

Research Article

Diversity of Ectomycorrhizal Fungi Associated with *Eucalyptus* in Africa and Madagascar

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Use of the Australian genus *Eucalyptus* in short rotation plantations in Africa and Madagascar has developed over the last century to such an extent that it is becoming the most frequently planted genus in Africa. In order to find ecologically well-adapted eucalypts, foresters have tested different species of various origins and the number of tested *Eucalyptus* species now exceeds 150 in Africa. Due to the ability of eucalypts to naturally form ectomycorrhizae, even in the absence of any controlled introduction of compatible ectomycorrhizal fungal partners, their introduction in new ecosystems has direct consequences for ectomycorrhizal fungus communities. A bibliographical compilation, together with original field observations on putative ectomycorrhizal fungi associated with eucalypts in Africa and in Madagascar, has been drawn up in two lists: one for Africa and one for Madagascar where surprisingly high fungal diversity was observed. The level of diversity, the putative origin of the fungi, and their potential impact on native ectomycorrhizal fungi are discussed. The development of eucalypts plantations will inexorably lead to the increase of exotic fungal species being potentially invasive in the considered region.

1. Introduction

Since colonial times, the African woodlands have been subjected to irreversible management policies that have resulted in the planting of large areas with exotic trees, for instance *Pinus* and *Eucalyptus*. In Mediterranean and tropical countries eucalypts are planted because they are generally fast-growing trees that make for a profitable business. Nowadays, eucalypt plantations cover approximately 1,8 Mha in Africa and are the most important planted genus on that continent [1]. In order to extend plantations and increase profits, it appeared necessary to find and select new eucalypt genotype adapted to different ecological situations. To that end, foresters started to test different *Eucalyptus* species of different origins, notably in Africa and Madagascar (e.g., [2, 3]). As a result, the number of introduced eucalypt species in African plantation trials now exceeds 150. Some of them are

used in commercial plantations as pure species or as hybrids [4]. The mass introduction of these exotic species in Africa definitely has consequences for local plant biodiversity and also for soil microbial communities such as ectomycorrhizal (ecm) fungi. Indeed, the ability of eucalypt species to form ectomycorrhizae, which are ecologically important symbioses that mainly associate homobasidiomycetous fungi, was observed for the first time in South Africa by Van der Bijl [5]. Since then, the ecm status of eucalypt species has been clarified [6] notably in Australia where a large diversity of fungal partner has been described [7–12]. Until now, ecm fungi found in Africa and Madagascar have resulted putatively from chance introductions, from compatibility with native ecm fungi, or from compatibility with ecm fungi from other exotic plantations. Indeed, the use of soil as an inoculant or any other source of inoculation that might bring ecm fungi from the tree's native area has not been reported

when establishing eucalypt plantations. Some controlled field inoculation trials using pure strains were set up, but only on very limited areas (e.g., [14]) and, in this case, the invasion of neighboring plantations by the introduced strains was not reported. Controlled field inoculation trials provide ways of entry for new ecm fungi that cannot be neglected, as is the case for China [15, 16]. However, the fungal species or even the strain reference might be known, enabling tracking in the plantation or in surrounding plantations. In Africa, we are in a situation where we have no proof of any propagation of a fungal species after the controlled inoculation of a eucalypt plantation. However, we are in a particular case where human activity, eucalypt plantations, has direct and mostly uncontrolled consequences for another compulsorily related biological community: ecm fungi.

Published papers, unpublished information, and authors personal data formed the basis of our work to synthesize the knowledge available on putative ecm fungi of eucalypt plantations in Africa and Madagascar. An annotated list of putative ecm fungi of eucalypts is given for more than 20 African countries and Madagascar.

2. Materials and Methods

A bibliographical search covering 30 years was carried out enabling us to uncover all the published papers and also a large share of the “grey literature” directly linked to our topic: ecm fungi associated with eucalypts in Africa and Madagascar. Written reports and all the oral reports of ecm partnerships have always to be considered with great caution and skepticism. Indeed, proving the ability of a tree species to form ectomycorrhizae with one particular fungal species is always a difficult task; the existence of other local or introduced ecm tree species in the vicinity of eucalypt plantations as well as the mistaken identification of the fungal partner can lead to misinterpretation. Definitely doubtful data are not considered in the rest of the paper and unreliable data are presented with a special mention of what needs to be considered with caution.

