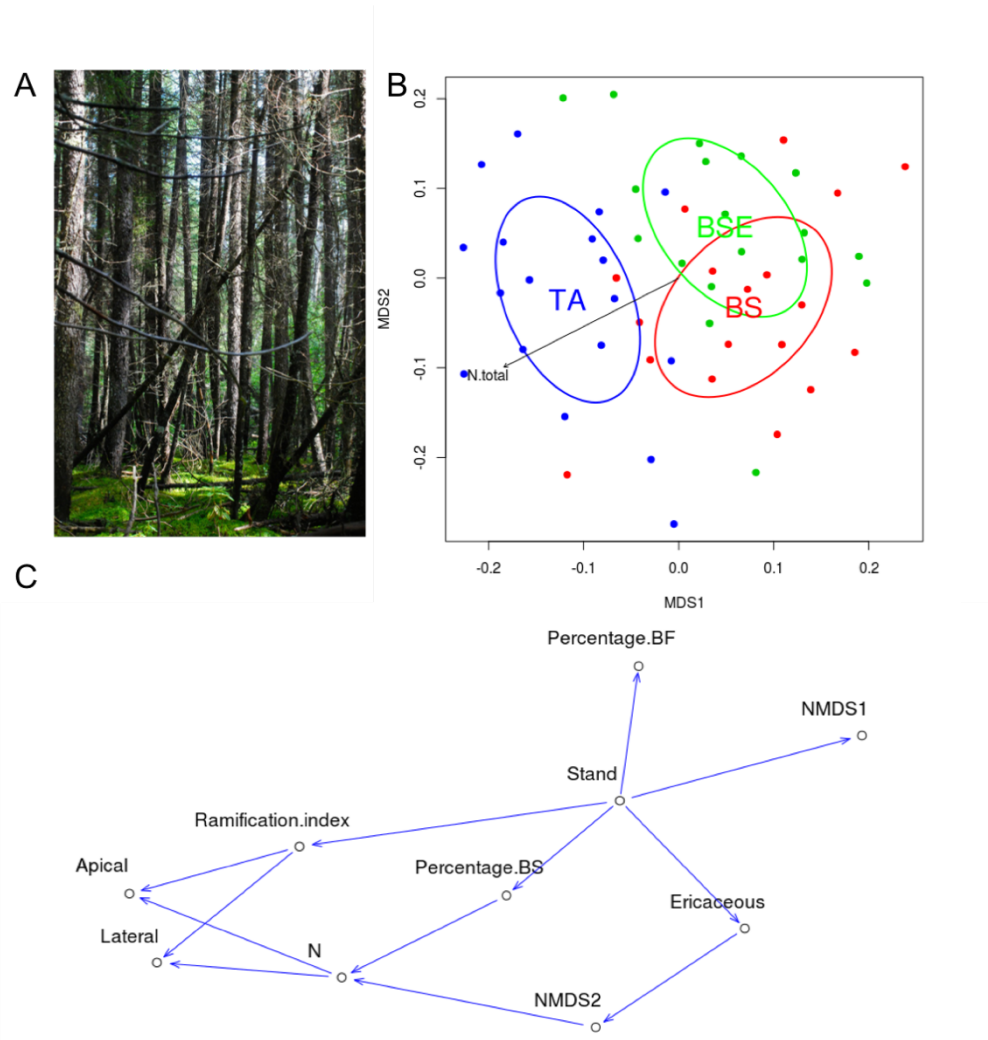


Figure 21: A, spruce forest with a clear forest gap where aspen can be observed; B, differences of EMF communities on fir saplings depending on dominant forest cover, and correlation with total N in fir needles, and C, possible interactions between EMF communities and fir growth revealed by path analysis (from ***Nagati et al., 2019****).*

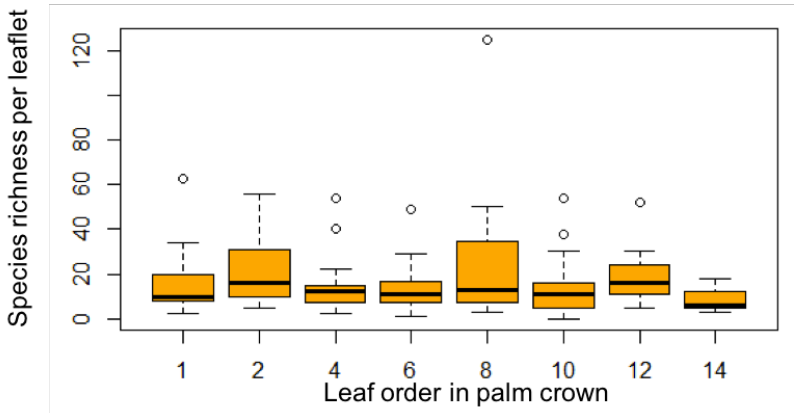


Figure 22: number of OTUs per 1 cm² of leaflet of Astrocaryum sciophilum*, showing the high diversity whatever the leaf age in a small surface.*

Through a collaboration with Université du Québec in Abitibi-Témiscamingue, I co-supervise the PhD of Mélissande Nagati, whose objective is **to investigate the role of EMF in boreal ecosystem dynamics at the ecotone between mixed forests and spruce forests**. We study an exceptional site, where *Abies balsamea* – the migrating tree species – grows better under *Populus tremuloides* than under *Picea mariana* (Fig 21A). These two species form patches and locally dominate. We have demonstrated that both forest patches host very contrasted fungal communities, both in soil (**Nagati et al., 2018**) and on young *Abies balsamea* (Fig 21B). We have also managed to show that *Abies* needles are richer in N under *Populus* (Fig 21B, **Nagati et al., 2019**). The presence of ericaceous shrubs has, on the contrary, a negative effect on the EMF communities (Fig 21C). Finally, we have compared the whole fungal communities with southern patches dominated by *Abies*, and we have shown that saprophytic fungi are more similar under *Abies* and *Populus* than under *Picea*. This PhD illustrates that *Abies* dynamics are the result of both positive and negative interactions, partly mediated by soil fungi and involving interactions with other plant.

c. Interactions within endophytic communities

In all my projects on EMF fungi, the host has been central, in the sampling, the questions, and often, the effects. Even if EMF can be generalist, and interactions with bacteria can also shape their diversity, leaving the host is not easy for an ecologist. By studying endophytic communities, I have tried **to question the role of the host, and the possible neutral distribution of those above-ground communities**. Through the ANR project SECIL, I supervise the post-doc of J. Donald, and we investigate the endophytes community in canopy leaves at the Nouragues station. We have shown that the host tree has an effect, together with the branch identity, and that neighbouring plants do not necessarily host more similar communities (**Donald et al., submitted**). Conversely, under the canopy, the basket-palm *Astrocaryum* sp. hosts endophytic communities more similar to its neighbours, probably through the accumulation of leaf litter coming from surrounding trees (**Donald et al., in prep**). Indeed, in other palm trees which do not accumulate leaf litter, a lower diversity of endophytic fungi is detected. The host effect can result partly from its morphological traits, and indeed, *Astrocaryum* sp. shares less endophytes with other *Astrocaryum* individuals than with their neighbouring tree species.

The structuring role of leaf and tree traits is increasingly recognized (Saunders et al., 2010; Sanchez-Azofeifa et al., 2012). It is for example part of the ongoing projects in French Guiana to try to test if drought-resistance traits is correlated with endophytic distribution. The genus *Astrocaryum* is well known for its slow growth and longevity (Charles-Dominique et al., 2003). In their review of endophytic diversity in the tropics, Arnold and Lutzoni (2007) suggested that leaf longevity could favour such a diversity. Through the project FUNCHEM, together with chemists interested in communities of slow-growing fungi (which may produce more complex metabolites), I studied endophytic communities of 0.5 to 28 yr-old *Astrocaryum* leaves in greater details. I hypothesized that **the long life-span of *Astrocaryum* leaves can favour a more diverse endophytic communities**. By sequencing the ITS1 barcode on 1-cm^2 leaf samples, I have observed that communities are less diverse and more homogeneous in older leaves than in young ones (Fig 22). Endophyte communities are highly diverse and not distinct between leaf ages. This result contrasts with the dynamics observed on *Theobroma cacao* leaves (Arnold and Herre, 2003), and probably reflects the high variability of communities sampled in the field.

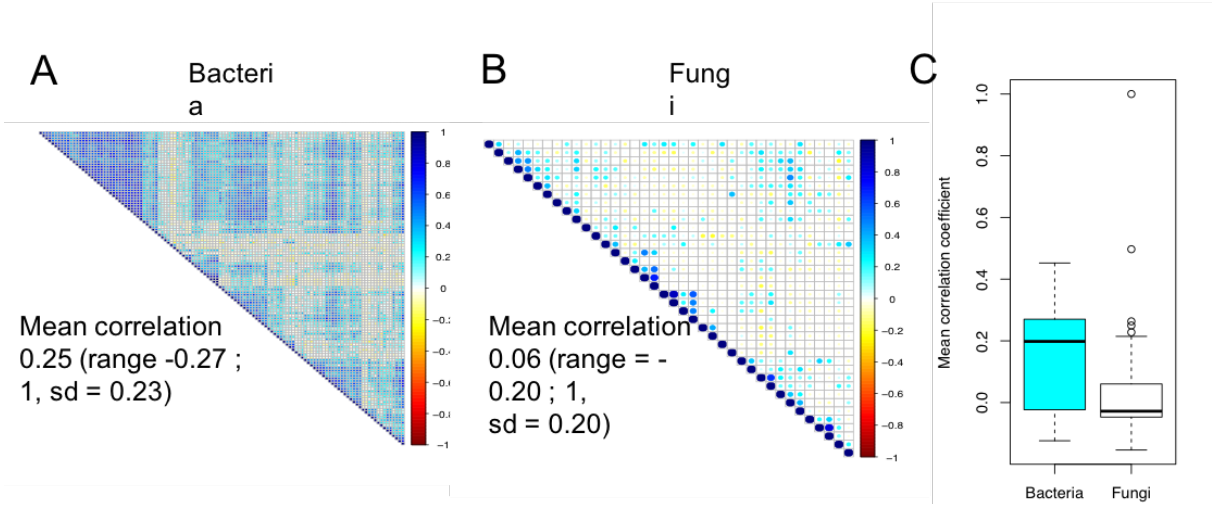


Figure 23: Interactions between OTUs in Posidonia *leaves, for bacteria (A) and fungi (B) and mean coefficient of correlation for a* Lulwoana *sp. (Gazal et al., in prep).*

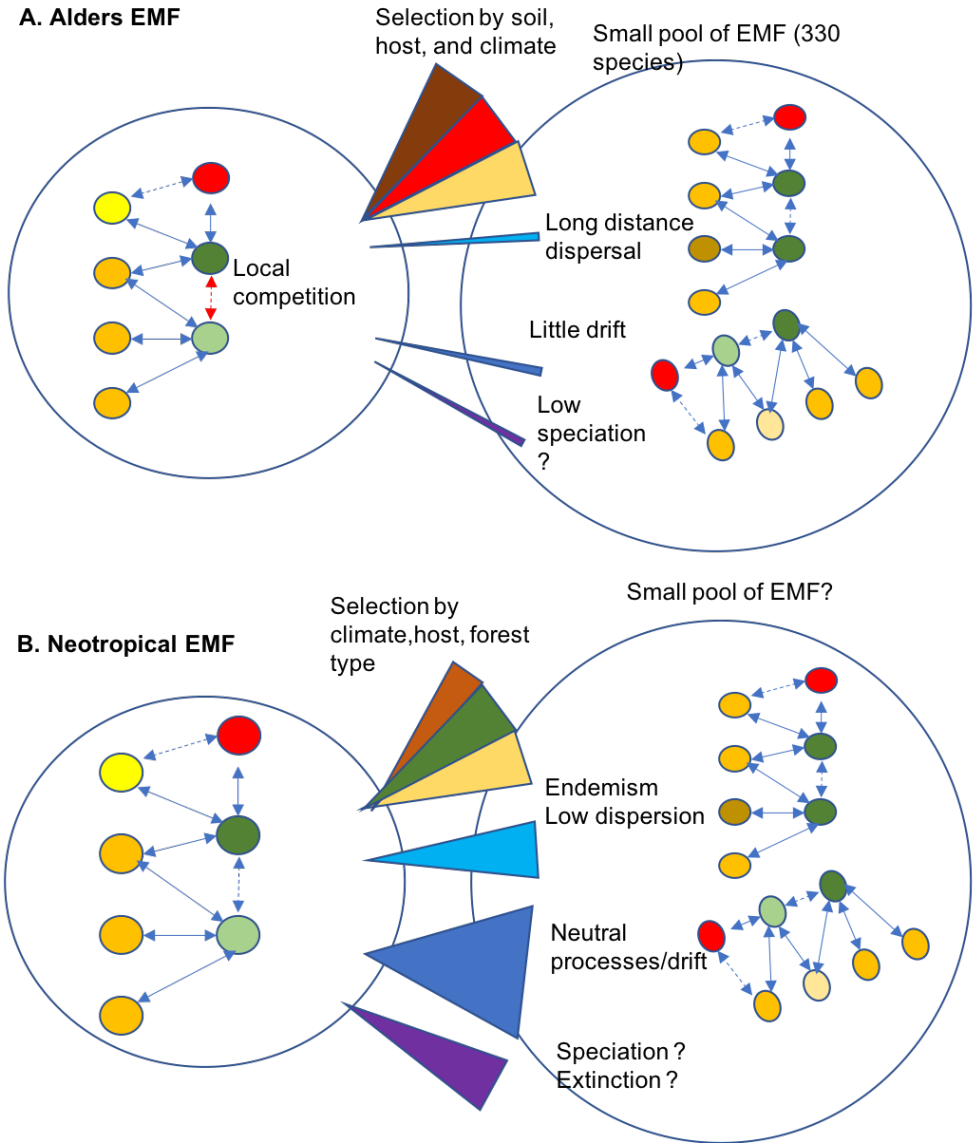


Figure 24: Synthesis of processes shaping EMF communities and specialization on the two model studied, Alnus *and Neotropical EM trees.*

The high diversity of fungi and bacteria detected within those leaves also raises questions regarding the interactions between micro-organisms. Interactions between endophytes represent a continuum going from parasitism to mutualism, including commensalism (Lindow and Brandl, 2003). Indeed, some competitors have anti-fungal properties, and are now used in agriculture, such as *Trichoderma* sp. (Degenkolb et al., 2006). Even epiphytic lichens can have anti-fungal properties (**Lagarde et al., 2018**). To progress in our understanding of microbial interactions within endophytic communities, I have collaborated with colleagues interested in interactions and bacterial communications, through the method of Quorum sensing. We have investigated a model plant hosting specialized fungi and diverse bacteria, *Posidonia oceanica* (Panno et al., 2013; Vohnik et al., 2015; 2016). Indeed, *Lulwoana* sp. (a dark-septate fungus) has been revealed only from sea grasses (such as *Posidonia*) in diverse locations (Torta et al., 2015). We hypothesized that **negative interactions between bacteria and fungi could contribute to fungal specialization in *P. oceanica* leaves**. I co-supervised the master 1 of Nina Gazal and sequenced fungal and bacterial barcodes (ITS1 and 16S respectively) in 89 samples of *P. oceanica*. Bacteria and fungi are clearly less abundant than in leaves of tropical trees and show distinct distribution patterns among *Posidonia* organs (roots, rhizome, leaves). Based on co-occurrence data, interactions between bacteria are more positive, and fungal interactions are rather neutral (Fig 23A, B, **Gazal et al., in prep**). Interestingly, one strain of *Lulwoana* qp. showed more positive interactions with bacteria than with fungi, but all interactions were mostly positive (Fig 23C, **Gazal et al., in prep**).

To summarize, through these diverse projects, I have confirmed that specialization is not neutral for alders and I have shown how interactions with other trees and bacteria can modify EMF and fungal specialization. The processes are different for alders and Neotropical trees, and for example dispersal may be more limited for tropical EMF than for the symbionts of alders. Parameters explaining EMF distribution are different, and specialization is variable for alders while it is mostly explained by host for Neotropical EMF. It is still too early to quantify the importance of each process, and some questions remain unanswered, such as the importance of speciation or extinction in the tropics (Fig 24). In French Guiana, the distribution of soil fungi has been studied and revealed that 50% of community variations can be explained by neutral models (Sommeria-Klein, 2017). Large-scale analyses of root symbioses by metabarcoding now have the power to evaluate the importance of neutral processes (Sommeria-Klein et al., 2016), and would allow quantifying the importance of distinct processes and factors influencing EMF diversity and specialization.

Building from these results, two subsequent pathways for research were possible, either going deeper in interactions, and searching for mechanisms leading to specialization, or searching for a more integrative level and studying factors shaping EMF communities and specialization. I have decided to investigate the second option, and will now focus on a higher level: the landscape.

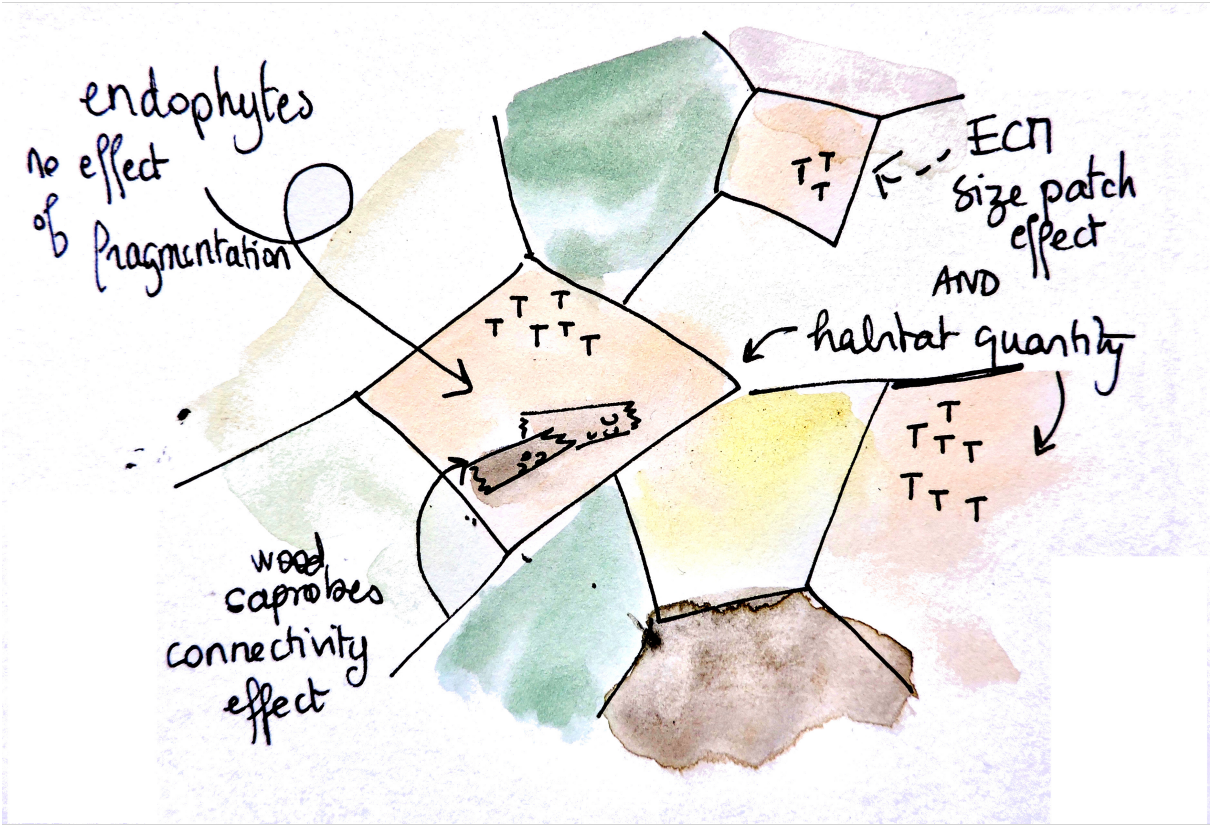


Figure 25: Effect of landscape on fungal communities, based on Grilli et al. 2017 ; watercolor by Mélanie Roy.

