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JANE OJA

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Temporal and spatial patterns of orchid mycorrhizal fungi in forest and grassland ecosystems

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Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers that are referred to in the text by Roman numerals:

I. **Oja J**, Kohout P, Tedersoo L, Kull T, Kõljalg U. 2015. Temporal patterns of orchid mycorrhizal fungi in meadows and forests as revealed by 454 pyrosequencing. *New Phytologist* 205: 1608–1618.

II. **Oja J**, Vahtra J, Bahram M, Kohout P, Kull T, Rannap R, Kõljalg U, Tedersoo L. 2017. Local-scale spatial structure and community composition of orchid mycorrhizal fungi in semi-natural grasslands. *Mycorrhiza* 27: 355–367.

III. Tedersoo L, Abarenkov K, Nilsson RH, Schüssler A, Grelet GA, Kohout P, **Oja J**, Veldre V, Jairus T, Ryberg M, Larsson K-L, Kõljalg U. 2011. Tidying up international nucleotide sequence databases: ecological, geographical, and sequence quality annotation of ITS sequences of mycorrhizal fungi. *PloS one* 6: e24904.

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V. Oja, J. (2016) 'Data from: Local-scale spatial distribution and community composition of orchid mycorrhizal fungi in relation to grazing and environmental effects in semi-natural grasslands'. University of Tartu; Institute of Ecology and Earth Sciences. http://dx.doi.org/10.15156/BIO/587446

The author's contribution to the publications and datasets:

I. developed the idea and experimental design, data collection, data analysis, interpretation of the results and manuscript preparation

II. participated in data collection, data analysis, interpretation of the results and manuscript preparation

III. participated in data analysis, interpretation of the results and manuscript preparation

IV. and V. created, managed and published datasets

1. INTRODUCTION

The Orchidaceae, with c. 28,000 species, is considered one of the largest and most widely distributed vascular plant families (Christenhusz & Byng 2016; Givnish et al. 2016). Recent molecular dating analyses indicated that the first orchids diverged in Austrialia c. 100 million years (My) ago, while most of the current orchid species originated in the Neotropics c. 84-64 My ago (Givnish et al. 2015, 2016). Orchids have unique flower morphologies and diverse set of lifestyles, which have enabled them to colonise a wide range of habitats from subarctic to tropical ecosystems. The highest number of orchid species occurs in the tropics and subtropics (Dressler 2005). The overall extraordinary diversification in Orchidaceae could be driven in part by the evolution of pollinia, epiphytism, the development of crassulacean acid metabolism photosynthesis, life in extensive tropical mountains and specialization on particular groups of pollinators (Givnish et al. 2015).

In nature, orchids reproduce and survive only by interacting with other organisms. Interactions with pollinators are required only for sexual reproduction, whereas association with fungi last throughout their lives (Waterman & Bidartondo 2008). More than a century ago, Bernard and Burgeff independently realised that fungi are essential for successful orchid seed germination (Rasmussen 1995). Unlike many other plants, dust-like orchid seeds (only 0.05 – 6.0 mm in size) are almost devoid of food reserves (Arditti & Ghani 2000), and therefore completely dependent on mycorrhizal fungi for further development. During the early development stages, fungal partners provide carbon (C) and other essential nutrients to the orchid (Dearnaley et al. 2012). This kind of nutritional strategy is called mycoheterotrophy (MH; Leake 1994). Many initially mycoheterotrophic orchids develop green leaves and become autotrophic, yet their poorly developed roots remain colonised by mycorrhizal fungi. Arguably these orchids may receive C from fungal partners even during the adult stage. However, the amount of C seems be too small and undetectable (Stöckel et al. 2014). On the other hand, some autotrophic orchids obtain C from both autotrophic photosynthates and associated fungi and are called partially mycoheterotrophic or mixotrophic (PMH; Gebauer & Meyer 2003; Julou et al. 2005; Selosse & Roy 2009). This kind of nutritional mode was discovered not long time ago thanks mainly to isotopic methods. With these methods, it was demonstrated that for some forest orchids the natural abundance of stable isotopes (^{13}C and ^{15}N) was intermediate between MH and photosynthetic plants at the same site (Gebauer & Meyer 2003). More recently, it has been shown that PMH is more widespread among orchids than previously assumed (Schiebold et al. 2018). Only a minority of orchids remain achlorophyllous as adults and are fully mycoheterotrophic throughout their life cycles. These species have evolved repeatedly from photosynthetic ancestors and potentially PMH orchids have been the intermediate step (Julou et al. 2005). Mycoheterotrophy is considered a mode of parasitism in plants, as there is no

known reward to the fungal partner (Merckx & Freudenstein 2010). Though the contribution of green orchids to the relationship has been debated for many years, the exact nature of the fungus-orchid relationship is still unresolved due to technical challenges in monitoring nutrient exchange between the fungus and orchid in the wild. A possibility of a mutualistic relationship has been suggested on the basis of a couple of in vitro studies that show transport of nutrients from the orchid to the fungus (Cameron et al. 2006, 2008) or the expression of genes implicated in mutualistic relationships (Perotto et al. 2014; Fochi et al. 2017). Alternatively, orchids may provide other possible benefits to fungi, such as vitamins or protection of hyphae (Selosse 2014).

