Chapter 8
Orchid Mycorrhizas in South America: Tropical and Subtropical Ecosystems

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8.1 Introduction

Orchids have fascinated enthusiasts and naturalists since at least the end of the eighteenth century (Cullen 1992). Certainly, Darwin's work (1862) inspired by highly specialized floral adaptations for attracting, deceiving, and manipulating insects to promote allogamy (Dressler 1981) was one of the most interesting and stimulating approaches for future generations of researchers. In addition, with about 30, 000 species and a worldwide distribution, Orchidaceae is the second most diverse family among angiosperms (Bánki et al. 2021). Its amazing floral shapes as well as the intricate relationships with both pollinators and mycorrhizal fungi make this plant group one of the most bizarre throughout the plant kingdom.

Among mycorrhizal associations (Peterson et al. 2004; Smith and Read 2010), orchid mycorrhiza (OM) is a special type that only occurs within Orchidaceae. Since orchids form minute seeds (like dust) with a reduced endosperm (Fig. 8.1) in

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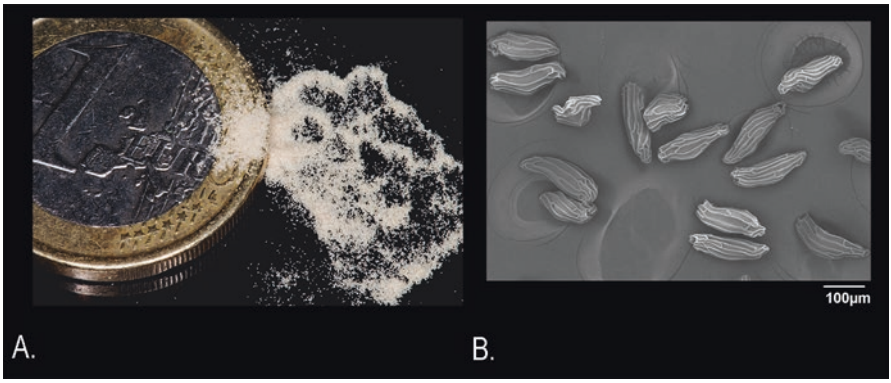

Fig. 8.1 Seeds of *Dichaea andina* orchid. This genus has one of the smallest sizes of seeds among Orchidaceae: (**a**) seeds like dust on one Euro coin, (**b**) view through scanning electron microscope (SEM). (Photo credit: Y. A. Alomía)

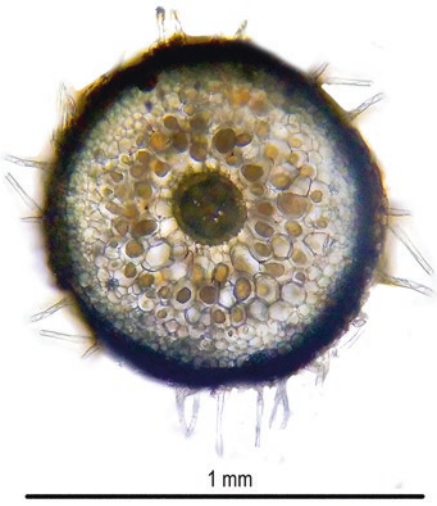

Fig. 8.2 Cross section of orchid root with pelotons (brown hyphal coils) formed by fungi into the parenchyma cells of cortex; view through of light microscope (200X). Photo credit: Y. A. Alomía

natural conditions, they need a fungal partner that provides the organic source to support the germination and seedling establishment (Bernard 1904; Rasmussen 1995; Brundrett 2017). This symbiosis is recognized for the formation of complex hyphal coils called pelotons within the root cortex tissue (Peterson et al. 2004; Zettler and Corey 2018) (Fig. 8.2).

In early stages of development, the plants are entirely dependent on the supply of nutrients and carbon by the orchid mycorrhizal fungi (OMF). In later stages, most species become green plants (i.e., photosynthetic orchids), and some species can obtain additional carbon supplies from fungi that remain until the adult stage. This mode of nutrition in which the plant gains carbon simultaneously from two sources, its own photosynthesis and the fungal supply, is called partial mycoheterotrophy

(Leake 1994; Gebauer 2018) (some authors use also the term mixotrophy; see Selosse et al. (2016)). In a broad sense, all orchid species are mycoheterotrophic in some state of the life cycle. Those species without chlorophyll as adults (i.e., non-photosynthetic orchids), which entirely rely on fungi throughout their lives for mineral and carbon nutrition, are called fully mycoheterotrophic orchids (Gebauer 2018).