Table 3: Contrasted effects of landscape on fungal communities

Fungi	Landscape element (significant in bold)	Publication
Wood-associated fungi and birch endophytes	**Edges, fragmentation**	Helander, 2007; Saikkonen, 2007; Abrego and Salcedo, 2014
root-associated fungal diversity	**Connectivity, patch area**	Vannette et al., 2016
Grape endophytes	Landscape composition	Fort et al., 2016a
endomycorrhizal and dark septate endophytes	Patch area	Grilli et al., 2012
EMF of *Alnus, Corylus, Crataegus*	Distance, **forest age**	Boeraeve et al. (2018)
specialist wood-associated fungi	**fragmentation**	Norden et al. (2013)
Generalist wood-associated fungi	fragmentation	Norden et al. (2013)

PRESENT/FUTURE DIRECTIONS

From community to landscape ecology

Projects	ARC, LONGTIME
Articles	Schwob et al., 2017; Mennicken et al., in prep; Gazal et al., submitted

Landscape ecology is an interdisciplinary field linking geography and ecology. This field was born initially in the first half of the XIXth century, a period during which vegetation and soil maps were produced, but exploded one century later (Wiens, 2008; Wu et al., 2013). Studies in landscape ecology have focused on plant, bird, and subsequently insect distributions, only recently including fungi (Grilli et al., 2017). Landscape ecology tries to understand how the landscape, through its heterogeneity, and its elements (patches, corridors) can explain species distributions. One major challenge to delineate patches, and therefore describe a landscape, is to identify the habitat of a species, and the distance at which it may disperse. For fungi, dispersal can occur over long distances (Vincenot and Selosse, 2017), and thus patches may be larger than patches for earthworms for example, which disperse vertically and over short distances. As a consequence, several landscapes can be drawn from a single environment, and this explains why in France, we have different corridors for fishes ("trame bleue"), for plants ("trame verte"), and now for bats ("trame noire", Sordello, 2017). However, landscapes are rarely defined for species (except for some endangered ones), but rather for habitats. Therefore, landscapes are often described through the surface of forests, fields, the presence of hedgerows, streams, and the connectivity between all these elements.

The importance of different elements of the landscape may differ among taxa, depending on their dispersal abilities (Fig 25). For fungi, recent studies have shown very contrasted patterns, depending on the community and the scale that are studied (Nordén et al., 2018 ; Table 3). Wood-associated fungi and birch endophyte communities are distinct at forest edges and are affected by forest fragmentation (Helander, 2007; Saikkonen, 2007; Abrego and Salcedo, 2014). In the lava-fragmented landscape of Hawaï, local root-associated fungal diversity increased with forest area, and fungal species composition is correlated with fragment connectivity (Vannette et al., 2016). On the contrary, landscape composition has no effect on grapevine foliar endophytic communities (Fort et al., 2016a), while patches of different habitats hosted very contrasted communities (Fort et al., 2016b). Grilli et al. (2015) have also shown that fragmentation does not shape communities of endomycorrhizal fungi associated with a ruderal forb. Previously, Grilli et al. (2012) had detected a strong relationship with patch size for endomycorrhizal and dark septate endophytes associated with a native host but not for fungi associated with an exotic host. Boeraeve et al. (2018) have also shown that EMF communities associated with three different hosts, *Alnus glutinosa, Crataegus monogyna* and *Corylus avellana,* are differently affected by the landscape. The distance between fragments does not explain change in communities, but forest age and host species have more of an effect. Interestingly, Nordén et al. (2013) have shown that specialist wood-associated fungi are more affected by fragmentation than generalist ones. Overall, Grilli et al. (2017) have concluded that in general, fragmentation negatively affects fungal diversity. Moreover, host, fungal nutritional mode and specialization may modify the tolerance of fungi to habitat disturbance. These recent results have rapidly changed my point of view on alder specialization.

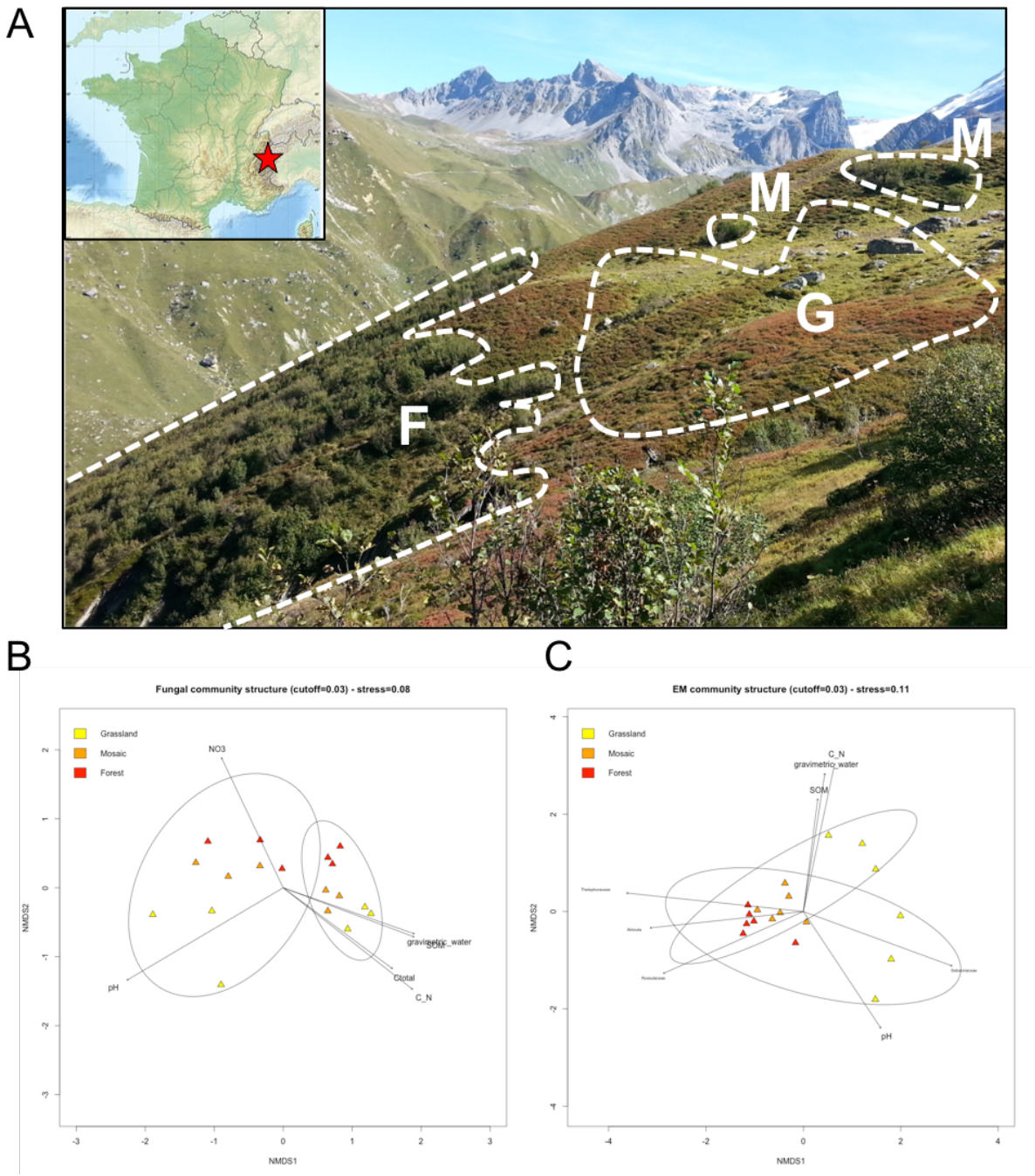


Figure 26: Recent landscape in the Vanoise, where alder stands are particularly extended (F) but also colonize the grassland (G) and form a mosaic (M) at the edge (A), and differences of soil fungi and EMF communities in this landscape (from ***Schwob et al., 2017****).*

Compared to other temperate trees, alders show a rather patchy distribution and extended stands are extremely rare. *Alnus alnobetula* is a montane shrub growing at the tree line, whose distribution is now extending over abandoned-pasture. In the Vanoise, extended populations can be found, representing one of the oldest alder stands in France (ca. 400 years old, with 80% of *A. alnobetula*, Anthelme et al., 2003). With G. Schwob, I have tried to understand how the landscape, through its fragmentation, can shape *Alnus*-EMF interaction and specialization. **We hypothesized that patches with a higher alder density would host more specific symbionts than isolated trees.** We did not detect an effect of alder density on EMF diversity, but we detected differences of EMF community structure and revealed a strong difference with grassland soil communities (Fig 26, **Schwob et al., 2017**). The sequencing of soil cores also revealed contrasting patterns among fungi, and saprophytic fungi distribution is opposed to EMF one. Specific symbionts are poorly distinguished by ITS1 barcodes (250 bp for Miseq) and we did not detect a strong difference between forest and edges. Interestingly, Boeraeve et al. (2019) also showed that soil communities are more affected by forest edge than root communities of *A. glutinosa*. All these examples illustrate the different responses of fungal communities to fragmentation and landscape structure.

Through a collaboration with A. Brin and E. Andrieux (DYNAFOR, Toulouse) on the Cevennes ancient forests, I have begun to get further involved in landscape ecology. The term "Ancient forests" does not refer to forest age or maturity, but rather to the permanence of a forest (Cateau, 2015). Ancient forests are defined in France from maps drawn by Cassini, who reported around 1755 the occurrence of forests in France. Ancient maps are precise enough to constitute a reference of the minimum extent of forests in France. Today, 30% of the French territory is covered by forests, three times more than in 1850. The forest surface was minimal at the beginning of the industrial period, where wood was intensely consumed, and most people were still living in the countryside. Therefore, ancient forests are defined from maps of 1850 (Cateau, 2015). Since then, an ancient forest can have been cut and replanted (Fig 27A), which explains the difference between ancient forests and mature forests. Interestingly, soils may well reflect the permanency of a forest's cover, and one can expect that soil fungi may be sensitive to such forest history. The literature is rich on forest ages than (e.g. Bonet et al., 2004; Richard et al., 2005), notably because forest managers have found many indicators of forest maturity among wood-associated fungi (Christensen et al., 2005). In the Cevennes National Park, a recent effort made to map ancient forest revealed a scattered distribution, hidden by the continuous forest cover. Today, 80% of the park is forested, but this landscape is apparently recent, as ancient forests represent only 20% of the surface (Fig 27B). As the forest fragmentation is low today, we have hypothesized that fungal communities may rather follow Fahrig's (2013) hypothesis, which assumes that connectivity may be less important than surface and habitat amount on species distribution. In other words, I have investigated **if the fungal diversity can be higher in ancient forest surrounded by a higher quantity of ancient forest, whatever the connectivity of these patches.** S. Mennicken worked on this project during her master 2, together with F. Kondratow (PhD supervised by A. Brin and E. Andrieu). Through the use of NGS, EMF, saprobes and pathogenic fungi have been sequenced from soil collected over 50 plots in the National Park (8 root cores per plot). We have shown that different guilds had distinct responses to the amount of habitat, and detected both the effect of soil chemistry and landscape (**Mennicken et al., in prep**). Interestingly, the surface of the central patch – where samples were collected- has no effect on fungal diversity, which contrasts with the results obtained on isolated stands in other ecosystems (Peay et al., 2007).

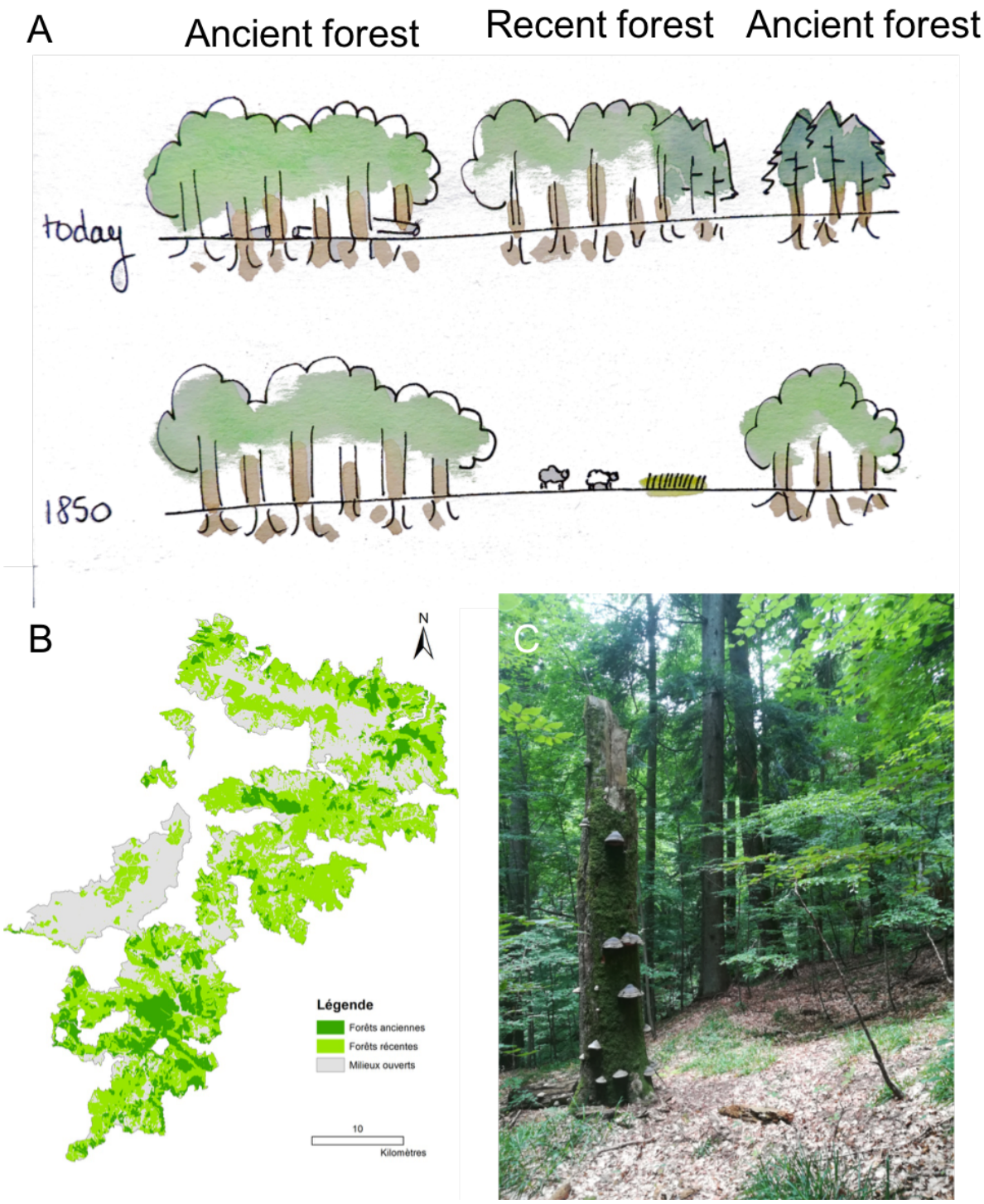


Figure 27: A, definition of ancient versus recent forest, from Cateau et al. (2015); B, distribution of ancient forests in Cevennes National Park and C, a mature and ancient beech forest of Maramures in Romania.

More recently, thanks to an interdisciplinary project with archaeologists and forest historians from Toulouse 2 University, I have sampled soil communities in ancient and recent forests located at the extreme north of the Carpathian Mountains (Romania). There are still pristine patches of forest in Ukraine, in the eastern Carpathians (Trotsiuk et al., 2012). In the Maramures (Fig 27C), forests are extremely tall, show numerous signs of maturity, and are characterized as old-growth forests (OGF). However, OGF have probably been exploited in the past, due to an intense local mining activity. Today, those old-growth beech forests are threatened by logging, even in protected areas (Knorn et al., 2013). Logging can deeply change forest structure and dynamics (Durak, 2010), and reserve managers are calling for research to monitor the diversity in these OGF. Compared to the Cevennes project, I have instead focused on the difference between ancient and recent forests within old-growth forests, and integrated more habitats and history descriptors. Within this project, I am testing **if fungal diversity is shaped not only by forest maturity but also by forest history**. For EMF, this might be the case, as Diédhiou et al. (2009, 2010a) have shown that the presence of Roman farms in the forest contributed to shape the distribution and the functions of EMF communities today. In another project, CERES (2018-2020), together with A. Brin, I aim at studying the effect of fragmentation and temporal continuity on diverse communities, including EMF, in the forests of southwestern France. To achieve this, I am studying the soil fungal diversity in both fragmented and extended forests, of either recent or ancient age. In this case, I am testing test **if fungal diversity is shaped by forest history and landscape structure** and I hope to involve a PhD student in this project soon.

In Amazonian forests, interactions between archaeologists and ecologists have also recently revealed the influence of history -linked with human history- on tree communities. Indeed, sites which have previously been heavily populated host the richest tree communities today (McMichael et al., 2017). Moreover, archaeologists have revealed clues on past uses for 82 plant families in the Neotropics (Levis et al., 2017). The Amazon may be a "*jardin sauvage"* or a "domesticated forest" (Barlow et al., 2012; Rostain, 2016). As Amazonian pre-colombian human populations have been highly connected and have been exchanging products (Rostain, 2017), they may have contributed to the dispersal of plants across the Amazon and have definitely modified some landscapes, such as raised fields, shell mounds or *terra preta* accumulations (Rostain, 2017). In French Guiana, clues of past occupancy are visible nearly everywhere along the streams, or close to inselbergs. In the forest, charcoal fragments and shards can be observed, and ring-ditched hills have recently been detected by LIDAR in so-called "pristine" forests.

Considering the abundance of EMF on slopes and close to inselbergs, I have contributed to a multidisciplinary project involving botanists and archaeologists, to understand the extent of which past forest history can shape EMF distribution in certain habitats in French Guiana. Among the habitats that have been massively occupied in the past, liana forest are particularly interesting, and host EM lianas such as *Gnetum* spp. and *Coccoloba* spp. On ring-ditched hills, pedologists suggest that soil has been removed, revealing the laterite crust and increasing the soil drainage when compared to surrounding forests. As a consequence, soil conditions may be similar on inselberg slopes and close to ring-ditched hills. I have therefore tested **if EMF could be favoured by past occupancy around ring-ditched hills**, during N. Gazal's Master 2 internship. By sequencing soil communities, we have produced comprehensive inventories (Fig 28A) and detected three EMF and one glomeromycota particularly associated with evidence of past human settlements (**Gazal et al., submitted**).