Orchid mycorrhiza (OrM) is characterized by the formation of fungal hyphal coiled structures – called pelotons – inside germinating seeds, protocorms (pre-seedling stages formed after germination), seedlings and roots of adult orchids (Fig. 1). Occasionally OrM fungi have also been found in rhizomes, tubers or corms (Rasmussen 1995). Pelotons can be found within parenchyma cells where they are surrounded by a plant-derived membrane and an interfacial matrix. The pelotons are constantly digested or collapsed and formed again either by any survived hyphae or by fungi penetrating from adjacent cells (Smith & Read 2008). Digestion of pelotons is one way how nutrients flux to the host orchid (Bougoure et al. 2014; Kuga et al. 2014). However, it has been shown that nutrient transfer can occur also from fully intact, unlysed pelotons (Kuga et al. 2014). It seems that both means of nutrient transfer can occur only in autotrophic orchids, as shown for protocorms of *Spiranthes sinensis* colonised by *Ceratobasidium* (Kuga et al. 2014).

Historically, the identification of OrM fungi was possible when fungi from orchid roots were isolated in a pure culture and thereafter inspected with microscopy. This method is considered to be time consuming and inefficient, mainly because many OrM fungi are either unculturable, grow too slowly, or rarely sporulate. Technical advances in molecular methods have greatly facilitated fungal species identification and thereby the range of OrM fungi has expanded (Taylor & Bruns 1997, 1999). A more recent approach, high-throughput sequencing methods, has allowed quick and more thorough characterization of fungal communities in orchid roots or in soil, and has offered new insights into OrM fungal community ecology (Jacquemyn et al. 2014; Ercole et al. 2015; McCormick et al. 2016; Waud et al. 2016a,b; Rock-Blake et al. 2017; Voyron et al. 2017). Although DNA sequencing based identification of fungi is highly appealing for studying OrM fungi, there can be several methodological complications. The most discussed question in molecular studies of OrM fungi has been the selection of primers (Taylor & McCormick 2008; Waud et al. 2014), whereas less attention has been paid to the quality of the reference database. The demand for high-quality reference datasets is most critical in large-scale sequence analyses because it is essentially impossible to evaluate each taxonomic assignment manually. It is known that the public sequence repositories contain a non-trivial number of incorrectly identified species and lack of metadata (Nilsson et al. 2006). In addition, these databases contain technical arte-

facts, such as chimeric or low read quality sequences (Nilsson et al. 2010). These shortcomings have been improved by regularly updated and manually curated databases (Abarenkov et al. 2010; Kõljalg et al. 2013).