Photosynthetic orchids are generally associated with fungi of the *Rhizoctonia* complex. This group consists of a phylogenetic heterogeneous assemblage that includes saprophytic, parasite, and endophyte species. Orchids also form mycorrhizas with fungi mainly included in the genera *Ceratobasidium*, *Tulasnella*, *Sebacina*, and *Serendipita* (Suárez et al. 2008; Taylor and McCormick 2008; Kottke and Suárez 2009; Weiß et al. 2016; Fritsche et al. 2021). On the other hand, partially mycoheterotrophic orchids, as well as fully mycoheterotrophic orchids, are associated with ectomycorrhizal fungi (*Russula*, *Thelephora*, *Tomentella*) of other nearby plants or with saprotrophic fungi (*Resinicium*, *Gymnopus*, and *Mycena*) (Martos et al. 2009; Zettler and Corey 2018).

Bernard (1904) reported the first record of mycorrhizal associations in orchids with *Rhizoctonia*-like fungi and proposed the first techniques for the cultivation of these fungi from sections of infected roots to promote seed germination. Morphologically, members of *Rhizoctonia* group share some common traits: hyphae without clamp connections branched at right angles, constriction of the hyphal branch, a septum close to the bifurcation site, and production of chains of swollen monilioid cells (Fig. 8.3). Detailed studies such as nuclear condition, septal ultrastructure, enzymatic activity, and the formation of anastomosis groups (Suárez et al. 2006, Suryantini et al. 2015, Thakur et al. 2018, Sathiyadash et al. 2020, Ghirardo et al. 2020, Nandeesha et al. 2021) can provide more taxonomic confidence. In addition, advances in molecular techniques have facilitated the identification of OMF mainly through sequencing of the internal transcribed spacer (ITS) region of ribosomal DNA (Kristiansen et al. 2001; Taylor and McCormick 2008; Kottke and Suárez 2009; Yokoya et al. 2015; Fritsche et al. 2021).

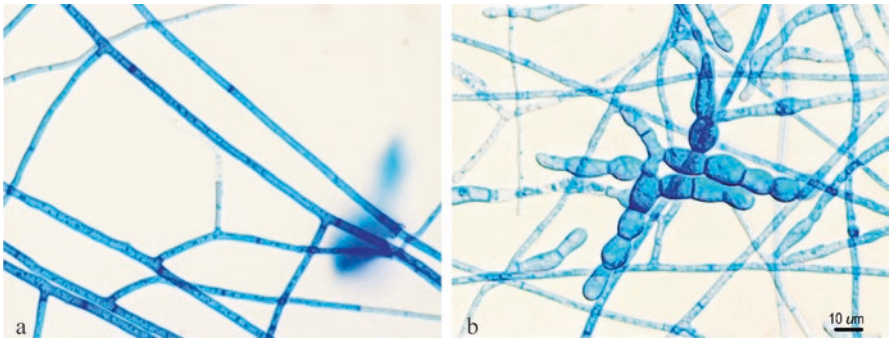

Fig. 8.3 Typical *Rhizoctonia* mycelium (*Ceratobasidium* sp.) stained with lacto-phenol blue; (**a**) branching pattern at 90, septum and constriction close to the bifurcation, (**b**) monilioid cells. Photo credit: Y. A. Alomía

An extensive literature has been published about the structure of orchid mycorrhiza, mechanisms of attraction, infection, nutrient exchange, phylogeny, and isolation techniques (Peterson et al. 2004; Smith and Read 2010; Dearnaley et al. 2012, 2016; Selosse et al. 2016; Swarts and Dixon 2017; Zettler and Corey 2018). Most of the knowledge on this topic comes from studies conducted in temperate ecosystems with terrestrial orchids (Kristiansen et al. 200; Gebauer and Meyer 2003; Bonnardeaux et al. 2007; Roche et al. 2010; Waterman et al. 2011; Jacquemyn et al. 2014, 2015; Těšitelová et al. 2015). In this chapter, a synopsis of the relevant literature on the interactions between OMF and their host plants in subtropical and tropical regions from South America is presented. After that, some perspectives and potential collaborations will be discussed.