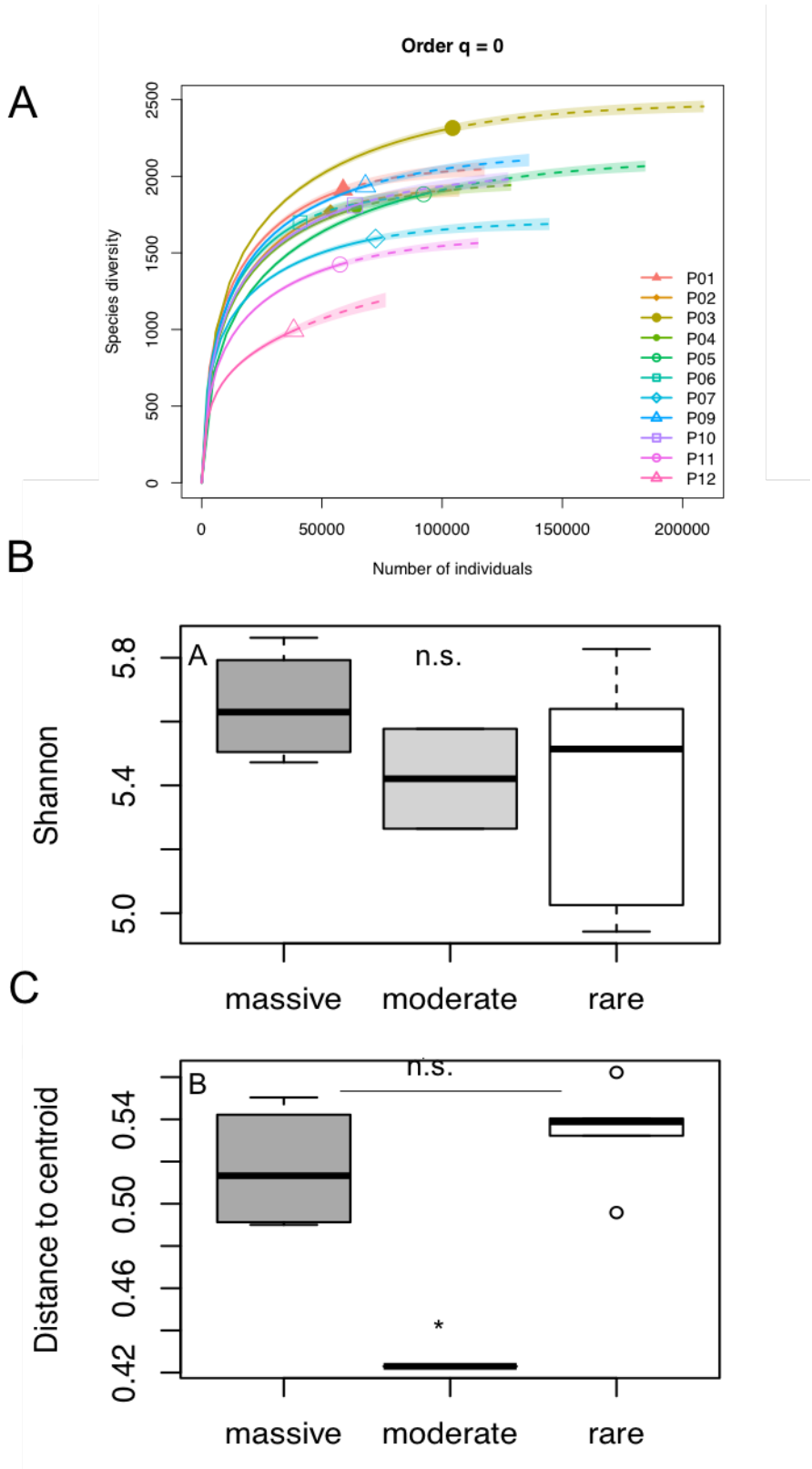


*Figure 28: A, species accumulation curves produced by sequencing environmental DNA from soil cores on 11 sites at Nouragues station, B, Shannon diversity of fungi on sites massively, moderately or rarely occupied in the past and C, distance to centroid in the NMDS, representing the beta diversity within each group (**Gazal et al., accepted**).*

Fungal diversity is not significantly different on massively occupied sites than on other sites (Fig 28B), nor is EMF diversity, and only sites moderately occupied in the past are more homogeneous (Fig 28C). More generally, EMF are abundant on slopes and in "*cambrousses*", a fact that confirms the preference of EMF for low-canopy forests. On ring-ditched hills, EMF can be favoured by canopy gaps and the occurrence of EM lianas or small trees. These results illustrate how neotropical EMF can survive in gaps, thanks to numerous and scattered favourable habitats, and eventually, thanks to past human uses.

The question remains if investigating fungal communities in general can be of interest for historical ecology studies. They have already been used but often as indicators. For example, the occurrence of spores of the coprophilous fungi *Podospora* or *Sporormiella* can indicate pasture in sediments (Orbay-Cerrato et al., 2017). In the Amazon, there is one puzzling question that may be solved by investigating not only EMF but also pathogenic fungi. Indeed, Neotropical forests are characterized by their tree diversity, and the high and density-dependent mortality, mediated by natural enemies (Levi et al., 2019) including fungi (Bagchi et al., 2010; Mangan et al., 2010). Increasing the density of species of cultivated plants in the forest may have been a challenge, and considering the deep soil modifications, one can wonder if the aim of these soil modification by humans could have been to decrease the abundance of saprobes and pathogenic fungi by increasing the soil drainage. Indeed, soils around crowned mountains are very different from *terra preta* described along the Amazon, where a higher organic matter content favours a rich saprophytic and bacterial community (Kim et al., 2007; Lucheta et al., 2016; 2017). Another use of fungi in archaeology can be linked to their dispersal ability. Indeed, evidence of occupancy may reflect local land uses, but the occurrence of indicators, that are habitat-specific and able to disperse, may also reflect changes at the landscape level. Searching for such indicators requires the production of reliable and comprehensive inventories of fungal communities, so that presence or absence records can be considered as reliable. At the EDB lab, efforts have been made to replicate PCRs, include 10% of negative controls, and now positive controls. Our sampling of fungi through NGS over 1 ha tend to show a saturation (**Gazal et al., accepted**), supporting the idea that soil DNA could be used to produce comprehensive sampling, and therefore to detect possible indicators.

To summarize, there are debates about the definition of landscape and the effect of landscape on fungal communities, but this integrative level of analysis could enlighten our understanding of the distribution pattern of EMF, both in temperate and tropical forests. Based on those recent projects, I am now developping projects focused on soil history and stability in order to understand not only if EMF could be more diverse in ancient forests, but also if mycorrhizal networks could be favoured in these stable habitats, and reciprocally, the extent to which fungi could contribute to forest resilience. An ecosystem's resilience reflects its capacity to recover after a perturbation, and managers are indeed searching to favour forest resilience, for example by increasing tree diversity or functional diversity in general (Thompson et al., 2009). During my short post-doc, I studied with F. Richard at CEFE (Montpellier) the effect of drought on EMF communities. We sampled EMF of *Quercus ilex* at Puechabon, where a rain exclusion system is settled since 15 years (-30% rain). We revealed only very small changes (**Richard et al., 2011**) and variations of EMF communities were mainly seasonal. Such observations illustrate the variability, but also the resilience of EMF communities, at least in ecosystems where EMF are abundant and EM trees dominate.

A

B

Figure 29: A, example of drawings used in tropical ecology teaching, to speak about plant diversity, size of fruits, and lack of EMF fruiting bodies, and B, example of drawing used in botany teaching with students and wine makers. Watercolors by Mélanie Roy.

Using landscape to reconnect students to ecology	
Projects	ACTUAAL
Articles	Roy et Caillon, submitted

Going from community ecology to landscape ecology has brought me closer to geography, not only in my research projects, but also in my teaching. Focusing on landscapes is relatively recent among educators, and becomes increasingly central in my pedagogy. The first classes I modified were botany and mycology, and the first step has been to interest students in learning about landscape through projects on their urban environment. Indeed, students are less and less interested in taxonomy, and rarely enjoy learning Latin names. Thanks to availability of "apps" to identify plants (such as Plantnet, Goëau et al., 2013), students are autonomous enough to perform inventories of wild plants in their own streets, trying to test if one dispersal mode was dominant over the others. In mycology, I have trained students to identify lichens growing in the city and in the countryside to determine pollution level. In both cases, involving students in participative surveys has really increased their investment in projects, and has brought interesting results. For example, inventories of lichens are often richer in central Toulouse as compared to the periphery. In the streets, long-distance dispersal is rare, and plants are often ant-dispersed. More theoretically, setting community ecology questions in relation to land use probably increases their interest for nature in towns (Pellegrini and Baudry, 2014) and such teachings now interest geographers as well. More recently and on a research level, I have begun to collaborate with J. Legall and study this increasing interest in urban areas of Buenos Aires and Mexico, where students are particularly disconnected from nature (ACTUALL project).

The second change in my courses, which is intimately linked with landscape ecology, is the use of drawings. This is extremely personal and uncommon in ecology (**Roy and Caillon, submitted**) while we teach our students how to draw plants in botany. Such drawings are useful for captivating students within a boring powerpoint and for sharing my passions for tropical diversity (Fig 29A). In anthropology and ethnology (Brunois, 2002), the role of drawings has long been dissected and many advantages have been underlined. Reciprocally, in art pedagogy, the ecology and the landscape are key elements for engaging students (Inwood, 2010) and raising their creativity (Neperud, 1997; Graham, 2007; Herzogenrath, 2009). More generally, the development of environmental art and even ecological art illustrates this long-term interest of artists for ecology (Brunner et al., 2013). Recently, some projects have highlighted the role of sketching in science (http://www.sciencesketches.org), but not particularly in ecology.

The third change in my teaching has then been to integrate both landscape-scale studies and drawings to build a pedagogical project linked with research questions in vineyards (fig 29B). Indeed, Toulouse University is surrounded by an agricultural landscape, especially vineyards. Close to Gaillac, vineyards are concentrated in Mediterranean microclimates and grow on limestones, sandy and clay-rich soils. This diversity of habitats and the occurrence of Mediterranean plants make vineyards particularly interesting for teaching botany in early spring. Rapidly, I have realized that not only students but also vintners are interested in plants and their landscape. With S. Caillon (CEFE, CNRS), I have begun investigating this relationship, through field teaching. The use of art is a real catalyst in this non-funded project, and enables the construction of a network of organic vintners, as a support for teaching and research (Fig 30A). Moreover, students are able to observe a rich plant community, with 133 plants identified over 48 inventories (10 m long transects, Fig 28B, C).

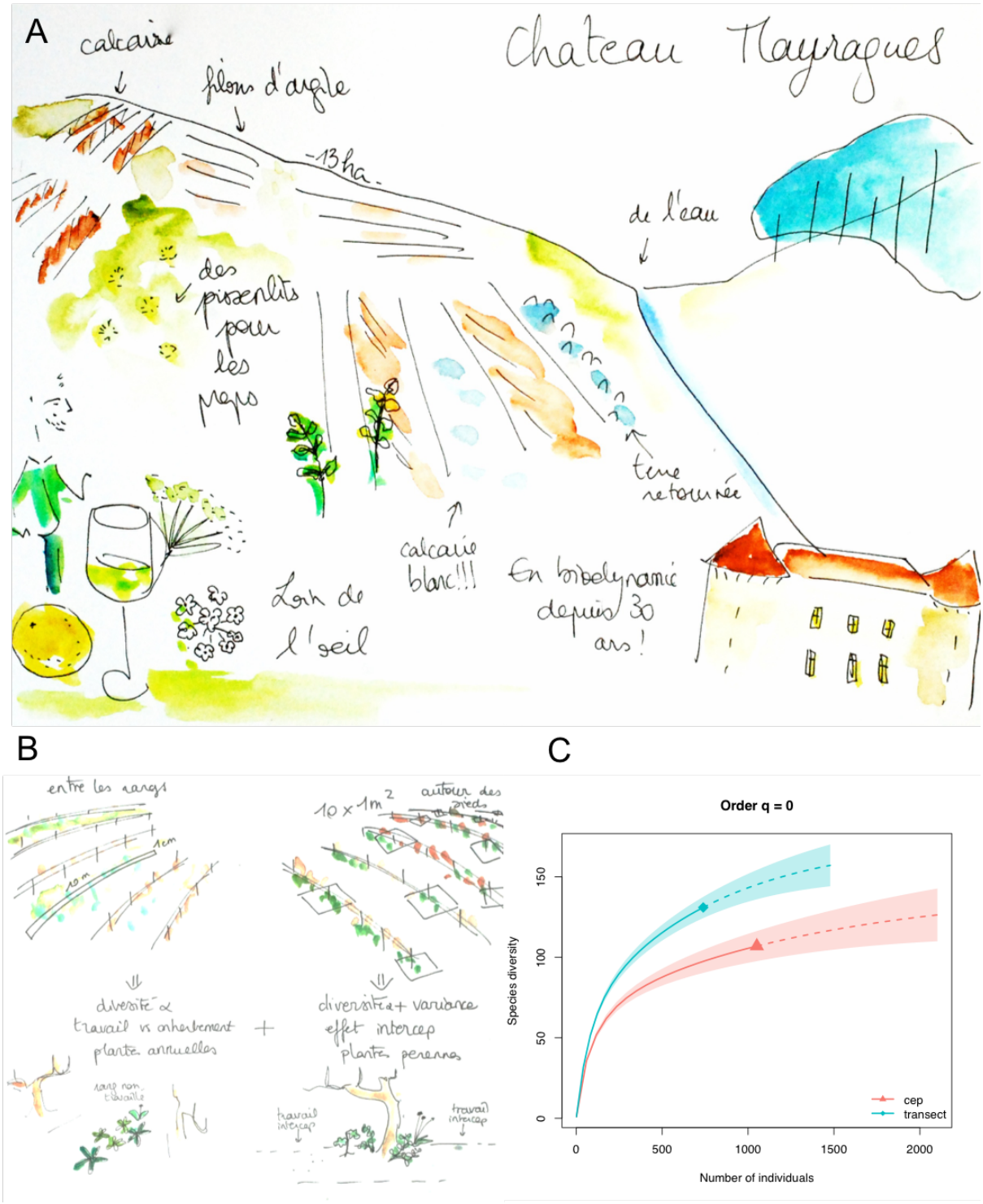


*Figure 30: A, drawing made by Mélanie Roy illustrating the enthusiasm of a wine maker and the integration of plants in his description of the vineyard (**Roy et Caillon, submitted**), B, inventory of plants in the inter-row and row, and C, species accumulation curves for row and inter-row inventories (over 9 vineyards and 28 transects).*

Gaillac appellation is not only one of the oldest vineyards in France (recorded from 200 yrs B.C.), but is also the most diverse in terms of grape varieties (Plageoles, 2009). Over the last century, up to 82 grape varieties have been reported and several are endemic, such as *prunelard*, *ondenc*, and *loin de l'oeil* varieties. Through field-based teaching, we have also observed that vintners are particularly innovative and use their landscape and the grape diversity in various ways to adapt their organic practice to local constraints. Thanks to a *"Make our planet great again"* project granted to D. Renard (CEFE, Montpellier), I will work with a PhD student (supervised by S. Caillon, 2019-2021) who investigates how practices and grape diversity contribute to vineyard resilience, estimated through the variability of harvests during the past 30 years (other estimators to be defined as well).

This project does not integrate fungi yet, but testing if mycorrhizal fungi can reflect differences in landscape and land use, and therefore contribute to vineyard resilience, would of course be extremely interesting. *Vitis sylvestris* var. *vinifera* is a domesticated liana associated with generalist endomycorrhizal fungi (Balestrini et al., 2010). Recent investigations of its interaction with surrounding plants have revealed possible carbon and nitrogen transfers from leguminous plants through mycorrhizal fungi (Cheng and Baumgartner, 2004; 2005; 2006). Moreover, projects on mycorrhizae try to detect possible protective effects against other fungal pathogens (Pozo and Azcón-Aguilar, 2007). However, in terms of diversity, the endomycorrhizal community may be of low variability at the scale of Gaillac and between grape varieties (Balestrini et al., 2010; Schreiner and Mihara, 2017) and the global fungal diversity might be more interesting to study. In the following projects, I have tried to integrate the methods and questions developed through those integrative teachings, to re-orient my research questions on EMF and fungi communities.

How to integrate ecological networks to study ecosystem resilience?	
Projects	CERES, GLOBNET, CHAMPLAIN
Article	Shefferson et al., 2016 ; 2018 ; Nagati et al., submitted

Fungi are heterotrophic. They are therefore involved in interactions, often with plants, but also with other soil organisms. The study of specialized interactions has illustrated the effect of bacteria and other soil fungi on EMF interactions and has raised more general questions on multitaxa interactions. The use of ecological networks to describe plant-fungi interactions can indeed be extended to other interactions, through co-occurrence data (Vacher et al., 2016b) and NGS data are beginning to be used to describe such networks (Bohan et al., 2017). There are still limitations, and for example species delimitation from short sequences (produced by NGS) may bias our description of networks (Bohan et al., 2017). Trying to describe ecological networks could be particularly interesting for estimating ecosystem resilience capacity, as more connected networks are supposed to increase ecosystem resilience (Thébault and Fontaine, 2010). Using NGS to characterize below-ground ecological networks involving EMF could allow detecting possible common mycorrhizal network (CMN), comparing ecological with functional common mycorrhizal network, and finally help to draw a more theoretical framework for fungal interactions.

Theories on ecological networks have been developed from the study of plant-pollinator interactions (Vasquez et al., 2009) and trophic chains. Interactions between plants and pollinators are highly variable, and mainly shaped by spatial heterogeneity (Moreira et al., 2015) and landscape (Ferreira et al., 2013).

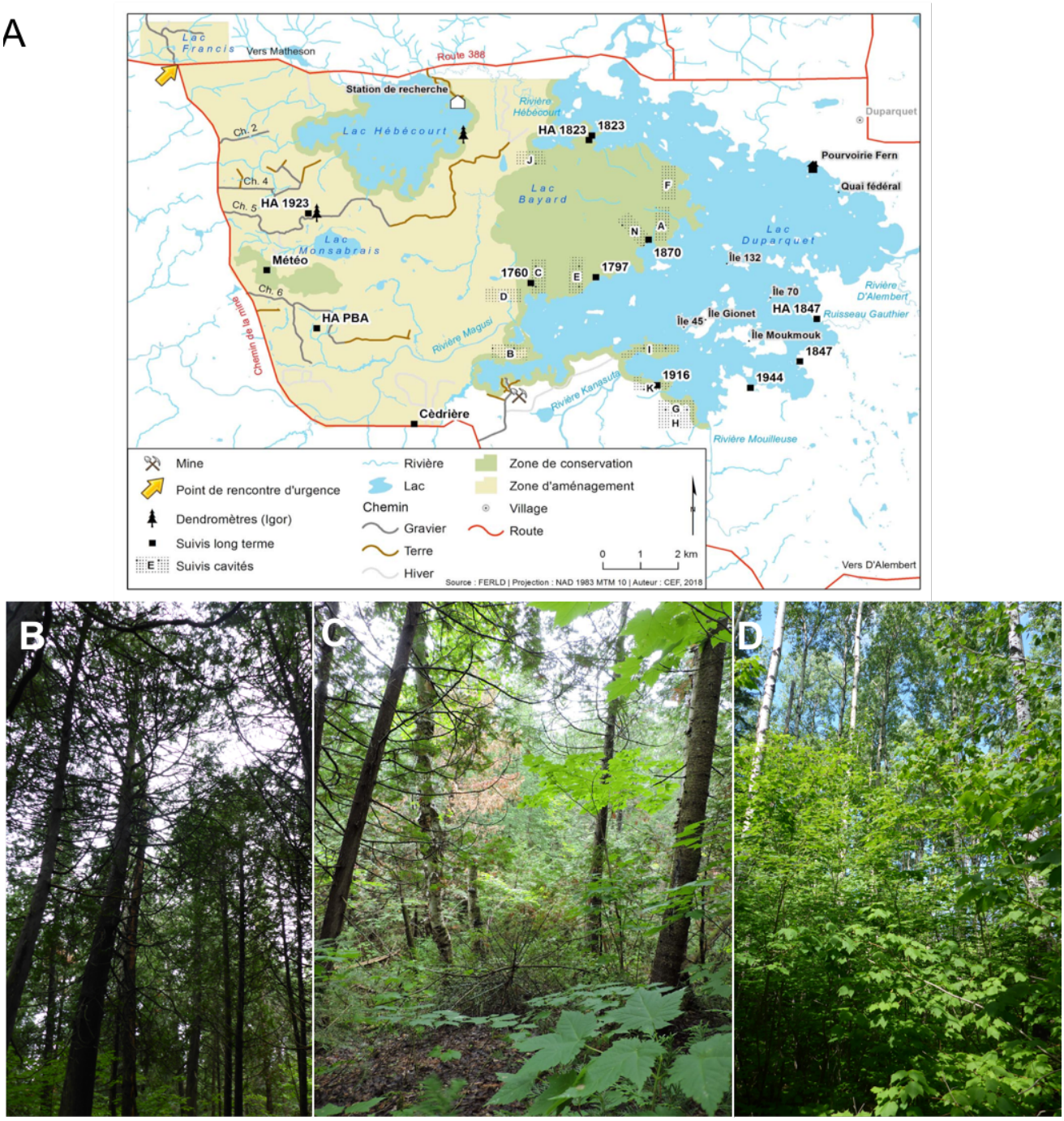


Figure 31: A, distribution of last fire events around the Duparquet Lake in Quebec. "Older" plots host conifer forest, more recent host a mixed wood, and the more recent host mainly poplars in the boreal forest.

These mutualist networks are often particularly nested and asymmetric compared to plant-herbivore networks (Bascompte et al., 2003; Nuismer et al., 2013). The nestedness of mutualist networks may contribute to network stability and more generally to ecosystem resilience (Thébault and Fontaine, 2010). Several articles suggest that a higher diversity in soils could also contribute to ecosystem resilience (Wagg et al., 2014; Bender et al., 2016), especially in agricultural fields, but there are still debates on the complexity-stability relationship (Jacqet et al., 2013). More generally, the review of Simard et al. (2012) highlighted that mycorrhizal networks may have both positive and negative feedbacks and could have different effects on ecosystem dynamics. Their role in ecosystem resilience is often assumed, but may not be obvious. For example, in boreal forests, EMF may promote fir migration to the north and contribute to rapidly changing forest dynamics (axis 3b).