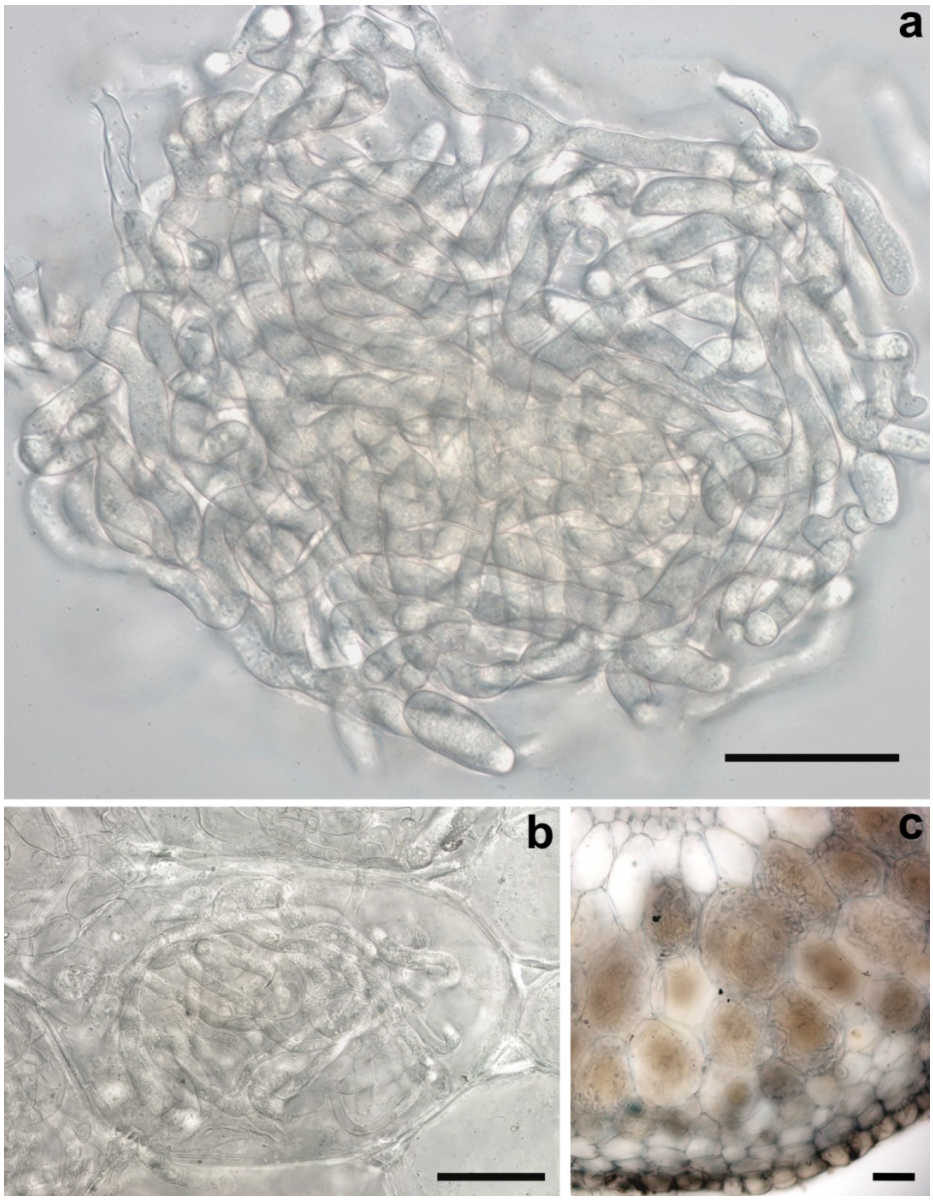

Figure 1. Morphological features of fungal structures in the roots of *Platanthera chlorantha*. a) A single coiled structure of OrM fungal hyphae or peloton outside roots. Scale bar = 50 µm. c) A single coiled structure of OrM fungal hyphae or peloton inside root tissue. Scale bar = 50 µm. b) Cross-section of a root showing fungal colonization. Scale bar = 100 µm. Photos by J.Oja.

Typically photosynthetic, autotrophic orchids associate with saprotrophic fungi from the Ceratobasidiaceae, Tulasnellaceae and Sebacinales (particularly Serendipitaceae), whereas most fully and partially mycoheterotrophic orchids associate with ectomycorrhizal (EcM) basidiomycetes, such as Thelephoraceae, Russulaceae (Dearnaley et al. 2012). Even EcM ascomycetes – related mostly to truffles – have been proved to form OrM associations with PMH orchids (Selosse et al. 2004). Associations with EcM fungi allow orchids to obtain C from surrounding autotrophic plants via shared fungal symbiont (McKendrick et al. 2000). Besides these aforementioned fungal taxa, several other fungal taxa can form OrM. In tropical and subtropical forests litter or wood-decaying saprotrophic fungi are able to support many MH orchids (Yamato et al. 2005; Ogura-Tsujita & Yukawa 2008; Martos et al. 2009; Ogura-Tsujita et al. 2009; Lee et al. 2015; Kinoshita et al. 2016). Often these saprotrophic fungal partners have been assigned to Mycenaceae (Martos et al. 2009; Ogura-Tsujita et al. 2009; Kinoshita et al. 2016) and Psathyrellaceae (Yamato et al. 2005; Ogura-Tsujita & Yukawa 2008). However, some MH orchids in tropical and subtropical forests have been shown to associate with EcM fungi (Roy et al. 2009; Okayama et al. 2012). Most recently, some photosynthetic, autotrophic orchids have been shown to be associated with certain saprotrophic fungi, again, belonging to Mycenaceae and Psathyrellaceae (Zhang et al. 2012; Yagame et al. 2013; Bayman et al. 2016). In one case, there is speculation that the green orchid *Cremastra appendiculata* associated with saprophytic *Coprinellus* (Psathyrellaceae) is instead PMH (Yagame et al. 2013). So far, the most unexpected example of fungal partners has been reported from some epiphytic and terrestrial autotrophic orchids in the tropics. These orchids were associated with members of the "rust" lineage of Atractiellomycetes (Pucciniomycotina, Basidiomycota; Kottke et al. 2010; Martos et al. 2012; Suárez et al. 2016). Taken together, a wide phylogenetic range of fungi have been reported to be able to form orchid mycorrhizal associations (Dearnaley et al. 2012). Yet, in this thesis we focus on OrM fungal taxa from the Ceratobasidiaceae, Tulasnellaceae and Sebacinales – the main group of mycorrhizal symbionts in most orchid species.