In addition, field surveys were organized in eucalypt plantations, notably in different African countries and in Madagascar; fungal fruiting bodies were systematically collected from the plantations. Litter and a few centimeters of topsoil were removed to search for hypogeous fungi on at least 4 m² in each plantation. Fungal specimens were deposited at the Museum National d’Histoire Naturelle de Paris (PC), France. In order to prove the ecm partnership, careful mycelium and root tracking were carried out in the field enabling us to assess physical links between fruiting bodies, ecm root tips, and the bearing trees.

Ectomycorrhizae histological studies were also carried out on materials collected in the field to reveal the fungal sheath and the Hartig net (Table 2).

3. Results

In Africa, 35 ecm fungal species are mentioned as being associated with 15 identified eucalypt species and a range

of unidentified species (at least five), along with hybrids (Table 1). *Pisolithus* was present and often highly dominant or even alone in almost all the plantations, as is the case in the West African dry tropics with *Pisolithus albus* in *E. camaldulensis* plantations (Figure 1(a)). The importance of the genus *Pisolithus* and to a lesser degree, the genus *Scleroderma*, was noteworthy (Figures 1(b) and 1(c)). The presence of the ubiquitous ecm fungus *Thelephora* sp. in the wet tropics was also noteworthy (Figure 1(d)). During the surveys ([13] in Table 1), ectomycorrhizae with a typical fungal sheath and a Hartig net (Figures 1(e) and 1(f)) were found in the vicinity of fruiting bodies.

In Madagascar, we collected 38 putative ecm fungal species from nine *E. robusta* plantations on the outskirts of Antananarivo (Table 3, Figures 2(a), 2(b), 2(c), 2(d), 2(e)). At these nine survey sites, *Pisolithus* was found only once and was far from dominant. In addition to this surprising diversity associated with *E. robusta*, two different *Pisolithus* species were found at two other sites in the southeast of Madagascar (Figure 2(f)).

4. Discussion

Ectomycorrhizal deficiency never seems to have been a problem in the early establishment of eucalypts. Ryvarden et al. [17] noted that selected trees form satisfactory partnerships with some introduced ecm fungi, notably *Pisolithus arhizus* which is now extremely abundant under eucalypts in Africa, and also with some elements of the indigenous ecm mycoflora. It is interesting to note that renantherous species of *Eucalyptus* known for their high dependence on ecm symbiosis [6] have been excluded by foresters due to their poor growth performance even in a Mediterranean climate (North Africa and South Africa), where the range of putatively adapted species is wide. During the process of eucalypt introduction and selection, foresters have neglected ecm symbiosis. This fact has probably led to the selection of tree species dependent little on ectomycorrhizae for early survival and growth. South America is also a place where eucalypts were abundantly planted and are found to be ectomycorrhizal with a range of ecm fungi ([13, 18–20, 42, 43] and Table 4). Some similarities with the African ecm fungi have to be mentioned, notably, the importance of genera *Scleroderma* and *Pisolithus*. On another hand, importance and diversity of genera *Descomyces*, *Hydnangium*, *Hymenogaster*, *Hysterangium*, and *Setchelliogaster* seems scarcer in Africa rather than in South America.

4.1. Fungal Diversity in Africa. According to Buyck [44], the native ecm fungi are unable to form ectomycorrhizae with exotic trees and consequently, eucalypts ecm fungi are limited to a few ecm fungal species that are now cosmopolitan. The observation made by Härkönen et al. [23] corroborated Buyck’s observation: the indigenous fungi cannot grow in symbiosis with the introduced trees. These assertions seem rather excessive; indeed records of typical European species such as *Amanita muscaria*, *A. phalloides*, *Paxillus involutus*, or *Rhizopogon luteolus* [21, 23, 32, 33] or typical African

TABLE 1: List of ectomycorrhizal fungi found associated with eucalypts in Africa with an indication of the country where the observation was made and the reference.