I have been involved in several projects related to ecological networks, but not focused on EMF nor on mycorrhizal networks. In GLOBNET ANR (2016-2020), the aim is to gather soil cores from temperate, boreal, and tropical zones, sequence several taxa, including fungi, and begin designing tools to study interaction networks between taxa based on co-occurrence. This ambitious project definitely allows a better understanding of plant-fungi interactions at a global scale. At a more regional scale, with I. Calderon-Sanou (PhD student of W. Thuiller), I have focused our sampling on a chronosequence of the boreal forest which has been well-described from the standpoint of fire age (Fig 31). This sampling enables the examination of how soil diversity changes along the chronosequence, but data may not be sufficient to test if networks are more connected in older forest patches. In the Amazon, the NEBEDIV ANR (2013-2018) has investigated specialisation of plant natural enemies, including fungi and insects. This project has gathered an immense set of data on variation of specialization and plant-fungi networks. As the sampling has focused on root interactions, mycorrhiza have been sequenced together with the rhizosphere community, and interactions may be more real than co-occurrence data in soil. However EMF may be rare, as EM hosts had not been targeted. Moreover, based on axis 2, EMF may be relatively rare and specific, and may not be involved in networks.

Back to roots: towards experiments to link ecological and common mycorrhizal networks in a biogeographic context

Ecological networks refer to potential interactions, but detecting shared OTUs on different tree species is of course insufficient to detect a possible common mycorrhizal network (CMN). Since the discovery of a possible organic carbon transfer between trees through shared EMF (Simard et al., 1997), some books have spread the idea that CMN are everywhere (such as “The secret life of trees”, P. Wohlleben, 2016), but this is definitely not the case. Indeed evidence for exchanges through common mycorrhizal networks is relatively scarce (Fig 32, Hoeksema, 2015), perhaps because facilitation can occur without a CMN (Bever et al., 2010). For example, shared fungi have been detected in Guinean monodominant forests (Diédhou et al., 2010a), but studies using isotopes have not revealed any transfer between trees. Moreover, Corrales et al. (2016) have not detected a CMN between *Oreomunnea* individuals in Mexican forests. Experiments are needed to detect functional CMN, for example by excluding shared hyphae with fine nets around trees (Booth, 2004; Hoeksema and Booth, 2010), or by tracing carbon or nitrogen isotopes between neighboring plants (Simard et al., 1997). Our knowledge is probably too limited to understand in which environmental conditions such exchanges can occur, and if temperate or boreal ecosystems favor such functioning.

Figure 32: How to isolate the effect of CMN, by cutting hyphae directly in soil (left) or enclosing saplings in a 50 micron-wide net, to allow only hyphae to grow, from Hoeksema et al., 2015.

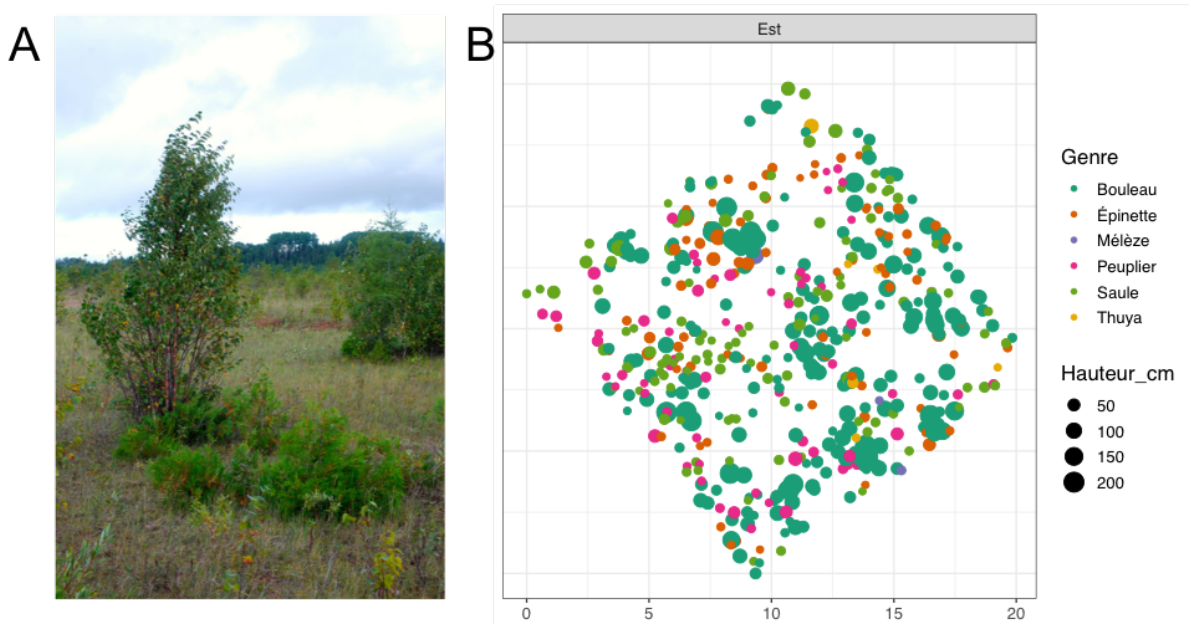


*Figure 33: A, recolonization of old mine field in the boreal forest showing young conifers and broad-leaved trees, and B, map of young saplings in a 20*20 m plot.*

Setting up more experiments in the field is challenging, but would be crucial to understand the ecological importance of exchanges through common mycorrhizal networks in a biogeographic context.

In the Canadian boreal forest, together with P. Marchand at UQAT, I have recently obtained a project to map interactions between trees and to investigate mycorrhizal and root connections between young trees (Funds from French Consulate in Canada). Indeed, in boreal ecosystems, *Populus balsamoides* and *Pinus banksiana* are both able to build root connections with other individual of the same species (Tarroux and DesRochers, 2010; Adonsou et al., 2016) and the question remains if such root grafts can contribute to facilitation between individual trees. Through two co-supervised student projects, we will therefore test **if positive spatial interactions between plants are correlated with fungal interactions** (shared fungi) or from root connections between individuals of the same species (Fig 33), or if on the contrary spatial aggregation results from a random process of dispersion. We have chosen to study such interactions in an unusual site, an abandoned mine, where up to 10 tree species could be recorded. This site began to be colonized by trees 50 years ago, and represents a simple system to study interactions between trees. Spatial aggregation can be used to target sites where CMN could occur, and this small project can be a base for future experiments on CMN in the field.

To study if mycorrhizal networks, or at least ecological networks between plants and fungi can contribute to ecosystem resilience, other options may be complementary. Indeed these descriptive projects do not include functional measures neither on ecosystem (e.g. decomposition rate) nor on mycorrhizal networks. Measuring functions of fungi may bring more evidence to estimate resilience capacity through a functional redundancy (Allison and Martiny, 2008; Griffiths and Philippot, 2013). This can be approached by reporting functional traits, and perhaps by sequencing more functional genes (Hannula and van Veen, 2016). Moreover, measuring functional consequences of networks may help to link below-ground and above-ground processes.

Through the PhD of M. Nagati, which I co-supervise, we began measuring traits of fir saplings (growth, nutrient status). Path analyses have revealed that the N content in fir needles is more related to EMF community structure than to the mycorrhization rate (**Nagati et al., 2019**), and that growth is negatively affected by the occurrence of ericaceous shrubs. These analyses suggest that EMF communities can be involved in facilitation of fir under aspen, and can be repeated in other ecosystems to investigate the functional consequences of below-ground networks. Studying plant fitness is central to understanding the functional consequences of CMN, and my studies on mycoheterotrophic orchids have also illustrated that plant survival may be an important parameter to follow (**Roy et al., 2013**b), especially for perennial species that could also be capable of dormancy (**Shefferson et al., 2016 ; Shefferson et al., 2018**).

Measuring resilience requires not only data on response traits, such as plant fitness or ecosystem diversity, but also a gradient or a time since perturbation, which is sometimes difficult to date and isolate in the wild. There is an on-going debate on how to measure resilience, and I would prefer to bring clues to measure traits that confer resilience (through functional redundancy, CMN) and how they correlate with EMF diversity, than to measure resilience per se. Such data could later be used by modelers to measure the total resilience of an ecosystem.

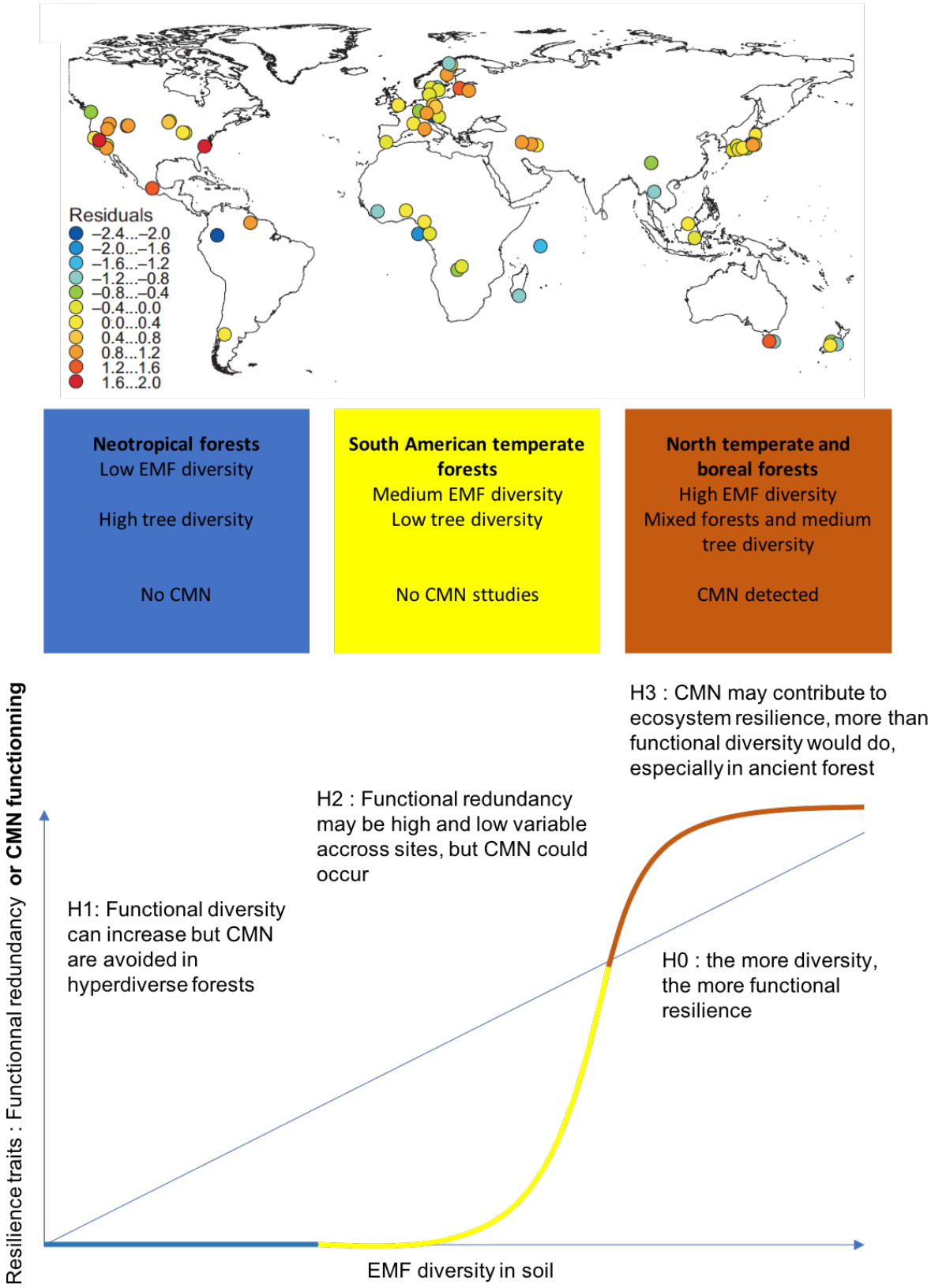


Figure 34: Hypotheses on links between EMF diversity and ecosystem resilience in a biogeographic framework.

Through the CERES project, with A. Brin, we are studying a gradient of fragmented forests, including ancient undisturbed forests, and focus on the impact of connectivity on below-ground diversity. This framework can also be used to study ecological networks involving fungi, as well as to set up experiments and investigate if young trees interact with surrounding ones through CMN. Moreover, by integrating a spatial and continuity gradient, this project allows testing hypotheses on landscape effect on EMF communities and their resilience. We would expect that the **less-fragmented and the more ancient forests would host more functional CMN and connected ecological networks**. Such results can be particularly interesting for forest managers or for understanding forest dynamics in a fragmented landscape. For example, in northern Quebec, the results of M. Nagati suggest that CMN could occur between fir and aspen, and may explain why fir regenerate better under aspen than under spruce. This result is also of interest in suggesting the utility of promoting mixed stands instead of monoculture, and thereby contributes to the search for more diverse and resilient forests (Thompson et al., 2009).

Another big challenge would be to replicate such experiments in ecosystems where CMN have never been detected and where EMF are relatively abundant. Until now, all experiments on CMN have been done in northern temperate forests, but southern temperate forests may function differently. For example, forest soils are generally richer in Patagonian forests than in boreal forests, and litter decomposition is controlled by nutrients rather than by temperature (Vivanco and Austin, 2019). Whilst networks have often been detected between distantly related species (for example orchids and trees), Patagonian forests are dominated by one or two Nothofagaceae that are possibly able to share fungi (Nouhra et al., 2013). As observed for alders, closely-related species may exclude each other, and the question remains whether CMN can occur in Nothofagaceae forests or more generally in southern temperate forests. Beyond the interest of studying CMN in these remote forests, there is a real need to understand and promote forest resilience (Thompson et al., 2009), especially in forests where regeneration failure has recently been observed, for example at the ecotone between *Araucaria* and *Nothofagus* forests (Zamorano-Elgueta et al., 2012; Cóbar-Carranza et al., 2014), and more generally in South American forests, which face both climate change and intense deforestation.

Following my previous results on EMF diversity, I would not expect CMN in neotropical forests, but a positive relationship between EMF diversity and functional diversity. In Southern temperate forest, CMN are theoretically possible (due to low specificity, Nouhra et al., 2013), but on the contrary functional diversity is relatively stable along an elevation gradient (Truong et al., 2019). I would expect CMN, but not necessarily favored by EMF diversity or functional diversity. Finally, in northern temperate or boreal forests, CMN have been detected, but the relationship with EMF diversity has not been investigated. I would expect a positive effect of temporal continuity (and ancient forests) on both functional diversity and CMN functioning (Fig 34). Testing those hypotheses would require a long-term and large-scale project, but through the CERES project, my collaborations at UQAT and now in Argentina, I am gathering colleagues to answer such questions with the methods developed in my previous projects (Fig 35, 36). The use of NGS will be essential to estimate EMF diversity, but networks will be described from root sampling, and eventually compared with networks drawn from co-occurrence data. The results of such a project would be a base for a more theoretical framework on mycorrhizal networks, and the links between ecological networks and CMN. Such a framework is clearly missing (Bahram et al., 2014) and will be useful even for forest managers and modelers interested in ecosystem resilience (Thompson et al., 2009).

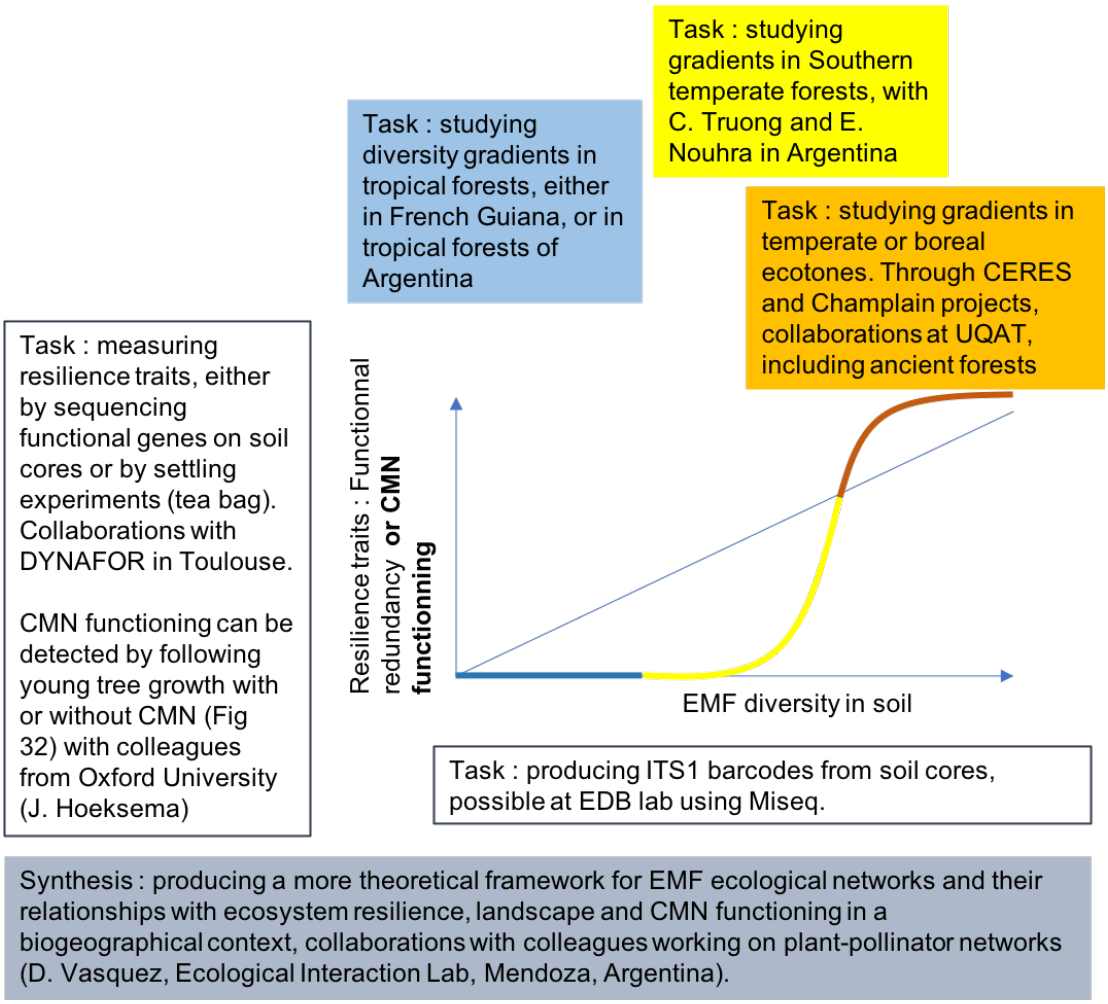


Figure 35: Scheme representing the different tasks and experiments to test hypotheses of Fig 34, and on-going and future collaborations with colleagues interested in such questions.

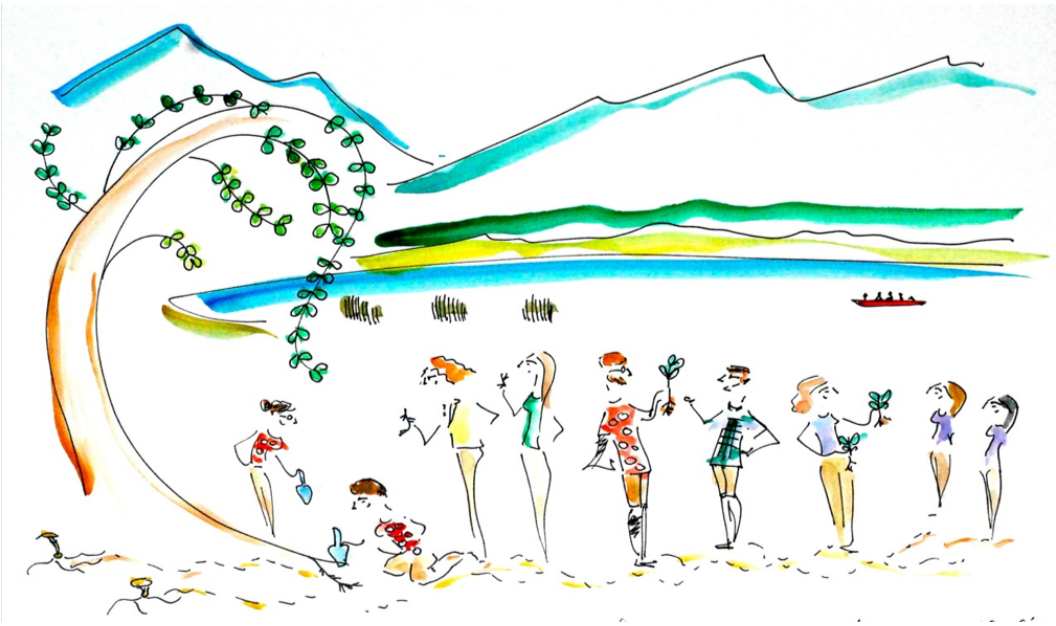


*Figure 36: An illustration of the dynamic network of colleagues and students interested in EMF in South America, sketched in Florianopolis (**Roy et al., 2017**) by Mélanie Roy.*

A parallel with mycorrhizal fungi and vineyards history: a project with students?