8.2 Studies on Orchid Mycorrhizae in South America

A great majority of studies on OM in South America are academic documents named as "gray" literature and deposited in the repositories of university libraries. Others are published in local scientific journals written in native languages (e.g., Spanish, Portuguese). We have compiled the studies conducted in Brazil, Colombia, and Ecuador (Table 8.1), where it was possible to identify the taxon or taxa of the orchids studied, the methods for the identification of mycorrhizal fungi, and their taxonomic determination. The names of the orchid and fungal species were preserved as reported. The contribution of OMF of other countries in the tropical region of South America (Venezuela, Guyana, Surinam, French Guyana, Perú, Bolivia) has been limited or is not available to consult.

Pioneering studies on OM in tropical zones of South America were presented in the early twenty-first century by Díaz et al. (2000) in Colombia, when they were exploring the mycorrhizal associations in several orchid species. This study used morphological traits of mycelium to identify the fungal partner as *Rhizoctonia* for all species, although the main aim of the research was to identify what type of plant secondary metabolites was producing in the tissues where the endophytes were found. Around the same time, in Brazil, the first studies on orchid mycorrhizae were beginning in the laboratory of Professor Maria Catarina Megumi Kasuya of the Federal University of Viçosa. This time, it included, in addition to morphological characterizations, genetic information (ITS sequencing and RAPDs) (Pereira 2001). The interest in this subject in the country then expands, resulting in several researches throughout the next decade (Table 8.1). Around 2002, in Colombia, mycorrhizal interactions began to be explored in economically important species such as *Vanilla planifolia* (Ordóñez et al. 2012), and, under the guidance of the second author of this chapter from the National University of Colombia, an important field of research in the country was opened, resulting in multiple studies (Table 8.1). Although Colombia and Brazil were the pioneer countries, Ecuador has established itself as the leading country in research on OMF in the region. Many of the studies carried out in this country are rigorous investigations that have been published in scientific journals (unlike Brazil and Colombia, where many reports are part of gray

Table 8.1 Studies on fungal associations with orchids in tropical South America: a timeline

Taxon	Fungal origin	Identification method	Reported OMF	Study focus	Reference	Country
Elleanthus, *Epidendrum*, *Liparis*, *Maxillaria*, *Odontoglossum*, *Oncidium*, *Pleurothallis*, *Sobralia*, *Stelis*	Fungal cultures	Morphological	*Rhizoctonia* sp.	Diversity, plant secondary metabolites	Díaz et al. (2000)	Colombia
Epidendrum rigidum, Isochilus linearis, Maxillaria marginata, Oncidium flexuosum, *Oncidium varicosum*, *Oeceoclades maculata*, *Polystachya concreta*	Fungal cultures, pelotons	Morphological, enzymatic assays, molecular (RAPD, RFLP-ITS)	*Epulorhiza* sp., *Epulorhiza repens*, *Epulorhiza epiphytica*, *Ceratorhiza* sp.	Diversity, morphological studies	Pereira (2001), Pereira et al. (2005a)	Brazil
Isochillus linearis, *Polystachya concreta*, *Gomesa crispa*, *Campylocentrum* sp., *Bifrenaria tyrianthina*, *Oncidium gracile*, *Epidendrum secundum*, *Pleurothallis limae*	Fungal cultures	Morphological, polyphenol-oxidases activity, molecular (nrDNA ITS/Sanger sequencing)	*Epulorhiza* sp., *Ceratorhiza* sp.	Diversity, phylogeny	Nogueira (2004)	Brazil
Bulbophyllum weddelii, *Epidendrum dendrobioides*, *Maxillaria acicularis*, *Oncidium gracile*, *Pleurothallis teres*, *Prosthechea vespa*, *Sophronitis milleri*, *Sarcoglottis* sp.	Fungal cultures	Morphological	*Epulorhiza* sp., *Ceratorhiza* sp. *Rhizoctonia*	Diversity, morphological studies	Nogueira et al. (2005)	Brazil
Oncidium flexuosum	Fungal cultures	Molecular (RAPD, RFLP-ITS)	*Epulorhiza repens*, *Epulorhiza epiphytica*, *Ceratorhiza*, *Rhizoctonia* sp.	Symbiotic seed germination	Pereira et al. (2005b)	Brazil

(continued)

Table 8.1 (continued)