Putative ecm fungi	Associated eucalypts	Countries	References
<i>Amanita muscaria</i> (L.) Hook	<i>E. camaldulensis</i> Dehnh.	MA	[1]
<i>Amanita phalloides</i> Fr. [§]	<i>Eucalyptus</i> sp.	TZ	[2]
<i>Amanita zambiana</i> Pegler & Pearce	<i>Eucalyptus</i> sp.	EAF	[3]
<i>Cantharellus densifolius</i> Heinem.	<i>E. grandis</i> W. Hill ex Maiden	ZA	[4]
<i>Cenococcum geophilum</i> Fr.	<i>E. camaldulensis</i>	MA	[1]
<i>Cenococcum geophilum</i> Fr. : Fr.	<i>E. gomphocephala</i> DC.	MA	[1]
<i>Chondrogaster pachysporus</i> Maire	<i>Eucalyptus</i> sp.	NAf	[5]
<i>Descomyces albus</i> (Klotzsch) Bougher & Castellano	<i>Eucalyptus</i> sp.	CA, NAF	[5]
<i>Hydnangium carneum</i> Wallr.	<i>E. globulus</i> Labill.	CA	[6]
<i>Hymenangium album</i> Klotzsch	<i>Eucalyptus</i> sp.	CA, NAF	[5, 7]
Hypogeous fungus (not determined)	<i>Eucalyptus</i> (hybrid)	CG	[8]
<i>Labyrinthomyces donkii</i> Malençon	<i>Eucalyptus</i> sp.	MA	[7, 9]
<i>Laccaria laccata</i> (Scop.) Fr.	<i>E. camaldulensis</i>	MA	[1]
<i>Laccaria lateritia</i> Malençon [§]	<i>Eucalyptus</i> sp.	ZR	[10]
<i>Laccaria lateritia</i> [§]	<i>E. maideni</i> F. Muell.	ZR	[11]
<i>Laccaria lateritia</i> [§]	<i>E. globulus</i>	CA	[6]
<i>Paxillus involutus</i> (Batsch) Fr.	<i>Eucalyptus</i> sp.	MA	[12]
<i>Paxillus involutus</i>	<i>E. camaldulensis</i>	MA	[1]
<i>Paxillus</i> sp.	<i>Eucalyptus</i> (hybrid)	CG	[8]
<i>Phlebopus sudanicus</i> (Har. & Pat.) Heinem.	<i>E. camaldulensis</i>	SE	[13]
<i>Phlebopus sudanicus</i>	<i>E. tereticornis</i> Sm.	SE	[13]
<i>Phylloporus</i> sp.	<i>Eucalyptus</i> (hybrid)	CG	[8]
<i>Pisolithus arhizus</i> (Scop. : Pers.) Rausch*	<i>Eucalyptus</i> sp.	ZR	[14]
<i>Pisolithus arhizus</i> *	<i>E. camaldulensis</i>	ZR	[11]
<i>Pisolithus arhizus</i> *	<i>E. umbellata</i> Domin	ZR	[11]
<i>Pisolithus arhizus</i> *	<i>E. microcorys</i> F. Muell.	ZR	[11]
<i>Pisolithus arhizus</i> *	<i>E. saligna</i> Sm.	ZR	[11]
<i>Pisolithus arhizus</i> *	<i>E. urophylla</i> S.T. Blake	CG	[15]
<i>Pisolithus albus</i> (Cooke & Masee) Priest	<i>E. apodophylla</i> Blakely & Jacobs	SE	[16]
<i>Pisolithus albus</i>	<i>E. camaldulensis</i>	BF	[13]
<i>Pisolithus albus</i>	<i>E. camaldulensis</i>	CI	[13]
<i>Pisolithus albus</i>	<i>E. camaldulensis</i>	MA	[13]
<i>Pisolithus albus</i>	<i>E. camaldulensis</i>	NG	[13]
<i>Pisolithus albus</i>	<i>E. camaldulensis</i>	SE	[16]
<i>Pisolithus albus</i>	<i>E. camaldulensis</i>	TH	[13]
<i>Pisolithus albus</i>	<i>E. camaldulensis</i>	TU	[13]
<i>Pisolithus albus</i>	<i>E. gomphocephala</i>	MA	[1]
<i>Pisolithus albus</i>	<i>E. grandis</i>	MA	[13]
<i>Pisolithus albus</i>	<i>E. pantoleuca</i> L.A.S. Johnson & K.D. Hill	SE	[16]
<i>Pisolithus albus</i>	<i>E. robusta</i> Sm.	SE	[16]
<i>Pisolithus albus</i>	<i>Eucalyptus</i> sp.	RW, BU	[17]
<i>Pisolithus microcarpus</i> (Cooke & Masee) G. Cunn.	<i>E. camaldulensis</i>	MA	[13]
<i>Pisolithus microcarpus</i>	<i>E. grandis</i>	MA	[13]
<i>Pisolithus marmoratus</i> (Berk.) E. Fisch.	<i>E. alba</i> Blume	CG	[13]
<i>Pisolithus marmoratus</i>	<i>E. grandis</i>	CG	[13]
<i>Pisolithus marmoratus</i>	<i>E. pellita</i> F. Muell.	CG	[13]
<i>Pisolithus marmoratus</i>	<i>E. urophylla</i>	CG	[13]
<i>Pisolithus marmoratus</i>	<i>Eucalyptus</i> (hybrid)	CG	[8]
<i>Rhizopogon luteolus</i> Fr. [#]	<i>E. camaldulensis</i>	ZR	[11]
<i>Rhizopogon luteolus</i> [#]	<i>E. microcorys</i>	ZR	[11]
<i>Rhizopogon luteolus</i> [#]	<i>E. saligna</i>	ZR	[11]