Resilience can also be measured with a diachronic approach, but for forest, ecosystem age is difficult to estimate, especially in ancient forests. In the vineyards, vintners usually have kept records of plantations, treatments, and especially transition to organic production. Today, a producer must wait three years before being certified as organic, but we have no idea about the time necessary for mycorrhizal fungi to recover from non-organic treatments. Changes are rapidly observed for soil properties, earthworms and bacteria (Costantini et al.,2015) but fungi were not targeted, while mycorrhizal fungi interest vintners more and more. Numerous studies have highlighted that organic vineyards host more plant and even mycorrhizal diversity (Bruggisser et al., 2010 ; Schmid et al., 2011 ; Nascimbene et al., 2012 ; 2013). My hypotheses on CMN and ecosystem resilience could also apply to vineyards, and in the future, with students (through my teaching on landscape ecology of vineyards), colleagues interested in landscape and wine (Sophie Caillon and Antoine Brin) and vintners, I will try to develop a project to study mycorrhizal diversity and more generally fungal functional diversity in vineyard soils, along a temporal continuity gradient (time since transition to organic), represented in Gaillac terroirs and integrating plant diversity (wild plants and grapevine varieties) and landscape heterogeneity.

Conclusions

From the diverse projects and experiences I have developed over the last nine years, I have collected different evidence to better understand the ecology, the evolution and the specialization of EMF-plant interactions. *Alnus*-EMF associations reveal a non-networking strategy, but variations of specialization in isolated populations. The distribution of EMF in the Neotropics confirms their rarity, but reveals favourable environments, notably in low-canopy forests. Their specialization is always extremely high, and probably limits the formation of any mycorrhizal network between trees. In boreal forests, EMF are less specialized, and together with saprophytic fungi, are involved in both positive and negative plant-plant interactions. In temperate forests, integrating the knowledge on ancient forests and soil history contributes to better understand EMF distribution. Finally, working with students in landscape ecology has convinced me to integrate more engaged questions and to collaborate with landscape/forest managers. The future research projects I imagine to build up with colleagues will be intimately linked with ecological networks, and will involve fungi, test the effects of landscape and soil history, include functional traits and field experiments, and finally, will be strongly connected with student projects and landscape managers. Perhaps to better integrate students, and to begin thinking more locally, all those experiences and projects could one day be transposed, not to local EMF, but rather to below-ground networks at a local landscape, the vineyards, where mycorrhizal fungi have only begun to be investigated from an ecological point of view, and could have a key role in the resilience of vineyards faced with faced with climate change.

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Curriculum vitae

Mélanie Roy, 27/10/1981, born in Kuujjuaq, Canada

*Maître de conférence*s since 01/09/2010, at UPS.

Laboratoire Evolution et Diversité Biologique, Equipe Diversification Ecologique et Evolutive des Populations, UPS – CNRS, UMR 5174. 118 route de Narbonne, 31062 Toulouse, France.

University degrees

1999	Baccalauréat, mention Très Bien
1999-2001	Classe préparatoire BCPST, Lycée Montaigne, Bordeaux.
2001-2005	Master of cellular and molecular biology – Ecole Normale Supérieure Lyon (8e/32), élève fonctionnaire)
2004	One year preparation to teaching at ENS Lyon Agrégation de SV-STU (66e).
2004-2005	Master 2 Ressources phytogénétiques et interactions biologiques -University Montpellier 2, mention Très Bien (1ère/11).
2005-2009	PhD in ecology and evolution of mycoheterotrophy by orchids, Centre d'Écologie Fonctionnelle et Évolutive, Montpellier, supervised by M.-A. Selosse. First prize of the French Botanical Society for the PhD (2009).

Professional experiences

2008/2009	ATER (teaching) at University Montpellier 2
2009/2010	Post-doctoral project on functional diversity of ectomycorrhizal fungi in Europe (6 months, INRA Cestas Pierroton).
2010/….	Maître de conférences (Assistant professor) at EDB, UPS
2014	Delegated by the CNRS in UMR EcoFoG for 6 months (Kourou, Guyane).
2017-2019	Associate professor at UQAT, Canada (only expert, no contract)

Teaching and transfer of knowledge

Summary

Since 2010, I teach at UPS but also in Albi University center. My teaching is closely related to my research on symbioses and has opened my research to biogeography and community ecology. I am responsible at UPS of a master 1 option on tropical ecology and co-responsible for the teaching of botany in Albi.

Site	Topic (* responsibility)	Type	Level
UPS	Biodiversité végétale	CM	L1
	Systématique végétale	TP	L3
	Mycologie	TP, TD, Terrain	L3
	Inventaires botaniques	Terrain	L3
	Macro-écologie et biogéographie	CM, TD	M1
	Ecologie évolutive	CM, TD	M1
	Phylogénie et méthodes comparatives	CM, TD	M1
	Biodiversité et vynamique des écosystèmes tropicaux*	CM, TD, TP, Terrain	M1
	Ecologie et Viticulture (Cultures perennes)	CM, TD, Terrain	L3 pro
	Interactions biotiques	CM, TD	M2 (BEE)
Centre Universitaire JFC, Albi	Biologie végétale*	CM, TD, TP	L1
	Biodiversité végétale*	Terrain	L3
IUT (UPS), Auch	Ecologie et viticulture	CM, TD, Terrain	L3 pro

In general, I teach 50% of my time to third-year students, mostly in the field, 40% of my time to master 1 and first year students, and 10% to Master 2 students. I usually do more than the requested amount of hours, and I am trying to reduce these extra hours.

Innovative teachings

Urban ecology through botany courses

In Albi and Toulouse, my third-year students learn botany, through practical courses and field trips. Since 2014, I have organized more local field trips, to vineyards, where they encounter vintners interested in plant diversity and uses, and in streets of Toulouse, Gaillac and Albi. My objective is to favor every-day observation of plants and to make students play with botany, through the use of **applications** such as PlantNet. Students produce an inventory of plants of their own street, and are evaluated on the basis of this document. They also report their data on **participative projects** such as *sauvage de ma rue*. Students are really invested in these inventories and colleagues at UPS have begun to be interested in urban ecology.

Cheese observations through mycology

Teaching microbiology is often restricted to the lab, while we encounter microorganisms every day in our food. In mycology, we give three practical courses on micro-organisms and since 2014, one of them is dedicated to the diversity of micro-organisms on cheese crusts. Introducing food as a topic is also a way to increase student enthusiasm and motivation.

Approaching the field in tropical ecology

In 2016, I became responsible for a course on the biodiversity of tropical ecosystems. However, teaching this topic to students who have never been to the tropics seems surrealistic. Since 2016, we teach three times in Toulouse Natural History museum, where they are greenhouses and tropical plants and collections, and go for one day to Pierre Fabre greenhouse and to the wood museum in Revel. During each visit, we meet colleagues who work in the tropics, such as botanists and forest managers. I always try to invite colleagues to talk to the students in this course, as they are interested in job opportunities in national park or reserves, and contacts could be useful for them later.

Introducing landscape in vineyard ecology

Since 2017, I have taught ecology to third-year students who have chosen a more professional career. I have created a course around the changing ecology of vineyard and teach the students to have a scientific point of view on vineyard adaptation to climate change. I try to give them a broader view on pathogenic fungi and their evolution, and consider the evolutionary ecology of grapevine. Those teachings are unique, as I focus not only on the vine but also the environment. I organize a three-day field trip to encounter vintners, and researchers on wine production and environment from the Institut de la Vigne et du Vin (IFV).

International courses

Abroad, I have been often invited to teach on ectomycorrhizae, especially in the neotropics. These courses are particularly important for training students in taxonomy to observe ectomycorrhizae, as this expertise is rare.

2014 In the Amazon, along the Rio Negro, I gave a one-month field trip on white sands, to students from Peru, Brazil, and USA (Supported by Trebediv project, IRD) with colleagues from INPA (Manaus) and Santa Catarina University (Florianopolis).

2015 Labex TULIP summer School, 13-17/07/2015, in the Pyrénées. Courses on ecological and mycorrhizal networks to international graduate and PhD students.

2016 During the Brazilian Mycology Congress in Florianopolis, I gave a three days course for students of Santa Catarina University. We collected ectomycorrhizae, observed them and discussed with international experts.

2019 In Buenos Aires, I have already given two courses, from the field to the lab, to observe and discuss the ecology of ectomycorrhizae, at Faculty of agronomy and Faculty of sciences of Buenos Aires University. Those one-day courses are short, but completely new to students.

Research activities : publication list and strategy

Summary and strategy

Since my PhD, I have published 38 peer-reviewed articles, two book chapters and eight articles in Society journals in French and English. Including my PhD, my h-factor reaches now 17.

Category	IF	Number (first author)
Peer-reviewed journals	IF>1	32 (8)
	IF<1	3
Society Journals/ Vulgarization journals	No IF	8 (5)
Book Chapters	In English	1
	In French	1 (1)

I still have not published as a last author, but I have submitted manuscripts as a last author twice this year (Gazal et al. and Schimann et al.). Even when I was PI of the grant that gave rise to the publication, I have let the last position to taxonomists, who trained me in mycology. There were a few conflicts about the last position, but I have always let that place, being the youngest on most projects. Beginning a few years ago, I let the first position to students, as they are more and more willing to write, and I keep the second position. The last position in that case remains for colleagues who co-supervised the students with me.

As I am convinced we have to work with taxonomists to know and preserve biodiversity, I have helped a lot of colleagues describe their specimens and publish articles in society journals. I recognize I should write more “big” papers on my data on French Guiana, and this is one of my objectives. However, “big” papers in taxonomy rely on species description, which are more likely to be accepted by specialized journals.

Finally, I continue to write for, and give conferences to a broad audience, in French. These publications are rarely recognized, but are useful locally, even for my students, who realize how interesting their research topic can be.

Peer-reviewed journals

1. **Roy M**, Dubois M-P, Proffit M, Vincenot L, Desmarais E, Selosse M-A. 2008. Evidence from population genetics that the ectomycorrhizal basidiomycete *Laccaria amethystina* is an actual multihost symbiont. *Molecular Ecology* 17: 2825–2838.

2. Pedersen HA, Watthana S, **Roy M**, Suddee S, Selosse M-A. 2009. *Cephalanthera exigua* rediscovered: new insights in the taxonomy, habitat requirements and breeding system of a rare mycoheterotrophic orchid. *Nordic Journal of Botany* 27: 460–468.

3. **Roy M**, Watthana S, Stier A, Richard F, Vessabutr S, Selosse M-A. 2009. Two mycoheterotrophic orchids from Thailand tropical dipterocarpacean forests associate with a broad diversity of ectomycorrhizal fungi. *BMC Biology* 7: 51.

4. **Roy M**, Yagame T, Yamato M, Iwase K, Heinz C, Faccio A, Bonfante P, Selosse M-A. 2009. Ectomycorrhizal Inocybe species associate with the mycoheterotrophic orchid *Epipogium aphyllum* but not its asexual propagules. *Annals of Botany* 104: 595–610.

5. Selosse M-A, **Roy M**. 2009. Green plants that feed on fungi: facts and questions about mixotrophy. *Trends in Plant Science* 14: 64–70.

6. Selosse, M. -A., Martos F., Perry B., Maj P., **Roy M.**, et Pailler, T. 2010. Saprotrophic fungal symbionts in tropical achlorophyllous orchids: Finding treasures among the 'molecular scraps'? *Plant Signaling & Behavior* 5 (4): 349-53.

7. Tranchida-Lombardo, V., **M. Roy**, E. Bugot, G. Santoro, Ü Püttsepp, M. Selosse, et S. Cozzolino. 2010. Spatial repartition and genetic relationship of green and albino individuals in mixed populations of *Cephalanthera* orchids. *Plant Biology* 12 (4): 659-67.

8. Richard, F., **M. Roy**, O. Shahin, C. Sthultz, M. Duchemin, R. Joffre, et M. -A. Selosse. 2011. Ectomycorrhizal communities in a Mediterranean forest ecosystem dominated by *Quercus ilex*: seasonal dynamics and response to drought in the surface organic horizon. *Annals of Forest Science* 68 (1): 57-68.

9. Kohout, P., T. Těšitelová, **M. Roy**, M. Vohník, et J. Jersáková. 2013. A diverse fungal community associated with *Pseudorchis albida* (Orchidaceae) roots. *Fungal Ecology* 6 (1): 50-64.

10. **Roy, M**., C. Gonneau, A. Rocheteau, D. Berveiller, J.-C. Thomas, C. Damesin, et M.-A. Selosse. 2013. Why do mixotrophic plants stay green? A comparison between green and achlorophyllous orchid individuals in situ. *Ecological Monographs* 83 (1): 95-117.

11. **Roy, M.,** J. Rochet, S. Manzi, P. Jargeat, H. Gryta, P. -A. Moreau, et M. Gardes. 2013. What determines *Alnus*-associated ectomycorrhizal community diversity and specificity? A comparison of host and habitat effects at a regional scale. *New Phytologist* 198 (4): 1228-38.

12. Těšitelová, T., J. Jersáková, **M. Roy**, B. Kubátová, J. Těšitel, T. Urfus, P. Trávníček, et J. Suda. 2013. Ploidy-specific symbiotic interactions: divergence of mycorrhizal fungi between cytotypes of the *Gymnadenia conopsea* group (Orchidaceae). *New Phytologist* 199 (4): 1022-33.

13. Gonneau, C., J. Jersáková, E. de Tredern, I. Till-Bottraud, K. Saarinen, M. Sauve, **M. Roy**, T. Hájek, et M. -A. Selosse. 2014. Photosynthesis in perennial mixotrophic *Epipactis* spp.(Orchidaceae) contributes more to shoot and fruit biomass than to hypogeous survival. *Journal of Ecology* 102 (5): 1183-94.

14. Henkel, T. W., A. W. Wilson, M. C. Aime, J. Dierks, J. K. Uehling**, M. Roy**, H. Schimann, F. Wartchow, et G. M. Mueller. 2014. Cantharellaceae of Guyana II: New species of *Craterellus*, new South American distribution records for *Cantharellus guyanensis* and *Craterellus excelsus*, and a key to the Neotropical taxa. *Mycologia* 106 (2): 307-24.

15. Gladieux, P., A. Feurtey, M. E. Hood, A. Snirc, J. Clavel, C. Dutech, **M. Roy**, et T. Giraud. 2015. The population biology of fungal invasions. *Molecular Ecology* 24 (9): 1969-86.

16. Buyck, B., P. -A. Moreau, R. Courtecuisse, A. Kong, **M. Roy**, et V. Hofstetter. 2016. *Cantharellus coccolobae* sp. nov. and *Cantharellus garnieri*, two tropical members of *Cantharellus* subg. *Cinnabarinus*. *Cryptogamie, Mycologie* 37(3): 391-404.

17. **Roy, M**., H. Schimann, R. Braga-Neto, R. AE Da Silva, J. Duque, D. Frame, F. Wartchow, et M. A. Neves. 2016. Diversity and distribution of ectomycorrhizal fungi from Amazonian lowland white-sand forests in Brazil and French Guiana. *Biotropica* 48 (1): 90-100.

18. Shefferson, Ri. P., **M. Roy,** Ü. Püttsepp, et M. -A.Selosse. 2016. Demographic shifts related to mycoheterotrophy and their fitness impacts in two *Cephalanthera* species. *Ecology* 97 (6): 1452-62.

19. Barbosa-Silva, A., C. L. Ovrebo, B. Ortiz-Santana, M. CA Sá, M. A. Sulzbacher, **M. Roy**, et F. Wartchow. 2017. *Tylopilus aquarius*, comb. et stat. nov., and its new variety from Brazil. *Sydowia*. 69: 115-122.

20. Delgat, L. & **Roy M**. *Lactifluus ceraceus* in Crous, Pedro W., Michael J. Wingfield, T. I. Burgess, A. J. Carnegie, GE St J. Hardy, D. Smith, Brett A. Summerell, J. F. Cano-Lira, J. Guarro, et J. Houbraken. 2017. Fungal Planet description sheets: 625–715. *Persoonia*: *Molecular Phylogeny and Evolution of Fungi* 39: 270.

21. De Crop, E., J. Nuytinck, K. Van de Putte, K. Wisitrassameewong, J. Hackel, D. Stubbe, K. D. Hyde, **M. Roy**, R. E. Halling, et P.-A. Moreau. 2017. A multi-gene phylogeny of *Lactifluus* (Basidiomycota, Russulales) translated into a new infrageneric classification of the genus. *Persoonia: Molecular Phylogeny and Evolution of Fungi* 38: 58.

22. Gryta, H., C. Van de Paer, S. Manzi, H. Holota, **M. Roy**, et G. Besnard. 2017. Genome skimming and plastid microsatellite profiling of alder trees (*Alnus* spp., Betulaceae): phylogenetic and phylogeographical prospects. *Tree Genetics & Genomes* 13 (6): 118.

23. **Roy, M.,** A. C. Pozzi, R. Gareil, M. Nagati, S. Manzi, I. Nouioui, N. Sharikadze, P. Jargeat, H. Gryta, et P. -A. Moreau. 2017. Alder and the Golden Fleece: high diversity of Frankia and ectomycorrhizal fungi revealed from *Alnus glutinosa* subsp. *barbata* roots close to a Tertiary and glacial refugium. *PeerJ* 5: e3479.

24. **Roy, M.,** A. Vasco-Palacios, J. Geml, B. Buyck, L. Delgat, A. Giachini, T. Grebenc, E. Harrower, F. Kuhar, et A. Magnago. 2017. The (re) discovery of ectomycorrhizal symbioses in Neotropical ecosystems sketched in Florianópolis. *New Phytologist* 214 (3): 920-23.

25. Schwob, G., **M. Roy**, S. Manzi, T. Pommier, et M. P. Fernandez. 2017. Green alder (*Alnus viridis*) encroachment shapes microbial communities in subalpine soils and impacts its bacterial or fungal symbionts differently. *Environmental Microbiology* 19 (8): 3235-50.

26. Gruhn, G., S. Dumez, P. -A. Moreau, **M. Roy**, Or. Morreale, H. Schimann, et R. Courtecuisse. 2018. The genus *Resinicium* in French Guiana and the West Indies: a Morphological and Molecular Survey, Revealing *Resinicium grandisporum* sp. nov. *Cryptogamie, Mycologie*. 38(4) : 469-484.

27. Hoeksema, J. D., **M. Roy,** G. Łaska, A. Sienkiewicz, A. Horning, M. J. Abbott, C. Tran, et J. Mattox. 2018. *Pulsatilla patens* (Ranunculaceae), a perennial herb, is ectomycorrhizal in northeastern Poland and likely shares ectomycorrhizal fungi with *Pinus sylvestris*. *Acta Societatis Botanicorum Poloniae.* 2018. 87(1):3572.

28. Lagarde, A., P. Jargeat, M. Roy, M. Girardot, C. Imbert, M. Millot, et L. Mambu. 2018. Fungal communities associated with *Evernia prunastri, Ramalina fastigiata* and *Pleurosticta acetabulum*: Three epiphytic lichens potentially active against *Candida* biofilms. *Microbiological Research* 211: 1-12.

29. Nagati, M., **M. Roy**, S. Manzi, F. Richard, A. Desrochers, M. Gardes, et Y. Bergeron. 2018. Impact of local forest composition on soil fungal communities in a mixed boreal forest. *Plant and Soil*, 432(1-2): 345-357.