Taxon	Fungal origin	Identification method	Reported OMF	Study focus	Reference	Country
Gomesa crispa, *Campylocentrum organense, Bulbophyllum* sp.	Fungal cultures	Morphological	*Ceratorhiza*, *Rhizoctonia*	Diversity, ultrastructural analyses	Pereira et al. (2005c)	Brazil
Stelis hallii, *S. superbiens*, *S. concinna*, *Pleurothallis lilijae*	Root tissue with pelotons, fungal cultures	Morphological, molecular (nucLSU and nrDNA ITS/Sanger sequencing)	*Tulasnella*	Diversity Phylogeny, ultrastructural analyses	Suárez et al. (2006)	Ecuador
Masdevallia coccinea	Fungal cultures	Morphological	Binucleate *Rhizoctonia*	Morphological studies	Ordoñez (2006)	Colombia
Cyrtopodium vernum	Fungal cultures	Morphological	*Rhizoctonia*	Diversity, symbiotic seed germination	Gonçalves et al. (2008)	Brazil
Several species of Pleurothallidinae	Root tissue with pelotons	Molecular (nucLSU/ Sanger sequencing)	Tulasnellales, Sebacinales	Diversity, Community ecology, Phylogeny	Kottke et al. (2008b)	Ecuador
Stelis hallii, *S. superbiens*, *S. concinna*, *Pleurothallis lilijae*	Root tissue with pelotons	Morphological, Molecular (nucLSU and nrDNA ITS/Sanger sequencing)	*Opadorhiza*, *Epulorhiza*	Diversity, Phylogeny, Ultrastructural analyses,	Suárez et al. (2008)	Ecuador
Epidendrum secundum	Fungal cultures	Morphological, Molecular (RAPD, ITS-RFLP, nrDNA ITS/Sanger sequencing)	*Tulasnella/Epulorhiza*, *Sebacina/Opadorhiza*	Morphological studies, Diversity	Pereira (2009)	Brazil
Epidendrum secundum	Fungal cultures	Morphological	*Epulorhiza* spp.	Morphological studies, Diversity	Pereira et al. (2009)	Brazil

Bletia, *Stelis*, *Pleurothallis*, *Octomeria*, *Maxillaria*, *Pseudolaelia*, *Epidendrum*, *Artorima*, *Elleanthus*, *Sobralia*, *Prosthechea*	Root tissue with pelotons	Morphological, Molecular (nrDNA ITS/Sanger sequencing)	Atractiellomycetes (Pucciniomycotina)	Diversity, Phylogeny, Ultrastructural analyses,	Kottke et al. (2010)	Ecuador
Epidendrum secundum	Fungal cultures	Morphological	*Epulorhiza* spp.	Symbiotic seed germination	Pereira et al. (2011)	Brazil
Hadrolaelia jongheana, *Hoffmannseggella cinnabarina*, *Hoffmannseggella caulescens*	Root tissue with pelotons	Molecular (nrDNA ITS/Sanger sequencing)	*Tulasnella*, *Sebacina*	Diversity, Phylogeny	Oliveira (2012)	Brazil
Oeceoclades maculata	Fungal cultures	Morphological	*Rhizoctonia*	Morphological studies, Symbiotic seed germination	Pessoa et al. (2012)	Brazil
Coppensia doniana	Fungal cultures	Morphological, molecular (nrDNA ITS/Sanger sequencing)	*Ceratobasidium*	Diversity, phylogeny, morphological studies, symbiotic seed germination	Valadares et al. (2012)	Brazil
Epidendrum rhopalostele	Root tissue with pelotons	Molecular (nrDNA ITS/Sanger sequencing)	*Tulasnella* (clades A and B)	Diversity, phylogeny	Riofrío et al. (2013)	Ecuador
Notylia sp., *Habenaria* sp., *Epidendrum melinanthum*, *Trizeuxis falcata*, *Maxillaria* sp., *Cranichis* sp., *Dichaea* sp.	Fungal cultures	Molecular (nrDNA ITS/Sanger sequencing)	*Ceratobasidium*, *Thanatephorus*	Diversity, phylogeny	Mosquera et al. (2013)	Colombia
Epidendrum hemiscleria	Pelotons	Molecular (nrDNA ITS/Sanger sequencing)	*Tulasnella violea*	Diversity	Cueva (2014)	Ecuador

(continued)

Table 8.1 (continued)