TABLE 1: Continued.

Putative ecm fungi	Associated eucalypts	Countries	References
<i>Rhizopogon luteolus</i> #	<i>E. umbellata</i>	ZR	[11]
<i>Rhizopogon vulgaris</i> (Vittad.) M. Lange#	<i>E. globulus</i>	CA	[6]
<i>Russula</i> sp.	<i>E. camaldulensis</i>	MA	[1]
<i>Scleroderma albidum</i> Pat. & Trabut**	<i>Eucalyptus</i> sp.	DZ, MA, CG, Saf	[5]
<i>Scleroderma bovista</i> Fr.	<i>E. camaldulensis</i>	MA	[1]
<i>Scleroderma capensis</i> Lloyd	<i>E. camaldulensis</i>	SE	[18]
<i>Scleroderma capensis</i> Lloyd	<i>E. robusta</i>	SE	[18]
<i>Scleroderma cepa</i> Pers.**	<i>Eucalyptus</i> sp.	RW BU	[17]
<i>Scleroderma cepa</i> **	<i>E. globulus</i>	CA	[6]
<i>Scleroderma citrinum</i> Pers.	<i>Eucalyptus</i> sp.	RW, BU	[17]
<i>Scleroderma flavidum</i> Ellis & Everh.	<i>Eucalyptus</i> (hybrid)	CG	[8]
<i>Scleroderma laeve</i> Lloyd**	<i>Eucalyptus</i> sp.	Saf	[5]
<i>Scleroderma polyrhizum</i> (J.F. Gmel.) Pers.**	<i>Eucalyptus</i> sp.	CA	[5]
<i>Scleroderma verrucosum</i> (Bull.:Pers.) Pers.***	<i>E. camaldulensis</i>	GU, SE	[19]
<i>Scleroderma verrucosum</i> ***	<i>Eucalyptus</i> sp.	GU	[18]
<i>Scleroderma verrucosum</i> ***	<i>E. robusta</i>	SE	[13]
<i>Scleroderma</i> sp.	<i>Eucalyptus</i> sp.	MW	[20]
<i>Scleroderma</i> sp.	<i>Eucalyptus</i> sp.	ZA	[20]
<i>Scleroderma</i> sp.	<i>Eucalyptus</i> sp.	ZW	[20]
<i>Scleroderma</i> sp.	<i>Eucalyptus</i> (hybrid)	CG	[8]
<i>Thelephora</i> sp.	<i>Eucalyptus</i> (hybrid)	CG	[8]
<i>Tricholoma</i> sp.	<i>E. camaldulensis</i>	MA	[1]

Legend: Countries: DZ: Algeria, NAF: North Africa, EAF: East Africa, SAF: South Africa, BF: Burkina Faso, BU: Burundi, CA: Canary Islands, CG: Congo, ZR: Democratic Republic of Congo, CI: Cote d'Ivoire, GU: Guinea, MA: Morocco, MW: Malawi, NG: Niger, SE: Senegal, RW: Rwanda, TZ: Tanzania, TH: Chad, TU: Tunisia, ZA: Zambia, and ZW: Zimbabwe. References: 1: [21, 22], 2: [23], 3: [24], 4: [25], 5: [26], 6: [27], 7: [28], 8: [29], 9: [30], 10: [31], 11: [32], 12: [33], 13: [34, 35], 14: [36], 15: [37], 16: [38], 17: [39], 18: [40], 19: [17], and 20: Authors' personal observations.