30. Pozzi, A. C., **M. Roy**, M. Nagati, G. Schwob, S. Manzi, M. Gardes, P. -A. Moreau, et M. P. Fernandez. 2018. Patterns of diversity, endemism and specialization in the root symbiont communities of alder species on the island of Corsica. *New Phytologist* 219(1): 336-349.

31. Schwob, G., M. Roy, C. A. Pozzi, A. Herrera-Belaroussi, et M. P. Fernandez. 2018. In planta sporulation of Frankia as a determinant of alder-symbionts interactions. *Applied and Environmental Microbiology*. 01737-18.

32. Seynabou S., M.-A. Selosse, M. Forget, J. Lambourdière, K. Cissé, A. G. Diédhiou, E. Rivera-Ocasio, H. Kodja, N. Kameyama, K. Nara, L. Vincenot, J.-L. Mansot, J. Weber, **M. Roy**, S. N. Sylla, A. Bâ. 2018. A

pantropically introduced tree is followed by specific ectomycorrhizal symbionts due to pseudo-vertical transmission. *The International Society for Microbial Ecology Journal*.12: 1806–1816

33. Shefferson, R. P., T. Kull, M. J. Hutchings, M.-A. Selosse, H. Jacquemyn, K. M. Kellett, E. S. Menges, R. B. Primack, J. Tuomi, K. Alahuhta, S. Hurskainen, H. M Alexander, D. S Anderson, R. Brys, E. Brzosko, S. Dostálik, K. Gregg, Z. Ipser, A. Jäkäläniemi, J. Jersáková, W D. Kettle, M. K McCormick, A. Mendoza, M. T Miller, A. Moen, D.-I. Øien, Ü. Püttsepp, **M. Roy**, N. Sather, N. Sletvold, Z. Štípková, K. Tali, R. J Warren, D. F Whigham. 2018. Drivers of vegetative dormancy across herbaceous perennial plant species. *Ecology Letters* 21 (5): 724-33.

34. Gruhn, G., P. Alvarado, N. Hallenberg, **M. Roy**, et R. Courtecuisse. 2018. Contribution to the taxonomy of *Sistotremastrum* (Trechisporales, Basidiomycota) and the description of two new species, *S. fibrillosum* and *S. aculeocrepitans*. *Phytotaxa* 379 (1): 27-38.

35. Accioly T., Sousa J.O., Moreau PA, Lecuru C., Silva B D.B, **Roy M.**, Gardes M., Baseia I.G., Martin M.P. 2019. Hidden fungal diversity from the Neotropics: *Geastrum hirsute*, *G. schweinitzii* (Basidiomycota, Geastrales) and their allies. *PLOS ONE* 14(2): e0211388.

36. Vleminckx J., H. Schimann, J. Orivel, **M. Roy**, M. Fichaux, V. Vedel, T. Decaëns, M. Lapier, J. Engel, P. Petronelli, G. Jaouen, C. Baraloto. 2019. Coordinated beta-diversity across five taxonomic groups in Amazonian rainforests. Accepted in Scientific reports

37. Nagati M., **M. Roy**, A. DesRochers, S. Manzi, Y. Bergeron, M. Gardes. 2019. Facilitation of balsam fir by trembling aspen in a boreal forest : does soil fungal communities matters ? accepted in Frontiers in plant science

38. Vanegas León M.-L., M. A. Sulzbacher, A. C. Rinaldi, **M. Roy**, M.-A. Selosse, M.-A. Neves. 2019. Are Trechisporales ectomycorrhizal or root endophytic? Accepted in Mycological Progress.

Society journals

1. Consiglio G, Contu M, **Roy M**, Selosse MA, Vizzini A. 2007. *Rhodocybe praesidentialis* spec. nov. Una nuova specie della sezione *Rhodocybe*. Addendum. *Rivista di Micologia dell'Associazione Micologica Bresadola* 50: 175–178.

2. **Roy, M**. et M. -A. Selosse. 2010. De la graine à l'adulte, de l'individu à l'espèce: des orchidées plus hétérotrophes qu'il n'y paraît? *Cahier de la Société Française d'Orchidophilie* 8: 185-94.

3. Selosse M.-A. et **M. Roy.** 2012. Les plantes qui mangent des champignons. *Dossier Pour La Science* 77.

4. **Roy, M** & Selosse. M. -A. La germination des orchidées, quoi de neuf ? *Revue de la Société Nationale d'Horticulture de France* 622.

5. Kohout, P., T. Malinová, **M. Roy**, M. Vohník, et J. Jersáková. 2013. Mycorrhizal and endophytic fungal communities associated with roots of *Pseudorchis albida* (Orchidaceae). *Lankesteriana International Journal on Orchidology* 13 (1-2): 142.

6. **Roy M,** Tomas W, Gareilh R, Claessens O, Tostain O, Leotard G, Sambin A, Ravet E. 2014. Diversité phylogénétique des orchidées de Guyane Française. *Cahier de la Société Française d'Orchidophilie* 8 : 99-118.

7. **Roy, M.** 2018. La mycohétérotrophie et le jardinier – un conte presque réaliste. *Revue de la Société Nationale d'Horticulture de France* 650.

8. **Roy M.**, V. Troispoux, E. Louisanna et H. Schimann. 2018. Diversité, distribution et écologie des champignons du mont Itoupé. *Les cahiers scientifiques du parc Amazonien de Guyane*, dossier spécial Itoupé 4(1) 59-64.

Book chapters

1. Hynson, N. A., T. P. Madsen, M. -A. Selosse, I. KU Adam, Y. Ogura-Tsujita, **M. Roy**, et Gerhard Gebauer. 2013. The physiological ecology of mycoheterotrophy. In Mycoheterotrophy, 297-342. Springer, New York, NY.

2. **Roy, M**. et Selosse, M. -A. 2015. les réseaux mycorhiziens in Analyse des réseaux sociaux appliquée à l'éthologie et l'écologie. in Sueur et al., Editions materiologiques, Paris.

3. Gazal N., S. Mennicken, S. Manzi, E. Lapied, A. Brin, T. Decaëns, **M. Roy**. Landscape-scale study of soil communities. Accepted Book chapter for *Studies in Historical Ecology*

Submitted manuscripts

Alexandre G. S. Silva-Filhao, L. Delgat, M.C.A. Sa, **M. Roy** & F. Wartchow. *Lactifluus paucipilosus* (Russulaceae, Russulales): a new species of *Lactifluus* subg. *Lactariopsis* from Brazilian semiarid highlands. Submitted to *Peersonia*

Delgat L., R. Courtecuisse, **M. Roy**, E. De Crop & A. Verbeken. *Lactifluus* (*Russulaceae*) in the Lesser Antilles: multi-gene phylogeny and morphological revision reveal high endemic diversity. Submitted to *Peersonia* (minor corrections)

Donald J., **M. Roy**, U. Suescun, A. Iribar, S. Manzi, L. Pelissier, P. Gaucher, J. Chave. A test of community assembly rules using the endophytic microbial communities of a tropical forest canopy. Minor revision, Journal of Ecology

Donald J., M. Barthelemy, N. Gazal, Y. Eveno, S. Manzi, V. Eparvier, D. Stien, **M. Roy**. Co-occurence and competitive activity structure tropical endophyte communites in a rainforest palm. Submitted to Frontiers in Plant Sciences

Jaouen G., C. araloto, B. Buyck, C. Decock, E. Louisanna, S. Manzi, **M. Roy**, A. Sagne, H. Schimann. Fungi of French Guiana: an online dataset to gather taxonomic, environmental and molecular data. Submitted to *Scientific data*

Roy M., A. Taudière, S. Manzi, D. Sincu, P.-A. Moreau, F. Richard, J. D. Hoeksema, M. Gardes. Mycorrhizal interaction networks among species of alders: from global to local patterns, submitted to *Journal of Ecology*

Schimann H., J. Vleminckx, C. Baraloto, J. Engel, G. Jaouen, E. Louisanna, S. Manzi, A. Sagne, **Mélanie Roy**. Tree communities and soil properties shape fungal community assembly in Neotropical forests
Submitted to *New Phytologist*

Submitted Book Chapter

Roy M. et Caillon S.. Rendre visible le sensible par un engagement artistique et scientifique. Portrait de la flore des vignes dans le cadre d'une co-construction lente avec les vigneron.nes de Gaillac. Chapter submitted to Presses Universitaires Grenoble Alpes.

Manuscripts in preparation

Braga-Neto R., F. Wartchow, H. Schimann, **M. Roy**, T. Henkel. Modelling the distribution of ectomycorrhizal fungi in South America

Durrington B., E. Verbruggen, U. Suescun, S. Manzi, J. Chave, M.-A. Selosse, **M. Roy**. Drivers of fungal distribution on tropical tree roots along a phosphorus gradient in French Guiana.

Fernandez L., Hackel J., Mike H., D. Frame, C. Decock and **M. Roy**. Interactions between ectomycorrhizal fungi and their hosts in low canopy forests.

Gazal N., **M. Roy**, S. Fagorold, E. Gomez, S. Manzi, D. Stien, R. Lami. Interactions between fungal and bacterial endophytes in *Posidonia oceanica*. In prep for *Marine Drugs*

Hackel J., P.-A. Moreau, R. Courtecuisse, B. Buyck, T. Henkel, S. L. Miller, E. de Crop, A.-M. Verbeken, M.-A. Neves, M. C. W. Jaeger, J. Duque, F.Wartchow, M. Sà, J.L. Cheype, E. Louisanna, H. Schimann, S. Garnica, G. M. Mueller, V. Hofstetter, S. Manzi, M. Gardes, **M. Roy**. Origins and diversification of Neotropical taxa in a cosmopolitan lineage of ectomycorrhizal fungi (Basidiomycota: Russulaceae). In prep for *Journal of Biogeography*.

Mennicken S., F. Kondratow, S. Manzi, E. Andrieux, **M. Roy**, A. Brin. Fungal diversity in and around ancient forests in Cevennes national Park. In prep for a special issue on landscape ecology in *Frontiers in Plant Science*.

Munoz F., H. Vogt-Schilb, D.Prat, **M. Roy** and B. Schatz. How do ecological strategies of temperate terrestrial orchids change along broad environmental gradients? to be resubmitted.

Ramon A., H. DeDeurwaerder, E. Verbruggen, H. Verbeeck, **M. Roy**. Fungal communities in liana forests from French Guiana.

Roy M., J. Hackel, S. Manzi, E. Louisanna, A. Iribar-Pelozuelo, D. Frame, M. Gardes, T. W. Henkel, C. Decock, P.-A. Moreau, R. Courtecuisse, H. Schimann. Diversity and distribution of ectomycorrhizal fungi in French Guiana. To be resubmitted.

Roy M. and T. Kuyper. Mixotrophy, mixology ? in prep for the *Mycological Society of the Netherlands*

Roy M. and Verbruggen E.. Rare ectomycorrhizal fungi in non-monodominant forests: What do the exceptions tell us? In prep for the *New Phytologist*.

Oral communications at congresses

Since 2010, I have given 15 talks in international conferences, and 6 more were given by my students.

1. F. Richard, M. Duchemin, **M. Roy**, M.-A. Selosse, 2009. Diversity of ectomycorrhizal fungi associated with Quercus ilex: temporal and spatial variability. Atelier de l'ESF sur l'écologie des communautés de champignons ectomycorhiziens, 6-8/12/09, Nancy, France (oral)

2. A. Franc, M. Duchemin, **M. Roy**, E. Legname, C. Plassard, 2009. ECM communities : traits or taxa assembly ? Atelier de l'ESF sur l'écologie des communautés de champignons ectomycorhiziens, 6-8/12/09, Nancy, France (oral)

3. **M. Roy**, J. Rochet, S. Manzi, P. Jargeat, H. Gryta, P. -A. Moreau and M. Gardes. Does host evolution shape alder-associated ectomycorrhizal fungi communities? 2011, Mycological Society of America, 3-8/08/2011, Fairbanks, Alaska, USA (oral).

4. **M. Roy**, J. Rochet, P.Jargeat, H. Gryta, S. Manzi, P.-A. Moreau, M. Gardes, 2012. Coévolution des aulnes et de leurs champignons mycorhiziens : une histoire de couples et de communautés. 07-08/09/2012, congrès MycoFrance, Nancy, France (oral)

5. **M. Roy**, J. Rochet, P.Jargeat, H. Gryta, S. Manzi, P.-A. Moreau, M. Gardes, 2012. Coevolution in *Alnus*-ectomycorrhizal fungi mutualism : from couples to communities. International Society of Symbiosis, 02-08/08/2012, Kracow, Poland (oral).

6. **M. Roy**, M.Nagati, J. Hackel, C. Collongeon, R. Gareillh, L. Graf, S. Manzi, H. Gryta, P. Jargeat, A. Herrera, A. Pozzi, P.-A. Moreau, M. Fernandez, M. Gardes, 2013. Biogéographie d'un mutualisme : les aulnes et leurs champignons ectomycorhiziens. Congrès du REID, 26/09/2013, Paris, France. (oral)

7. **M. Roy**, 2013. Diversity and discovery of Ascomycota and endophytes in French Guiana, Rencontres d'étude des Ascomycota, 01-08/06/2013, Somiedo, Espagne (oral).

8. M. Nagati, W. Thomas, R. Gareilh, O. Claessbesn G. Leotard, A. Sambin, O. Tostain, E. Ravet **M. Roy**, 2014. Diversité phylogénétique des orchidées de Guyane Française. Congrès de la Société Française d'Orchidophilie, 16/04/2014, Blois, France (oral présenté par M. Nagati).

9. **M. Roy**, H. Schimann, R. Braga-Neto, L. Fernandez, J. Hackel, S. Manzi, R. Angelica Elias Da Silva, J. Duque, D. Frame, C. Decock, M. A. Neves. Diversity, distribution and specificity of ectomycorrhizal fungi in the Amazonian lowlands. International Conference on Mycorrhiza, 3-8/08/2015, Flagstaff, Arizona, USA (oral).

10. **M. Roy**, H. Schimann, S. Manzi, A. Sagne, G. Gruhn, C. Lechat, J. Fournier, H. Voiry, S. Welti, C. Decock, P.-A. Moreau, T. Henkel, R. Courtecuisse. 2015. FLAG : Fungi of the Lesser Antillas and French Guiana. Congrès Bibliothèque du Vivant, 24/06/2015, Paris, France (oral)

11. **M. Roy**, H. Schimann, R. Braga-Neto, L. Fernandez, J. Hackel, S. Manzi, R. Angelica Elias Da Silva, J. Duque, D. Frame, C. Decock, M. A. Neves. 2016. Diversity and host-specificity of ectomycorrhizal fungi from inselbergs of French Guiana. VIIIe Congress of Brazilian Mycology. 3-6/10/2016, Florianopolis, Brazil (oral).

12. **M. Roy**, H. Schimann, R. Braga-Neto, L. Fernandez, J. Hackel, S. Manzi, R. Angelica Elias Da Silva, J. Duque, D. Frame, C. Decock, M. A. Neves. 2016. High diversity and high specificity of ectomycorrhizal fungi communities associated with trees from low canopy forests in French Guiana. Association for Tropical Biology and Conservation. 17-21/06/2016, Montpellier, France (oral).

13. **M. Roy**, H. Schimann, R. Braga-Neto, L. Fernandez, J. Hackel, S. Manzi, R. Angelica Elias Da Silva, J. Duque, D. Frame, C. Decock, M. A. Neves. 2016. Diversité et distribution des champignons ectomycorhiziens au Brésil et en Guyane. Journée Jean Chevaugeon, 23-27/01/2016, Aussois, France (oral).

14. Nagati M., S. Manzi, P.-A. Moreau, M. Gardes, **M. Roy.** 2016. Les champignons des aulnes corses sont-ils endémiques ? Journée Jean Chevaugeon, 23-27/01/2016, Aussois, France (oral).

15. **M. Roy** & S. Caillon. 2017. De la scientificité à la une gestion créative multidimensionnelle : échanges de savoirs autours des plantes rencontrées dans le vignoble gaillacois. Colloque d'Anthropologie, University of Lausanne, Switzerland. 13/12/2017 (oral, invited)

16. S. Mennicken, F. Kondratow, **M. Roy**, E. Andrieu, A. Brin. 2017. Influence de la quantité de forêt anciennce dans le paysage sur la diversité et la composition des communautés de champignons. Rencontres d'écologie du Paysage. 23-26/10/2017, Toulouse, France (oral)

17. Nagati M., **M. Roy**, S. Manzi, A. DesrRochers, Y. Bergeron, M. Gardes. Effect of canopy cover and micro-organisms on the establishment of balsam fir in the boreal forest. North European Forest Mycologist Congress, Uppsala, 09/02/2018

18. **M. Roy**, A. Taudière, P. -A. Moreau, F. Richard, J. D. Hoeksema, M. Gardes. 2018. En quoi les changements d'échelles et de mesures peuvent-ils éclairer la spécialisation de l'association aulnes-champignons ectomycorhiziens ? Journées Francophones des mycorhizes, 27-29/06/18. Dunkerque, France (oral)

19. **M. Roy**, A. Taudière, P. -A. Moreau, F. Richard, J. D. Hoeksema, M. Gardes. To network or not ? Variations in host-ECM fungi interactions. 2018. Symposium on ecology of mycorrhiza, Leiden, Netherlands, 29/10/18 (oral, invited)

20. Nagati M., **M. Roy**, S. Manzi, A. DesrRochers, Y. Bergeron, M. Gardes. Effets des micro-organismes sur l'établissement du sapin en forêt boréale. Colloque de la chaire en aménagement forestier durable, Lorrainville, Canada, 30/11/2018.

21. Nagati M., **M. Roy**, S. Manzi, A. DesrRochers, Y. Bergeron, M. Gardes. Les mycorhizes sont-elles impliquées dans l'établissement du sapin en pessière à mousse ? Colloque du centre d'étude sur la forêt, Chicoutimi, Canada, 01-02/05/2019.

Invited conferences in labs

Locally or internationally, I am frequently invited by my colleagues to give talks, and I do enjoy these more private interactions, as compared with international congresses.

1. **M. Roy** , Schimann H., Sagne A. , Moreau P.-A., Welti S., Lechat C., Fournier J., Gruhn G.' Manzi S., Luisana E., Pelozuelo A., Decock C., Henkel T., Courtecuisse R., Gardes M. 2014. Conférence invitée à la Mycothèque de l'Université Catholique de Louvain. 09/10/2014 (oral, invited).

2. **M. Roy** et al. 2015. Ecology and evolution of ectomycorrhizal fungi in the Amazonian lowlands, or how to search for networks in hyper-diverse primary forests. Invited conference at Institute of Applied Sciences, Toulouse, France, 19/09/2015 (oral, invited).

3. **M. Roy** et al. 2015. L'Amazonie, un bon coin à champignons ? Conférence invitée, FRAIB, Toulouse, France. 04/06/15 (oral, invited)

4. **M. Roy**. 2015. Phylogéographie d'un mutualisme : les aulnes et leurs champignons ectomycorhiziens. Invited conference at INRA, Pierroton, 5/03/2015 (oral).

5. **M. Roy**, et al. Des réseaux…partout ? Distribution et écologie des réseaux mycorhiziens. Invited conference at UQAT, Rouyn Noranda, Québec, Canada, 30/08/16 (oral).

6. **M. Roy**, et al. Diversity and distribution of alder and its symbionts: impact of recent migration and climate changes. Invited conference at University of Bialystok, Poland, 13/07/2016 (oral).

7. **M. Roy** et al. From biogeography to ecology of ectomycorrhizal symbioses in the Neotropics, invited conference at Université Lille 1, 14/06/2016 (oral).