Taxon	Fungal origin	Identification method	Reported OMF	Study focus	Reference	Country
Vanilla calyculata, *V. odorata*, *V. rivasii*	Fungal cultures, root tissue with pelotons	Molecular (nrDNA ITS/Sanger sequencing)	*Tulasnella* *Ceratobasidium*	Diversity, symbiotic seed germination	Alomia (2014), Alomia et al. (2017)	Colombia
Epidendrum marsupiale, *Odontoglossum pardinum*	Root tissue with pelotons	Molecular (nrDNA ITS/Sanger sequencing)	*Tulasnella*, *Ceratobasidium*, Sebacinales	Diversity	Guzmán and Moreno (2014)	Ecuador
Epidendrum secundum, *Acianthera limae*, *Polystachya concreta*	Fungal cultures	Molecular (nrDNA ITS/Sanger sequencing)	*Epulorhiza repens*, *E. epiphytica*	Diversity	Nogueira et al. (2014)	Brazil
Cyrtopodium paludicolum, *Cyrtopodium saintlegerianum*	Fungal cultures	Molecular (nrDNA ITS/Sanger sequencing)	*Rhizoctonia*, *Tulasnella*	Diversity, symbiotic seed germination	Carvalho (2015)	Brazil
Ionopsis utricularioides, *Psygmorchis pusilla*	Fungal cultures	Molecular (nrDNA ITS/Sanger sequencing)	*Ceratobasidium*	Diversity	Valadares et al. (2015)	Colombia
Cyrtochilum flexuosum, *Cyrtochilum myanthum*, *Maxillaria calantha*	Root tissue with pelotons	Molecular (ITS2/ Illumina sequencing)	Serendipitaceae, Ceratobasidiaceae, Tulasnellaceae	Diversity, community ecology	Cevallos et al. (2016)	Ecuador
Teagueia spp.	Root tissue with pelotons	Molecular (nrDNA ITS/Sanger sequencing)	*Tulasnella*, Atractiellales (Pucciniomycotina)	Diversity, phylogeny, evolutive implications	Suárez et al. (2016)	Ecuador
Maxillaria spp.	Fungal cultures	Morphological	*Tulasnella*, *Ceratobasidium*	Diversity	Rodriguez & Lora (2016)	Colombia
Stanhopea tricornis	Fungal cultures	Morphological	*Rhizoctonia*	Diversity	Córdoba-Díaz et al. (2015)	Colombia

Prescottia sp., *Oeceoclades maculata*, *Arundina bambusifolia*, *Vanda* sp., *Cattleya tigrina*, *Cattleya walkeriana*	Pelotons	Morphological	*Epulorhiza*, *Ceratorhiza*, *Moniliposis*, *Rhizoctonia*	Diversity, symbiotic seed germination	Minamiguchi (2017)	Brazil
Cyrtochilum flexuosum, *Cyrtochilum myanthum*, *Cyrtochilum pardinum*, *Epidendrum marsupial*, *Maxillaria calantha*	Root tissue with pelotons	Molecular (ITS2/ Illumina sequencing)	*Agaricales*, *Cantharellales*, *Thelephorales*, *Hymenochaetales*, *Sebacinales*, *Atractiellales*	Diversity, community ecology	Cevallos et al. (2018)	Ecuador
52 orchid species: *Stelis* (18 spp.), *Pleurothallis* (13 spp.), *Maxillaria* (9 spp.), *Epidendrum* (5 spp.), *Elleanthus* (3 spp.), *Artorima* (1 sp.), *Prosthechea* (1sp.), *Sobralia* (1sp.), *Oncidium* (1 sp.)	Root tissue with pelotons	Molecular (nrDNA ITS/Sanger sequencing)	*Tulasnellaceae*, *Serendipitaceae*	Diversity, mutualistic networks	Herrera et al. (2018)	Ecuador
Cyrtochilum myanthum, *Stelis superbiens*	Fungal cultures	Molecular (nrDNA ITS/Sanger sequencing)	*Tulasnellaceae*, *Ceratobasidiaceae*	Diversity	Novotná et al. (2018)	Ecuador
Zygopetalum mackayi, *Z. pedicellatum*	Fungal cultures	Molecular (nrDNA ITS/Sanger sequencing)	*Tulasnella*	Diversity	Regina et al. (2019)	Brazil
Oncidium luteopurpureum, *Oncidium lehmannii*	Fungal cultures	Molecular (nrDNA ITS/Sanger sequencing)	*Ceratobasidium*	Diversity	Henao-Mejía et al. (2020)	Colombia