* *Pisolithus arhizus* is a temperate European species described from acidic soils and associated with trees like *Quercus*, *betulus*, or *pinus*. Its presence in Africa associated with introduced Australian species is unlikely. Our assumption is that the specific epithet "arhizus" is erroneous.

**The systematic of *Scleroderma* are complex and the erroneous use of specific epithets in the identification of this species has to be kept in mind.

***In the absence of any indication on the subspecies, the possibilities of synonymy with other species are multiple.

#*Rhizopogon* is a genus mostly associated with pines and some temperate deciduous trees. A poor mycorrhizal colonization of eucalypt roots by these *Rhizopogon* can be considered; indeed *Rhizopogon* spp. differed markedly in their ability to form ectomycorrhizas according to their taxonomical section and host plant [41].

§The presence of these temperate taxa in tropical countries has to be carefully considered; confusion with local tropical taxa might be possible.

TABLE 2: Color, diameter, fungal mantle thickness, and Hartig net depth of ectomycorrhizae *in situ* collected in Senegal on 3 species of *Eucalyptus*.

Fungal species	Color	Diameter (μm)	Mantle thickness (μm)	Hartig net depth (μm)
<i>E. apodophylla</i> X <i>Pisolithus albus</i>	bY	190 \pm 20	20 \pm 4	23 \pm 7
<i>E. camaldulensis</i> X <i>Pisolithus albus</i>	bY	240 \pm 22	26 \pm 6	24 \pm 2
<i>E. robusta</i> X <i>Pisolithus albus</i>	bY	210 \pm 18	22 \pm 4	20 \pm 6
<i>E. camaldulensis</i> X <i>Scleroderma capensis</i>	W	215 \pm 23	20 \pm 4	18 \pm 8
<i>E. robusta</i> X <i>Scleroderma capensis</i>	W	190 \pm 16	16 \pm 3	24 \pm 4
<i>E. camaldulensis</i> X <i>Scleroderma verrucosum</i>	W	150 \pm 22	14 \pm 6	23 \pm 5

species such as *Amanita zambiana*, *Cantharellus densifolius*, or *Phlebopus sudanicus* [24, 25, 45], indicate possibilities for some native fungi, or for fungi introduced with other exotic species such as pines, to form ectomycorrhizae with eucalypts. The presented data clearly show that the level of fungal diversity in Africa remains very low under eucalypts: only 34 ecm fungal species were recorded since 1918 [5]! The easily disseminated (by wind and rain splashing) and

largely distributed genus *Pisolithus* is present and dominates in most plantations; other records always seem exceptional. A regular increase in fungal diversity, due to new uncontrolled introductions, to the extension of plantations to new climatic and soil conditions, and to the ageing of some plantations creating favorable conditions for the development of late stage ecm fungi is unavoidable. With the increasing importance of eucalypt plantations in Africa, we have here an



FIGURE 1: Example of ectomycorrhizal fungi and ectomycorrhizae of eucalypts in Africa. (a) *Pisolithus albus*; (b) *Pisolithus marmoratus*; (c) *Scleroderma flavidum*; (d) *Thelephora* sp.; (e) golden yellow ectomycorrhizae of *Pisolithus albus* with *E. camaldulensis*; (f) cross-section of an ectomycorrhizae of *Pisolithus albus* with *E. camaldulensis*. The bar represents 50 μm .

interesting area to improve our knowledge on the role played by ecm diversity in the sustainability of eucalypt plantations.

On the other hand, the presence of ecm fungi associated with eucalypts has not yet been reported under native ecm trees. Presumably there is incompatibility between eucalypt ecm fungi and those of the indigenous African ecm trees (e.g., *Azelia* spp., *Brachystegia* spp., *Berlinia* spp., and *Isobertlinia* spp. among the Caesalpiniaceae; *Monotes* spp., *Marquesia* spp. among the Dipterocarpaceae; *Uapaca* spp. among the Euphorbiaceae).