8. **M. Roy**. 2017. Metabarcoding specimens, roots and soil to search for ectomycorrhizal fungi in the Neotropics. Invited conference at Viçosa University, Brazil, 22/02/17 (oral)

9. **M. Roy** & H. Schimann. 2018. Diversity and distribution of ectomycorrhizal symbioses in French Guiana and in the Neotropics from the field to the course. Conference at Naturalis institute, Leiden, Netherlands, 16/04/18 (oral, invited)

10. **M. Roy**. 2018. What interaction networks tell us about plant, and fungi ecology. Invited conference at Agronomy Faculty, Buenos Aires, Argentina, 21/12/18 (oral)

11. **M. Roy**. 2018. To network or not ? Distribution and ecology of ecological networks between plant and fungi in the neotropical forests. Invited conference at Ecology Department of Buenos Aires University, Argentina, 18/12/18 (oral)

12. **M. Roy**. 2019. Biogeography of ectomycorrhizal symbioses in the neotropics. Invited conference at Cordoba University, Argentina, 08/02/19 (oral)

13. **M. Roy**. 2019. Are mycorrhizal networks the rule ? digging into ectomycorrhizal fungi ecology in the neotropics. Invited conference Mendoza University, Argentina, 04/02/19 (oral)

14. **M. Roy**, 2019. To network or not ? Distribution and ecology of ecological networks between plant and fungi from the boreal to the neotropical forests. Invited conference at IRBV, Montréal, Canada, 19/06/19 (oral)

Posters

1. **M. Roy**, 2013. What can we learn from albino individuals in orchids? Symposium du New Phytologist, 14-16/05/2013, University of Calabria, Italy (poster).

2. **M. Roy**, J. Hackel, S. Manzi, E. Louisanna, A. Iribar-Pelozuelo, A. Buffard, D. Frame, M. Gardes T. Henkel, C. Decock, P.-A. Moreau, R. Courtecuisse, H. Schimann. 2014. Are Ectomycorrhizal fungi so rare in the Neotropics? Diversity of ectomycorrhizal symbioses in French Guiana. Symposium du New Phytologist, 19-21/05/2014, Zurich, Switzerland (poster).

3. J. Hackel, P.-A. Moreau, R. Courtecuisse, B. Buyck, T. Henkel, S. L. Miller, E. de Crop, A. Verbeken, M.A. Neves, M. C. W. Jaeger, J. Duque, F. Wartchow, M. Sà, J.-L. Cheype, E Louisanna, H. Schimann, S. Garnica, G. M. Mueller, V. Hofstetter, S. Manzi, M. Gardes, **M. Roy**. 2014. Origins and diversification of neotropical taxa in a cosmopolitan lineage of ectomycorrhizal fungi (Basidiomycota: Russulaceae). International Mycology Conference, 3-8/08/2014, Bangkok, Thailand (poster présenté par J. Hackel).

4. Nagati M. M. Roy, S. Manzi, Y. Bergeron, M. Gardes. Communautés fongiques en forêt boréale : ce que le metabarcoding nous révèle. Colloque de Centre d'Etude sur la Forêt, Montréal, 01-02/05/2017.

Conferences for societies

1. **M. Roy**, 2012. Les orchidées des racines truffées de champignons en tout genre. 15e Congrès « Alliances au pays des racines 2012 » de la Société Nationale d'Horticulture de France, 25/05/2012, Paris, France (oral)

2. **M. Roy** and H. Schimann, 2014. Café des sciences dédié aux champignons de Guyane. Organisé à Kourou par l'association Canopée des Sciences.

3. **M. Roy**, 2015. Les orchidées mangeuses de champignons. Muséum d'histoire naturelle de Gaillac.

4. **M. Roy**, 2016. Des champignons voyageurs. Muséum d'histoire naturelle de Gaillac.

5. **M. Roy**. 2017. Les fromages sous la coupe des mycologues. Conférence-dégustation organisée par l' Association Mycologique Toulousaine.

6. **M. Roy**. 2018. Mixotrophy, or how to mix? Annual meeting of the Mycological Society of the Netherlands, Utrecht, Netherlands, 14/04/18 (oral, invited)

Supervising experience

Licence

At UPS, students are not required to undertake a practical internship, but I have supervised four students, who wanted to discover research before the first year of their master.

Thomas Wesley, came once a week to be trained in molecular biology. He produced sequences of orchids from French Guiana and learned how to produce phylogenies for several genera (Roy et al., 2014). He is now a research engeneer in a private company.

Esther Gomez, attended my lecture in Albi University. Since her first year, she wanted to work with me on orchids or fungi, and she made a first internship during her third year, to work on endophytes of *Posidonia oceanica* and their phylogeny. She later worked in master 1 with Didier Stien, and her help in sampling was useful for a master 2 student a few years later. A publication is now in process, and she is included among the authors (Gazal et al., in prep). She is now working in a natural reserve in the Pyrénées.

Quentin Fabregal was a former student in Albi, and also applied for a practical internship in the vineyard. He inventoried plant diversity and his internship really improved the pedagogical material for botany teaching. The year after, he got a "service civique" thanks to his knowledge on plants. He is now in master 1 with me and still works on vineyards and mycorrhizae, and we will now try to publish his results.

Morgan Ada spent 6 months working in mycology during a year off (L3). She was motivated by tropical fungi and their diversity, and she spent three months in Toulouse producing sequences of *Geastrum*, and three months in French Guiana to learn more on these fungi. Her work contributed to collaborations with taxonomists from Brazil (Accioly et al., 2019). She is now in master 1 at UPS.

Master 1

I teach mostly in Master 1 Ecology at UPS, and met numerous and great students. I have always tried to teach them molecular biology and community ecology, to involve them in research discussions, and to encourage them to cooperate with other students, in master 1 or master 2. More recently, I have trained some to analyse environmental sequences or at least, I made them familiar with those techniques.

Jocelyn Soulard was my first student in 2011. He was motivated to work on fungi and to conduct some field work. We sampled around Toulouse and tried to detect shared partner between poplars and alders. These data were useful for a project of my colleagues in EDB, but we did not publish these data. He is still working in ecology and did a PhD in New Zealand.

Adeline Lepape was more interested in phylogenies, and did her stage on Ascomycota phylogeny, to confirm if some alder symbionts are specific. Her stage internship confirmed a low specificity, and was useful for the team's work on alders (**Roy et al., 2013a**).

Raphaël Gareilh, did a master 1 in 2012, and then 6 months as a technician in 2013. We studied alder symbionts in Georgia (Roy et al., 2017) and produced sequences of orchids (Roy et al., 2014). She decided quite quickly to be a technician, and I designed her internship to learn mostly molecular biology and barcoding. She is now a technician in a private lab in Toulouse.

Louis Graf, did a master 1 in 2012 too, and worked on *Alnicola* phylogeny, to position samples from Alaska. He did a brilliant master 1, and revealed several species that should be described by taxonomists. He moved to Korea the year after, as he got directly a PhD position. He still works on algae phylogeny there.

Mélissande Nagati started to work with me in 2013 as a master 1. She worked on alders in Corsica and collaborated with Adrien Pozzi, PhD student in Lyon (**Pozzi et al., 2018**).

Jan Hackel did his stage also in 2013, and worked on fungi associated with alders in Germany. He produced sequences that are now integrated into a larger database (Roy et al., submitted) and began working on fungi phylogeny.

Laura Fernandez was the first student to be trained in next generation sequencing, in 2015. She analysed the sequences isolated from neotropical tree roots in French Guiana, and revealed a high specificity there (**Fernandez et al., in prep**). The data still have to be published but need to be confirmed first. She is now working in environment at SNCF in France.

Mike Hélion did his master 1 in 2017, and wanted to learn more on tropical ecology. He tested tools to identify tropical mycorrhizae and moved to Montpellier to learn more on tropical ecology. He is now searching for a more applied job. His work supported Laura's observations and they will publish together (**Fernandez et al., in prep**).

Nina Gazal joined EDB lab in 2016, and began working on fungi in 2017. She did a brilliant Master 1 on interactions between endophytes, and we are now trying to write a paper on her work (**Gazal et al., in prep**).

Alexandre Ramon was a brilliant student in botany, and began working with me in 2018. He analysed NGS sequences produced from liana roots, and was particularly good at it. He is now in master 2 at EDB and has applied for a PhD position with Antoine Brin and I.

Tristan Lafont-Rapnouil applied for a practical internship in 2019 with Philippe Marchand (UQAT) and me, and has just finished his analyses. He studied how spatial interactions could bring clues for below-ground interactions in the boreal forest. We had the funding to allow him travel and stay in Quebec for two month, and will welcome in Toulouse another master 1 student from UQAT during the next autumn.

Master 2

Thanks to my diverse research projects, I have been able to fund master 2 students nearly every year. I have supervised or co-supervised 7 students, and sometime supervised students both in

M1 and M2. In M2, I try to show my students the different steps of research, from the field, even in French Guiana, to the publication or congresses. I have tried to make them more responsible for their data and experimental choices and to test their own hypotheses.

Cédric Gonneau, co-supervised with Marc-André Selosse, at CEFE, 2010.
He worked on mixotrophic orchids and did field experiments to understand if such orchids could cope with shade by increasing their exchanges with fungi. He wrote an article from his experiments (**Gonneau et al., 2014**) and did a PhD in Nancy later.

Circé Collongeon, full supervision, M2 BEE, UPS, 2013
During her internship, she studied populations of alders in Quebec and in Alaska to understand their biogeography. She was willing to do research again, after a 7-years break, but finally did not pursue research after this experience. Circé is a very passionate person, and she is now in New Caledonia teaching scuba-diving.

Mélissande Nagati, full supervision, M2 BEE, UPS, 2014
Her master 2 was focused on restricted populations of *A. cordata* and *A. maritima*, and she tried to understand the extent to which their specificity was shaped by isolation. She produced sequences, and analyses, and worked later with a PhD student of Lyon (**Pozzi et al., 2018**). The data she produced contributed to a synthesis on alders (**Roy et al., in prep**). She had the opportunity to present data to a first congress (French Orchid Society) and I have included her in a paper on orchid phylogeny (**Roy et al., 2014**).

Jan Hackel, full supervison, M2 BEE, UPS, 2014
Jan also wanted to follow in Master 2. During the summer 2013, I involved him in the field in French Guiana, to collect mycorrhizae of neotropical trees around inselbergs. We observed and collected several Russulaceae, and decided to focus his master 2 on Russulaceae biogeography. He did a great job, and we realised we could not finish without collaborations, as Russulaceae represent an extremely diverse and widespread family, even in the neotropics. He is now preparing a paper, including new sequences produced, and has already contributed to a paper with colleagues from Gant herbarium (**De Crop et al., 2017**).

Sophie Mennicken, full supersion, M2 EA, ENSAT, 2017
Sophie was extremely motivated to work in French Guiana, on fungal communities of ancient occupied sites, but she had to face a major strike in French Guiana and could not access the sites. After one month waiting, I decided to change her topic and we began a sampling in landscape ecology with Antoine Brin, in Cevennes National Park. She did the sampling, the sequencing, the analysis, in five months and produced a brilliant manuscript. Her results were very important for A. Brin's PhD student, and we are now working on a common publication (**Mennicken et al., in prep**). She is now working on orchids in a PhD study, in Czech Republic.

Nina Gazal, co-supervision with Antoine Brin (50%), M2 BV, UPS, 2018
The master 1 of Nina was very promising, and we managed to go to French Guiana together. Her Master 2 aimed at testing, if sites occupied in the past were richer in ectomycorrhizal fungi, in the pristine forest of French Guiana. She did the fieldwork, the molecular biology and the analyses, and produced a very solid work. We have already submitted her results (**Gazal et al.,**

submitted) and her results are followed by other colleagues in French Guiana. She has recently got a PhD position.

Benjamin Durrington, co-supervision with Marc-André Selosse (25%, MNHN), and Erik Verbruggen (25%, Antwerp University), M2 Erasmus Mundus, 2018
Benjamin is American, studied in England, Belgium, France and Australia, and contacted me to work on tropical mycorrhizae. He studied the specificity of neotropical mycorrhizae along a phosphorus gradient. Erik Verbruggen did the field work and I supervised Benjamin's analyses and molecular biology. We are now working on a paper together (**Durrington et al., in prep**). Benjamin is now in Miami and would like to get a more practical job in botany.

PhD

Rapidly after my recruitment, and thanks to colleagues in other labs, I had the opportunity to work with PhD students, for example A. Pozzi and G. Schwob in Lyon and A. Sagne in EDB and EcoFoG. For A. Sagne, I was really invested, and worked with her during her stay in Toulouse and my CNRS delegation in French Guiana. The first student I officially co-supervised decided to stop his PhD and return to a job in pharmacy. It was difficult to admit but he had a different professional and personal goal. I have always tried to support him, even after he stopped his PhD. More recently, I co-supervised Mélissande Nagati's PhD. I was perhaps more conscious of the difficulties a student could face during a PhD, and so were my colleagues. Mélissande defended on 27th of august 2019.

Yannick Eveno, Grant from labex CEBA, 2014-2016, supervised by Didier Stien (Director, CNRS Banyuls, 50%) and I ("co-encadrante", 50%). MNHN.

Bio- and chimiodiversity of endophytic communities

Yannick decided to begin a PhD after his pharmacy studies, he was highly motivated by the field and the lab. His PhD was in between ecology and chemistry, and he intended to relate micro-organisms' activity with their interactions, detected from community analyses and NGS. He produced 400 strains of endophytes, and invested most of his time in lab experiments. I helped him mostly for the NGS analyses, and we had regular contacts either by Skype or by meeting for "analyses weeks", as he was mainly based in Gif-sur-Yvette. During the second PhD committee, he announced he wanted to stop his PhD, he had other ambitions, and wanted to go back to pharmacy. We did not at all expect this decision, but indeed, writing was particularly difficult. He stopped his PhD three months later, and was very positive about his decision. He rapidly searched for a more applied job. He is now employed by a private company in pharmacy in Lille. I am now trying with Julian Donald, in post-doc, to publish part of his data, and he will be involved as a co-author (**Donald et al., submitted**).

Mélissande Nagati, Grant MITAC from Quebec Region, "Co-tutelle" between UQAT and UPS, supervised by Yves Bergeron ("Directeur", 25%, UQAT) and Monique Gardes ("Co-directrice", 25%, UPS), Annie DesRochers ("Co-encadrante", 25%, UQAT) and me ("Co-encadrante", 25%, UPS). Mélissande is enrolled in UQAT and UPS.

Canopy and micro-organisms effect on fir establishment in the boreal forest

After her M1 and M2 with me, Mélissande wanted to pursue a PhD on fungal ecology. The year before, with Monique Gardes, we had stimulating discussions with Yves Bergeron, who suspected that fungi were implied in fir regeneration in the boreal forest. He funded a year of salary for Mélissande, so that she could apply for a grant in Québec. During that year, we applied for a MITAC grant and got a 4-year position for Mélissande. She began at the end of 2015 and will finish in August 2019 (28/08/19).

Her PhD focused on the role of fungi in fir regeneration in the boreal forest. She spent the first year in Quebec describing the ecosystem and fungal diversity in the boreal forest, learning NGS analyses in Toulouse, and revealed a huge diversity on her sites (**Nagati et al., 2018**). The second year, she followed the growth and survival of young firs in the boreal forest, and launched glasshouse experiments on fir germination, on different boreal soils. The third year, she collected the roots of young firs, and showed that tree growth was not related to fungal diversity, but rather to the identity of the dominant tree (**Nagati et al., 2019**). The fourth year, she collected the samples from her glasshouse experiment, and wrote her PhD (deposited on the 16th of May, 2019) and a third article on fir germination and soil effect (**Nagati et al., in prep**).

As a "co-encadrante", I have been really invested in Mélissande's PhD, and searched for funding to allow her to travel and attend congresses and workshops (in Canada, France, Sweden) and achieve her experiments. Mélissande is really autonomous, and enjoyed being abroad, but we managed to keep a regular contact, with stimulating discussions, throughout these four years. We often organized skype meetings with Monique Gardes, and exchanged papers and manuscripts. She has spent 18 months in Toulouse, and I have been to Quebec for the field, and later for discussions. She is now applying for a Post-doctoral contract in Quebec, on fungi, and is still motivated by research.

She is also invested in vulgarization and won a prize for "mon projet nordique" (2017, Institut Nordique de Quebec). Thanks to this prize, she was invited in Iceland, to the Arctic Circle Assembly (October 2017). She also presented her work in a radio program in Quebec ("Chronique Forêt : Réseautage sous la surface du sol", Radio Canada, 14/08/18) and published an article in French (Nagati M. 2017, Les champignons des sols forestiers : des alliés invisibles. Progrès, *Forestier* N°222).

Post-doctoral contracts

Julian Donald, one year post-doc on SECIL ANR Grant, 2018

Julian applied for a post-doc position with Jérôme Chave and me, on fungal endophytes. He came to learn NGS techniques and analyses, and after one year submitted two papers. He is now in EDB lab for a second post-doc, has kept his interest for endophytes and has presented his results in congresses (British Ecological Society congress, Association for Tropical Biology and Conservation congress). As his PhD was also on tropical ecosystems, I have involved him in my tropical ecology course. He enjoyed teaching, and students really enjoyed his field experience.

Councils and committees

PhD committee

Felix Lallemand, supervised by Marc-André Selosse, MNHN (2015-2018)
Felix did his PhD on “Evolution des interactions mycorhiziennes et de la mycohétérotrophie chez les orchidées “ . He focused on orchid mixotrophy, and worked on albino metabolism and genetic. He is now a post-doc and develops his own activity in a “think tank”.

Jury

Every year, I contribute to evaluate master 1 and 2 students, for masters “Biologie Végétale” and “Ecologie”, Master 2 “Ecologie et Anthropisation” and “Biodiversité Ecologie et Evolution” at UPS (from 2 to 4 students to evaluate).

PhD

Tristan Cordier, examiner for his PhD, “Structure des assemblages fongiques de la phyllosphère des arbres forestiers et effet potentiel du changement climatique”, supervised by Marie-Laure Desprez-Loustau, Cécile Robin and Corinne Vacher, University of Bordeaux 1 (2014).

Anne Houlès, “rapporteur” for her PhD, “Principe de facilitation appliqué à la restauration écologique de sites miniers dégradés : suivi des communautés ectomycorhiziennes au cours de successions végétales assistée par *Acacia spirorbis*“, supervised by Marc Ducousso and Philippe Jourand, University of Montpellier (2017).

Sofia Gomes, examiner for her PhD, "ecology, taxonomy and biogeography of mycoheterotrophic plants”, supervised by N. Soudzilovskaia, University of Leiden and Naturalis Institute (2018).

HDR

A. Diedhiou, “rapporteur” for his HDR, “Diversité et rôles des champignons mycorhiziens dans les écosystèmes forestiers et agricoles”, University of Montpellier (2017).
N.B : to evaluate A. Diedhiou HDR, I got a special authorization from the DRED (University of Montpellier)

Councils and evaluations

Councils
Member of Labex TULIP Pedagogical council since 2016.
Member of the scientific council of French Phytopathology and Mycology Society since 2016.
Co-responsible of the ATER commission for Biogéoscience Department (UPS) since 2018.

Evaluations

France	Involved in PRAG recruitment for Albi University center. project evaluation for the ANR (1)
Belgium	project evaluation for the Research council of University of Leuven (2)
Canada	CV and project evaluation for the Natural and Engineering Research Council of Canada

Reviewing activities

Member of *Mycorrhiza* editorial board.

Since 2010, I have reviewed 72 papers, and I regularly review papers for the *New Phytologist* (20), *Molecular Ecology* (11), *Mycorrhiza* (10), *Fungal Ecology* (6), *Frontiers in Plant Science* (3), *Symbiosis* (3), *Biotropica* (2), *Annals of Botany* (2), *Plos One* (2), *Forest Ecology* (1), *Trends in Ecology and Evolution* (1), *the Botanical Review* (1), *Ecology Letters* (1), *Proceedings of the Royal Society* (1), *Vertigo* (1), *Canadian Journal of Forest Research* (1), *FEMS Microbiology* (1), *Genetica* (1), *Planta* (1), *BMC Genomics* (1), *Diversity and Distributions* (1), *Journal of Ecology* (1).

International exchanges and scientific animation

Visiting students

Through my different projects, students from other labs have often been involved. I have welcomed them to be trained in NGS, discuss fungi ecology, and exchange with local colleagues and students. To facilitate these exchanges, I am also **associate professor at UQAT** since 2016. In Argentina, we have begun a convention between UPS and Buenos Aires University, to facilitate student exchanges and collaborations.

Tamara Malinova-Tesitelova, University of Ceske Budejovice, Czech Republic, supervised by Janza Jerza, 1 month (2013).
Tamara came to EDB lab during the end of her PhD, to write common papers on orchid mycorrhizae. Reciprocally, I was invited for one month in her university in 2012. We managed to publish three papers together thanks to these exchanges (**Kohout et al., 2013a ; 2013b ; Tesitelova et al., 2013**).