(continued)

Table 8.1 (continued)

Taxon	Fungal origin	Identification method	Reported OMF	Study focus	Reference	Country
Cattleya jongheana	Fungal cultures	Morphological, Molecular (nrDNA ITS/Sanger sequencing)	*Tulasnella*, *Serendipita*	Morphological studies, diversity, phylogeny	Freitas (2021)	Brazil
Dichaea andina	Fungal cultures	Molecular (nrDNA ITS/Sanger sequencing)	*Ceratobasidium*	Diversity	Alomia et al. (2022)	Colombia

References: *mtLSU* mitochondrial large subunit ribosomal gene; *nucLSU* nuclear large subunit ribosomal gene; *nrDNA ITS* nuclear ribosomal internal transcribed spacer gene; *ITS-RFLP* restriction fragment length polymorphism of the fungal nuclear internal transcribed spacer region; *RAPD* random amplified polymorphic DNA. In the "study focus," we refer as morphological studies to those where the macroscopic characteristics of the mycelium are described and an optical microscope is used for the microscopic traits. In contrast, ultrastructure analyses are more detailed studies of the anatomy of fungi on the characteristics of hyphae and other mycelial organs, using transmission electron microscopy

literature). Professor Juan Pablo Suárez from Universidad Técnica Particular de Loja (Ecuador) as the leader in this field with the academic collaboration of Professor Ingrid Kottke (University Tübingen, Germany) has proposed a more evolutionary and ecological perspective on this type of association, including detailed ultrastructural analyses by transmission electron microscopy and community ecology approaches (Kottke et al. 2008a; Kottke and Suárez 2009; Kottke et al. 2013; Suárez and Kottke 2016).

The initial studies identified the fungi associated with orchids from the isolation of the mycelium that was morphologically characterized (Díaz et al. 2000; Pereira 2001). This approach required a great knowledge of fungi or the consultation to experts and did not provide very precise determinations due to the lack of reliable taxonomic characters to reach the species level, which would only be possible by obtaining the teleomorph or sexual phase of the isolated strain. In the region, unlike the temperate zones, obtaining teleomorphs was not a method addressed among the scientific community. With advances in molecular biology, the first genetic identifications were made with the random amplified polymorphic DNA (RAPD) and restriction fragment length polymorphism (RFLP) methods (Pereira 2001, Pereira et al. 2005a). Later, with the new findings on Sanger sequencing and the primers designed to capture the genetic information of the groups of mycorrhizal fungi frequently found in orchids (Kristiansen et al. 2001, Taylor and McCormick 2008), many researchers bypassed the time-consuming phase of isolation of mycelium in vitro to obtain the genetic information from root tissues infected with orchid mycorrhiza, verifying the presence of pelotons (Suárez et al. 2006; Kottke et al. 2008b; Suárez et al. 2008; Kottke et al. 2010; Oliveira 2012; Valadares et al. 2012; Alomía et al. 2017). The most studied genes are those of the nuclear ribosomal internal transcribed spacer (nrDNA ITS) gene and to a lesser extent those of the mitochondrial large subunit ribosomal (mtLSU) and nuclear large subunit ribosomal (nucLSU) regions. Sanger sequencing is the most widespread approach and is still used today for studies in which the strains are not required to be used in germination experiments or to be conserved in mycelium banks for later purposes. Although recent next-generation sequencing (NGS) techniques with Illumina technology offer more complex and robust information on fungi associated with orchids (Cevallos et al. 2016, 2018), this approach is not the most used due to the costs involved, which are not necessarily within the common financial source availability of researchers from developing countries in the region.