4.2. *The Case of Madagascar.* In Madagascar 80% of the vascular plants were considered to be endemic [46]. It also has one of the highest concentrations of endemic plant families: nine families represented by a total of 19 genera ca. 90 species [47, 48]. Of these, the ectotrophic Sarcolaenaceae [49] represent 56 species. Plantations of the Central Plateau are widely dominated by one single species: *E. robusta*. Among the 38 putatively ecm fungal species found associated with *E. robusta*, some red cap *Russula* sp. and *Cantharellus eucalyptorum* are marketed locally as edible, and the latter



FIGURE 2: Example of putative ectomycorrhizal fungi of *Eucalyptus robusta* in Madagascar. (a) *Amanita* sp.3; (b) *Cantharellus eucalyptorum*; (c) *Cantharellus congolensis*; (d) *Rubinoboletus* sp.; (e) *Russula* sp.3; (f) *Pisolithus* sp.

is exported to the surrounding countries. The number of ecm fungi found associated with *E. robusta* in a one-year survey was larger than the number of ecm fungi found in the whole of continental Africa since more than 80 years of observations. *Amanita*, *Boletus* (s.l.), *Cantharellus*, and *Russula* are the dominating genera found under *E. robusta*; on the other hand, members of the Sclerodermataceae were rarely observed. The presence of Madagascan endemic plant

taxa able to form ecm in eucalypt plantations or in the nearby surroundings as been carefully explored and none of the already known ecm families such as Sarcolaenaceae, Rhopalocarpaceae, Caesalpiniaceae, or Euphorbiaceae has been found. Other grass and shrubs growing under the canopy of eucalypts plantations were arbuscular mycorrhizal or for a few of them, nonmycorrhizal (unpublished). To conclude, this striking difference has yet to be elucidated.

TABLE 3: List of ectomycorrhizal fungi found associated with *Eucalyptus robusta* and *Eucalyptus* sp. in Madagascar.

Fungal species	Observation sites	Herbarium N ^o (*)
Associated with <i>E. robusta</i>		
<i>Amanita bojeri</i> Buyck [#]	Anjozorobe	MG47
<i>Amanita</i> aff. <i>citrina</i>	Manjakandriana	MG23
<i>Amanita</i> aff. <i>luteolus</i>	Anjozorobe	MG44
<i>Amanita</i> aff. <i>phalloides</i>	Anjozorobe	MG35
<i>Amanita</i> aff. <i>rubescens</i>	Antananarivo	MG21
<i>Amanita</i> sp.1	Ampitambe	MG14
<i>Amanita</i> sp.2	Anjozorobe	MG20
<i>Amanita</i> sp.3	Anjozorobe	MG49
<i>Amanitopsis</i> sp.1	Manjakandriana	MG32
<i>Boletus</i> aff. <i>cyanopus</i>	Manjakandriana	MG26
<i>Boletus</i> sp.1 [#]	Anjozorobe	MG19
<i>Boletus</i> sp.2 [#]	Antananarivo	MG28
<i>Boletus</i> sp.3 [#]	Anjozorobe	MG38
<i>Boletus</i> sp.4 [#]	Anjozorobe	MG45
<i>Cantharellus congolensis</i> Beeli	Antananarivo	MG16
<i>Cantharellus eucalyptorum</i> Buyck & Eyssartier [#]	Anjozorobe	MG15
<i>Cortinarius</i> sp.1 [#]	Antananarivo	MG31
<i>Pisolithus albus</i>	Anjozorobe	MG24
<i>Rubinoletus</i> sp.1	Mandrake	MG13
<i>Rubinoletus</i> sp.2 [#]	Antananarivo	MG18
<i>Rubinoletus</i> sp.3 [#]	Mantaso	MG27
<i>Russula</i> sp.1	Antananarivo	MG33
<i>Russula</i> sp.2	Anjozorobe	MG34
<i>Russula</i> sp.3	Antananarivo	MG36
<i>Russula</i> sp.4	Anjozorobe	MG39
<i>Russula</i> sp.5	Antananarivo	MG40
<i>Russula</i> sp.6	Antananarivo	MG41
<i>Russula</i> sp.7	Anjozorobe	MG42
<i>Russula</i> sp.8	Anjozorobe	MG46
<i>Scleroderma cepa</i> [#]	Ambohimanga	MG25
<i>Scleroderma</i> sp.1 [#]	Mahaela	MG12
<i>Scleroderma</i> sp.2 [#]	Anjozorobe	MG50
<i>Scleroderma verrucosum</i> [#]	Antananarivo	MG17
<i>Xerocomus</i> sp.1 [#]	Falamangua	MG11
<i>Xerocomus</i> sp.2 [#]	Manjakandriana	MG22
<i>Xerocomus</i> sp.3	Manjakandriana	MG30
<i>Xerocomus</i> sp.4 [#]	Antananarivo	MG43
Associated with <i>Eucalyptus</i> spp.		
<i>Pisolithus albus</i> [#]	Fanjahira	MG86
<i>Pisolithus</i> sp. [#]	Petriki	MG85

*Herbarium samples have been deposited at the Museum National d'Histoire Naturelle de Paris (PC), France.