Mariana Sà, University of João Pessoa, Brazil, supervised by Felipe Wartchow, 10 months (2014-2015).

Mariana wanted to learn molecular biology before starting a PhD. She was interested in ectomycorrhizal fungi, especially Russulaceae. She applied for a Brazilian Grant ("Sandwich") and stayed for 10 months in Toulouse in 2014. She was trained in molecular biology on herbarium specimens, compared her results with phylogenies and taxonomy and visited European herbaria to compare specimens (Lille, Paris, Gant) and meet colleagues in taxonomy.

Her work allowed the description of a new species of *Tylopilus* (**Barbosa-Silva et al., 2017**), and she worked with Jan Hackel during his M2.

Claudèle Ghotsamekontchou, UQAT, PhD supervised by Yves Bergeron, 1 month (2018).

Claudèle came for one month to learn NGS techniques, and study ectomycorrhizal fungi diversity on aspen roots in the boreal forest. He rapidly became autonomous and is now using NGS for his analyses. Mélissande Nagati is working with him at UQAT and we hope the synthesis will produce a final article for both of them.

Supun Madhumadhawa Pawuluwage, UQAT, Master 1, supervised by Philippe Marchand, 3 months (2019).

Supun will come in autumn 2019. He is now working with Tristan Lafont Rapnouil and will test if positive spatial interactions could be explained by shared mycorrhizal fungi. He will learn NGS analyses and molecular biology in EDB lab. His stay is funded by the French Consulat in Québec.

Visiting scientists

During two years (2011-2013), I was co-responsible of external seminars in the lab and I invited mainly colleagues from Montpellier, but also taxonomists, such as **Cony Decock** (Mycothèque de Louvain) and **Terry Henkel** (Humboldt State University, California, USA). I am still really invested in international exchanges and regularly invite and welcome colleagues from France and abroad.

Thanks to the Labex TULIP, I managed to get grants and invite two colleagues to discuss future projects, exchange with colleagues at EDB, and teach in M2 BEE.

Jason D. Hoeksema, University of Mississippi, USA, three weeks (2016).
Jason is an expert on plant-fungi coevolution and he invited me in spring 2016 for a two-weeks course on coevoluton. We used his stay at EDB to work on alder-fungi coevolution and submitted a first paper on this topic (**Roy et al. submitted**). We also handled experiments together in Poland, and published a paper on the unusual ectomycorrhizae of a forest-dwelling herb, *Pulsatilla patens* (**Hoeksema et al., 2018**).

Diego Vasquez, CONICET, Mendoza, Argentina, two weeks (2019).
During my stay in Argentina, I met Diego to discuss and compare mycorrhizal networks with his background on ecological networks. We decided to apply for a visiting scientist grant, and we plan several meetings, in Argentina and France, to think about this comparison and develop a project in Argentina.

Invited visits

Reciprocally, I have been invited for several invited conferences in labs (see section invited conferences) but also for stays abroad. From the UPS, I received a mobility grant to sample in **Alaska** (2011, 2500^{E}) and in **Canada** (2016, 2500^{E}).

Ceske Budejovice University, collaboration with Jana Jerza, one month (2012)
During this stay, I brought my expertise on fungi and we sampled orchid roots in diverse habitats in Czech Republic. I also collected alder-fungi in old growth forests in South Moravia. This stay, together with the visit of Tamara Malinova, allowed us to write three articles (**Kohout et al., 2013a ; 2013b ; Tesitelova et al., 2013**).

Smithsonian South Field Station, collaboration with Jason D. Hoeksema, two weeks (2016).
Teaching in Arizona, with Judith Bronstein, was a revolution for me, and my pedagogy. I was responsible for botany and geology teaching, and discussed coevolution with Judith and the students, through their short projects and articles. With Jason D. Hoeksema, we still collaborate, and we have recently deposited a project for a **summer school in 2020, in Brazil (Campinas), funded by the *New Phytologist***.

Viçosa University, collaboration with Marc-André Selosse, two weeks (2017).
Marc-André Selosse had a sabbatical in Viçosa University, and welcomed me with Melissa Bocayuva to join the field work, and teach on fungi. This stay was a good opportunity to discuss about endophytic fungi and discover Viçosa state, from a biogeographical point of view.

Organization of congresses and symposia

Congrès de Mycologie et Phytopathologie (Journée Jean Cheveaugeon), 25-29/01/2016, Aussois, France. co-responsible for the Taxonomy and Ecology symposium with Marc-André Selosse.

Association for Tropical Biology and Conservation, 20-24/06/2016, Montpellier, France. co-responsible for the tropical interactions symposium with K. McGuire.

Brazilian Mycological Congress, 05-09/09/2016, Florianopolis, Brazil. Co-responsible for tropical ectomycorrhiza symposium with M.-A. Neves and A. Vasco-Palacios.

Congrès de Mycologie et Phytopathologie (Journée Jean Cheveaugeon), 22-26/01/2018, Aussois, France. Co-responsible of the congress with E. Gaulin and S. Raffaele.

International Mycology Congress, 16-21/07/2018, Panama. Co-responsible for a symposium on tropical ectomycorrhizae, with M.-A. Neves and A. Vasco-Palacios.

Salon vins et fromages de l'UPS, 14/03/2019, Toulouse, France. Responsible for invited conferences on vineyard landscapes in a changing world.

New Phytologist symposium on plant-fungi co-invasion, 20-22/06/2020, Campinas, Brazil. Involved in courses for students during this workshop.

Funded research projects

List of projects

Following my recruitment in 2010, I immediately began searching for research grants, in France and abroad, with colleagues on plant-fungi interactions and mycology. I managed to receive in total **574,342**[E] at EDB (**141,861**[E] as a PI). I was PI on my first projects and rapidly joined larger groups of colleagues and became a co-Pi. I am often responsible for tasks in larger projects, or give a hand, for example for the fieldwork in other projects, such as ANR METABAR and GLOBNET. I am now trying to get a CRCT to be able to manage a larger project on network biogeography and resilience, and launch more experimental projects.

ORCHID: Phylogenetic diversity of orchids in French Guiana
Société Botanique de France/Société française d'Orchidophilie
PI : **M. Roy** (50%)
2011-2012
3,200[E]

As orchids rarely produce flowers, botanists have been interested by the use of barcodes to identify orchids. In this project, I sequenced 382 specimens of orchids from French Guiana, including reference specimens. We published the sequences and a synthetic paper (**Roy et al., 2014**), showing how diverse are orchids in French Guiana, especially *Vanilla*. I did not submit more projects on orchids as it became a very sensitive project in French Guiana and their sampling was more and more limited.

REFUNG: Fungal diversity in Glacial Refugia
EC2CO - Microbien
PI: **M. Roy** (50%)
2012-2015
59,711[E]

This project aimed at studying alder symbionts (bacteria and fungi) in glacial refugia. I organized the fieldwork, in the Caucasus, the Carpathian mountains, Czech Republic, Germany, Corsica, Poland and Italy, and involved colleagues from all these countries. I supervised the molecular biology and students in master 1 on this topic. This project completed a sampling in France on fungi (**Roy et al., 2013a**). Thanks to the sampling of bacteria, I worked with a PhD student, A. Pozzi (UCBL, in Lyon) to analyze the patterns for both symbionts (**Roy et al., 2017 ; Pozzi et al., 2018**). I also collected leaves, and H. Gryta and G. Besnard analyzed the plant diversity in Europe (**Gryta et al., 2017**).

FUNGUY: Diversity of fungi from French Guiana
Projet annuel LABEX CEBA
PI : **M. Roy** (30%) and H. Schimann (EcoFoG, Kourou, Guyane Française)
2012
29,650[E]

This project allowed me to invite 11 experts for two weeks in French Guiana. We gathered more than 1000 specimens, and began describing new species (**Henkel et al., 2013 ; Barbosa-Silva et al., 2017; Crous et al., 2017; Gruhn et al., 2017, 2018, Accioly et al., 2019**). Most species are still to be described, but specimens are stored in the MNHN herbarium and more taxonomists have been involved. In this project, I organized the fieldwork at Nouragues field station, supervised the sequencing in Toulouse, phylogenetic analyses, and interactions with taxonomists. This project was an essential stepping stone toward following projects in French Guiana on fungal diversity.

MYCOTIN: MYcorrhizal COmmon network of Trees on Inselbergs
Projet CNRS Nouragues
PI: **M. Roy** (20%)
2013
8000^{E}

In this project, we aimed to identify networks between neotropical trees. I organized the fieldwork, the sampling, supervised the molecular biology and sequencing and analyses. In this project, C. Decock identified fungi and D. Frame the host plants. We also collected Russulaceae and material for a master 2 in EDB. We did not detect networks, and needed more observations on Myrtaceae roots. Thanks to recent observations, we can now prepare a publication (**Fernandez et al., in prep.**).

FLAG: Funguy from Lesser Antillas and French Guiana
Bibliothèque du Vivant
PI: **M. Roy**
2012-2013
25 sequencing plates (circa 12,500^{E})

This grant allowed only sequencing, and supporting the sequencing of specimens from French Guiana and ectomycorrhizal roots. It allowed the production of reference barcodes for fungi. I was responsible for the sampling and DNA extraction, and PCR products were then sent to MNHN. I handled this project with S. Manzi, engineer in EDB lab.

FUN-CHEM: Functional chemodiversity.
Project central LABEX CEBA.
PI: Christophe Duplais (EcoFoG, Cayenne, Guyane Française)
2014-2016.
11,900^{E} to EDB.

In this project, I was responsible for a task on endophyte diversity. I organized the fieldwork in French Guiana, supervised the isolation of strains and their sequencing. This project supported the PhD experiments of Y. Eveno, and was a great base for further projects (SECIL).

ARC: réseau d'étude de la dynamique des aulnaies vertes anciennes.
Regional project (Région Rhônes-Alpes).
PI : Maria-Fernandez (Ecologie Microbienne, UCBL, Lyon, France)

2015.
Only expertise in EDB

In this project, I was involved as an expert on ectomycorrhizal fungi of alders. I contributed to discussions, and to the fieldwork. I supervised the molecular analyses and soil sequencing and analyses. We recently published a paper on those old-growth alder stands (**Schwob et al., 2017**).

NEBEDIV: effect of Natural Enemies on Beta Diversity in tropical forest.
ANR Blanc.
PI: Christopher Baraloto (EcoFoG and now Florida International University)
2014-2018.
153,900^{E} to EDB

In this Project, I was involved in a task on fungi specialization and diversity. I contributed to the fieldwork in Brazil, and supervised the sequencing of root-associated micro-organisms in EDB. I handled experiments to improve plant identification and supervised students to confirm ectomycorrhizal symbioses. The sampling was longer than expected and the project is not yet finished. Thanks to the fieldwork in Brazil, I published a first paper on white sands (**Roy et al., 2016**).

DIADEMA: DIssecting Amazonian Diversity by Enhancing a Multiple taxonomic-groups Approach.
Project central LABEX CEBA.
PI: Christopher Baraloto (EcoFoG and now Florida International University)
2014-2016
72,100^{E} to EDB

In this project, I contributed to the task on biodiversity inventories, and sampled fungi in Mont Itoupé, Saül, Kaw, Laussat and Mitaraka. I was responsible for the identification of fungi and interactions with taxonomists, contributed to fill the database on fungi and supervised students on fungal phylogenies. We have already published our database and some inventories (**Roy et al., 2018 ; Schimann et al., 2019**) and submitted a synthesis on our analyses.

MITAC: Can mixing of tree species improve resilience and productivity of boreal forests?
PI: Yves Bergeron (UQAT et UQAM, Canada)
projet MITACS (Québec, financement semi-industriel).
2015-2019.
only expertise in EDB

This project funded Mélissande Nagati's PhD. I was only expert in this project but Mélissande produced very interesting results on microorganisms in the boreal forest.

SECIL: Study of leaf endophytic fungi : Exploration and valorization of biosourCed Innovative antibacterial metaboLites.
ANR Franco-Suisse.
PI: Didier Stien (CNRS, Banyuls, France) and J.-L. Wolfender (University of Geneva)

2015-2019.
79,040^{E} to EDB.

In this project, I was responsible for a task on endophytes communities. I contributed to the field in French Guiana, supervised master students and involved Julian Donald as a Post-Doc. I supervised the metabarcoding at EDB, and acquired impressive datasets on endophytes communities and strains. I also helped my colleagues in chemistry identifying their strains with phylogenies. We are currently writing papers on this project (**Donald et al., submitted ; Donald et al., in prep ; Gazal et al., in prep**), and my colleagues in chemistry isolated very promising strains.

LONGTIME: Long Term Impact of ancient Amerindian settlements on Guianese Forests.
Project central LABEX CEBA.
PI: Jean-François Molino (AMAP, Montpellier, France) and G. Odonne (LEESIA, Guyane)
2016-2018.
15,000^{E} at EDB

In this project, I was responsible for a task on soil biodiversity, and organized the fieldwork for 8 researchers and students in French Guiana. I supervised the soil sequencing and biodiversity analyses for fungi, bacteria and earthworms and the master 2 of Nina Gazal. We have already submitted a book chapter about our methods (**Gazal et al., submitted**) and a master 2 (Isis Poinas), supervised by Maxime Rejou-Méchain (AMAP, Montpellier), is now gathering our data with archaeological data.

DROUGHT: Functional diversity and response to drought in tropical forests.
Project central LABEX CEBA.
PI: Damien Bonal (EEF, Nancy, France)
2016-2018.
23,000^{E} at EDB.

In this project, I was co-responsible for a task on micro-organisms associated with trees and their interaction with drought stress. I focused on mycorrhizae and gathered mycorrhizae along a phosphorus and rainfall gradient in French Guiana, that was analysed by B. Durrington during his master 2 (**Durrington et al., in prep**). The project also focused on endophytes of leaves and branches and the sequencing was finally handled in C. Vacher's lab, through another master 2.

DIAMOND: Dissecting and monitoring Amazonian diversity.
Project central LABEX CEBA.
PI: Jérôme Murienne (EDB), Jérôme Orivel (EcoFoG, Kourou, Guyane Française)
2016-2018.
137,541^{E} at EDB

In this project, I contribute to improve databases on fungal barcodes and fungal phylogenies. The ABC Saül is tightly linked with this project, as fungi identified by experts are useful to analyze metabarcoding short sequences.

RECO-RECO: Importance des réseaux mycorhiziens et des connexions racinaires dans la revégétalisation des parcs à résidus miniers.
Projet Champlain, financé par le Consulat de France au Québec.
PI : **Mélanie Roy** (40%) and Philippe Marchand (UQAT, Canada).
2018-2019.
14,000^{E} at EDB.

Champlain projects aim at promoting exchanges of students and researchers. In this project, I supervise a master 1 student in France and one in Québec, I organize the fieldwork in northern Québec, and train students in NGS analyses in EDB. My colleagues P. Marchand and N. Fenton will visit Toulouse, and have supervised a master 1 from UPS and trained him in spatial analyses.

ABC Saül : Atlas de la Biodiversité Communale de Saül.
AFB
PI: Laurent Gode (Parc National Amazonien de Guyane)
2018-2020.
Only expertise in EDB

In this project, I am responsible for mycological inventories and lead a group of 8 experts, organize field trips to Saül (3) and a mushroom exhibition in French Guiana, supervise a master student and the molecular biology on the collected specimens. We aim at publishing a booklet on fungi from French Guiana for the National Park. Moreover, this project is an excellent way to transfer my knowledge on fungi to the National Park.

CERES : Connectivité des écosystèmes forestiers et rivulaires de l'espace SUDOE.
Inter-Reg SUDOE
PI: Sébastien Chauvin (FORESPIR, Toulouse, France)
2018-2020.
1 272,214^{E} euros (only expertise in EDB, collaboration with DYNAFOR)

In CERES, I am involved as an expert on fungi diversity. This project focuses on ecosystem connectivity and the response of bat, invertebrate and fungal communities. I will contribute to the sampling in the Pyrénées, the DNA extraction and sequencing and finally the analyses on fungi. We have also deposited a PhD subject for this project.

ACTUAAL: Accompagner les Transitions de l'Urbain Anthropocène en Amérique latine : l'école comme laboratoire des futurs écosystèmes urbains
CNRS – Ecosystèmes Urbains 2019
PI: Julie Legall (CEMCA, Mexico)
2019
25,000^{E} (only expertise in EDB)

Through my teaching on urban diversity, and my projects on landscape ecology, I have begun interacting with colleagues in geography. In this project, I am responsible for plant inventories with two schools of Buenos Aires and Mexico. I will identify plants and teach the pupils how to recognize and observe plants. Julie Legall and her students will then detail how pupils use this

knowledge. This project is tightly connected with my botany course and will involve my students at Toulouse in 2020.

MULTIMYCO :
Annual project LABEX CEBA
PI : **Mélanie Roy** (40%) and Francis Brearley (University of Manchester, Great Britain)
2019
14,800^{E}

Ectomycorrhizae are rare in French Guiana but endomycorrhizae are on the contrary extremely diverse. Thanks to this project, we gather expertise on both microorganisms and will study the specialization process on *Dicorynia guyanensis* roots. In this project, I organize the field, and contribute to analyses. Christina Hazard, in post doc at Ecole Centrale de Lyon, is responsible for the sequencing and Jennifer Rowntree in Manchester University will sequence the plant microsatellite. This project is short, but very stimulating and benefits from the expertise of Francis Brearley and myself in French Guiana.

Field experience and expertise

Through my diverse research projects, I have organized and joined projects in very diverse forests around the world. Fieldwork is essential in my research and expertise, and I have tried to transmit this passion to students, and involve taxonomists – who are often free-lance experts – in my field trips to French Guiana.

Boreal forests	Fieldwork in Québec (2), and Alaska (1)
Temperate forests	Fieldwork in Cevennes national Park, Vanoise, Corsica Germany (Black forest), Romania (Carpathians), Poland (Tatras), Czech Republic (White Carpathians), Georgia (Colchis), Italy (Sorentino)
Tropical forests	French Guiana (14), Brasil (2)

Recently, I have been involved as an expert for *Office National des Forêts* in French Guiana. This expertise has allowed me to contribute to inventories in Trinité reserve avec fund my projects on fungi around inselbergs.

Around Toulouse, I organize field days for the Natural History Museum of Gaillac, on orchids and urban ecology, and for the Tarn CPIE.

Five selected articles

I have focused my research on three models, alder-EMF symbiosis, neotropical EMF and more recently boreal ecosystems. I have chosen 5 articles, to reflect these three topics, and show the results of collaboration with other PhD students (A. Pozzi) and present Mélissande Nagati's first article.

1. **Roy, M.,** J. Rochet, S. Manzi, P. Jargeat, H. Gryta, P. -A. Moreau, et M. Gardes. 2013. What determines *Alnus*-associated ectomycorrhizal community diversity and specificity? A comparison of host and habitat effects at a regional scale. *New Phytologist* 198 (4): 1228-38.

2. **Roy, M.,** A. C. Pozzi, R. Gareil, M. Nagati, S. Manzi, I. Nouioui, N. Sharikadze, P. Jargeat, H. Gryta, et P. -A. Moreau. 2017. Alder and the Golden Fleece: high diversity of *Frankia* and ectomycorrhizal fungi revealed from *Alnus glutinosa* subsp. *barbata* roots close to a Tertiary and glacial refugium. *PeerJ* 5: e3479.

3. Pozzi, A. C., **M. Roy**, M. Nagati, G. Schwob, S. Manzi, M. Gardes, P. -A. Moreau, et M. P. Fernandez. 2018. Patterns of diversity, endemism and specialization in the root symbiont communities of alder species on the island of Corsica. *New Phytologist*. 219(1): 336-349.

4. **Roy, M**., H. Schimann, R. Braga-Neto, R. AE Da Silva, J. Duque, D. Frame, F. Wartchow, et M. A. Neves. 2016. Diversity and distribution of ectomycorrhizal fungi from Amazonian lowland white-sand forests in Brazil and French Guiana. *Biotropica* 48 (1): 90-100.

5. Nagati, M., **M. Roy**, S. Manzi, F. Richard, A. Desrochers, M. Gardes, et Y. Bergeron. 2018. Impact of local forest composition on soil fungal communities in a mixed boreal forest. *Plant and Soil*, 432(1-2): 345-357.