8.3 Research Interests

Some studies explored more than one topic in relation to the fungus-orchid associations. However, most studies (46%) have been focused on determining the diversity of OMF associated with few orchid species of interest. Phylogeny, morphological, and symbiotic seed germination studies are other of the main topics addressed (16%, 12%, and 11%, respectively). Ultrastructure and community ecology

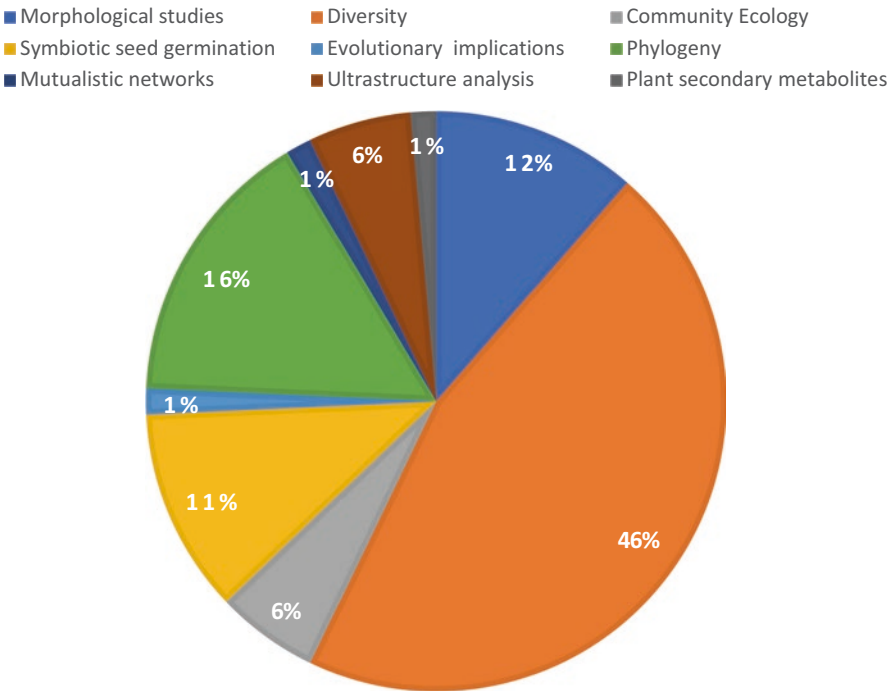

Fig. 8.4 Main studied topics in the OMF-orchid interaction from tropical and subtropical ecosystems in South America

researches are hardly representative (6%), while evolutionary implications, mutualistic networks, and metabolic aspects are the least explored topics (1%) (Fig. 8.4). We did not find studies aimed at understanding physiological topics of the OMF-orchid interaction.

These data indicate that basic questions are still being asked in the region as most of the studies describe the diversity of fungi associated with orchids. Few studies ask analytical questions that lead to a better understanding of the interactions between orchids and fungi. This may in part because a low resource availability limits the development of complex issues, such as those related to physiological or biochemical effects on each partner. Since the biodiversity of orchids in tropical South America is so extensive, the knowledge of OMF diversity is far from complete.

8.4 Challenges and Perspectives

Surprisingly, in tropical regions of South America where the Orchidaceae is especially diverse (Meisel et al. 2015; Kirby 2016), studies on orchid mycorrhiza symbiosis are underrepresented. However, in the last 20 years, the interest in endophytic

orchid fungi, both mycorrhizal and non-mycorrhizal, has increased in the region (Herrera et al. 2010; Hernández and Alomía 2020).

Future directions for OMF include: (i) The developing of a broader understanding of OMF. Although most studies focus on fungal diversity, they do not understand the evolutionary implications of the orchids and OMF relationship. We encourage collaborations with the international scientific community to continue investigating complex questions that allow us to understand the role of mycorrhizae in the evolutionary success of tropical orchids. (ii) The developing of new fungal culture techniques to be able to use OMF in bioassays since many OMFs are difficult to grow under in vitro conditions. (iii) To publish for a wider audience. We found that most of the studies are in the "grey" literature. For this, it is necessary to generate innovative research that sparks interest in the academic community. (iv) The application of the information produced on OMF for orchid conservation, orchid propagation, and plant protection (Otero et al. 2013). Orchid conservation programs rarely use OMF technologies to propagate endangered orchids. Similarly, orchid growers do not use OMF for propagation. To develop the enormous potential of the region in the cultivation of orchids, we invite companies interested in the production of orchids such as "Ecuagenera" in Ecuador, "Lima Orquídeas" in Perú, and "Colombo Orquídeas," "Orquídeas del Valle," "Orquídeas Eva," and "Libia Orquídeas" in Colombia, to be linked with the academy so that through research projects, added value will be generated in their business. More specifically, the use of mycorrhizae in the cultivation of orchids can contribute to enhancing production and reducing costs in sexual propagation (seeds) represented by asymbiotic media. Furthermore, OMF could also reduce the development time for flower production, generating significant financial gain for orchid sellers.

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