[#]Indicates when the observation was carried out by tracking the mycelium from fungus fruiting bodies up to fine ectomycorrhizal roots and the trunk.

4.3. *Hypotheses on the Possible Origins of ECM Fungi in Eucalyptus Plantations.* Until now, the rational use of ecm fungi by eucalypt plantations has been poorly developed in Africa. Inoculations with selected ecm strains are still restricted to some experimental plantations [14]. The origin of the ecm fungi found associated with eucalypts in Africa and in Madagascar has yet to be elucidated. At least, three hypotheses

can be put forward: (1) chance introductions from Australia of (fully) compatible ecm fungi (e.g., *Pisolithus* spp.), (2) compatibility with some "broad host" ecm fungi growing in native African forests, and (3) compatibility with some ecm fungi growing in other exotic plantations (e.g., pine plantations). In any event, further studies are necessary to unravel the origins of the fungi in eucalypt plantations.

TABLE 4: List of some ecm fungi and associated eucalypt hosts spontaneously found in South America: Brazil (BR), Uruguay (UR), and Argentina (AR).

Fungal species	Host tree	Country
<i>Chondrogaster angustisporus</i>	<i>Eucalyptus</i> spp.	BR, UR
<i>Chondrogaster</i> sp.	<i>E. dunnii</i>	BR
<i>Descomyces fusisporus</i> sp. nov.	<i>E. cinerea</i>	AR
<i>D. varians</i> sp. nov.	<i>E. camaldulensis</i>	AR
<i>Descomyces</i> sp.	<i>E. dunnii</i>	BR
<i>Hydnangium archeri</i> (Berk.) Rodway	<i>E. camaldulensis</i>	AR
<i>H. carneum</i> Wallr.	<i>E. cinerea</i> , <i>E. camaldulensis</i>	AR
<i>Hydnangium</i> sp.	<i>E. grandis</i>	BR
<i>Hymenogaster rehsteineri</i> Bucholtz	<i>Eucalyptus</i> spp.	AR
<i>Hysterangium affine</i>	<i>Eucalyptus</i> spp.	BR
<i>Hysterangium gardneri</i> E. Fisch.	<i>E. camaldulensis</i>	AR
<i>H. inflatum</i>	<i>Eucalyptus</i> spp.	BR
<i>Labyrinthomyces</i> sp.	<i>E. dunnii</i>	BR
<i>L. laccata</i> var. <i>pallidifolia</i> sp.	<i>E. dunnii</i>	BR
<i>L. proxima</i> sp.	<i>E. dunnii</i>	BR
<i>Laccaria</i> sp.	<i>E. grandis</i>	BR
<i>Pisolithus albus</i>	<i>Eucalyptus</i> spp.	BR
<i>P. marmoratus</i>	<i>Eucalyptus</i> spp.	BR
<i>P. microcarpus</i>	<i>Eucalyptus</i> spp.	BR
<i>Pisolithus</i> sp.	<i>E. grandis</i>	BR
<i>Scleroderma albidum</i> sp.	<i>E. dunnii</i>	BR
<i>S. areolatum</i> sp.	<i>E. dunnii</i>	BR
<i>S. bougheri</i> sp.	<i>E. dunnii</i>	BR
<i>S. cepa</i> sp.	<i>E. dunnii</i>	BR
<i>Scleroderma</i> sp.	<i>E. grandis</i>	BR
<i>Setchelliogaster tenuipes</i> (Setch.) Pouzar	<i>E. camaldulensis</i>	AR
<i>Setchelliogaster</i> sp.	<i>E. dunnii</i>	BR
<i>Thelephora</i> sp.	<i>E. grandis</i>	BR

Curiously, in Madagascar, the level of fungal diversity observed under *E. robusta* is comparable to the diversity level of native ectotrophic forests [49]. The possibility that ecm fungi associated with *E. robusta* in Madagascar are of Australian origin has to be explored. Comparisons of our material collected under eucalypts (Table 2) with native Australian specimens and with samples of ecm fungi from native Madagascan ectotrophic forests are necessary to unravel the origins of the fungi observed in eucalypts plantations in Madagascar.

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