Seed germination and nutrition of adult plants is often facilitated by the same fungal taxa. However, some orchids switch or expand their OrM fungal partners during the development stages from seedling to adults (Rasmussen et al. 2015 and references therein). It has been shown that the seedling stage appears to be the developmental step when the diversity of symbiotic fungi is smaller compared to the germinating seeds and mature orchids (Bidartondo & Read 2008; Jacquemyn et al. 2011a; Zi et al. 2014). Changes in fungal communities associated with orchid roots have been described throughout different plant phenological stages, mostly from leafing to dormancy (Taylor & Bruns 1999; Rasmussen & Whigham 2002; Huynh et al. 2009; Kohout et al. 2013; Ercole et al. 2015). Most of these studies have reported a continuous presence of mycorrhizal fungi, but in some cases the abundance of fungal colonisation and the composition of fungal taxa have shown variations (Taylor & Bruns 1999; Rasmussen & Whigham 2002; Ercole et al. 2015). Besides the phenological

stage of orchids, mycorrhizal infection can be linked to the age of roots (Rasmussen & Whigham 2002; Shefferson et al. 2005) or different environmental stresses (McCormick et al. 2006). For example, in stressful conditions, orchids switch to new fungal partners due to the disappearance of the main fungal partner (McCormick et al. 2006).

Due to the crucial role of OrM fungi in plant survival, it has been constantly assumed that the distribution of these fungi determines the abundance and spatial distribution of orchid populations (McCormick & Jacquemyn 2014). Very little is known about the distribution and ecological requirements of OrM fungi, particularly those that associate with photosynthetic orchids. The biogeographical overview of OrM fungi suggests that OrM fungi associated with photosynthetic orchids are widespread and occur – like orchids – in varied habitats (Jacquemyn et al. 2017a). However, these fungi are independent of the distribution of orchids and most likely they are litter and soil saprotrophs, endophytes, EcM or necrotrophic pathogens (Roberts 1999; Tedersoo et al. 2010; Oberwinkler et al. 2013; Veldre et al. 2013). Tracking the distribution of these fungal taxa in nature is challenging, as they do not form conspicuous fruitbodies. Nevertheless, there is some indirect evidence of their distribution and abundance in the soil that has been revealed by the orchid seed-sowing method. In this method seeds are buried and retrieved in the field inside packets which retain seeds, but allow fungal hyphae to pass through and promote germination (Rasmussen & Whigham 1993). Results of several seed-sowing studies suggest that the presence of OrM fungi declines with increasing distance from the photosynthetic adult plants (e.g. Perkins & McGee 1995; Jacquemyn et al. 2007, 2012b; but see Masuhara & Katsuya 1994). While successful germination of seeds can be intertwined by abiotic and biotic factors (Batty et al. 2001; Diez 2007), molecular techniques provide better evidence of fungal distribution and abundance in soil. These recent studies have also demonstrated the distance-dependent decline in OrM fungal abundance (McCormick et al. 2016; Waud et al. 2016a, b; but see Voyron et al. 2017). Nonetheless, some OrM fungi are extremely sporadic and often even undetectable in soil adjacent to orchid roots (Voyron et al. 2017; Egidi et al. 2018). Within sites, orchid population dynamics are driven by the abundance of OrM fungi rather than solely by their distribution (McCormick & Jacquemyn 2014; McCormick et al. 2018). The factors that affect the abundance of OrM fungi have been less studied. McCormick et al. (2012) showed that organic amendments affect the abundance of mycorrhizal fungi.

In summary, though we are still lacking a comprehensive understanding of the factors shaping the fungus-ochid relationship, studying the aspects of this relationship using complementary methods holds the greatest promise of providing a better understanding of the factors that determine the occurrence and persistence of orchids in the wild and possible implications of their conservation strategies. Numerous studies have focused on finding specific fungus-orchid associations and their impact on orchid rarity (Bailarote et al. 2012; Waud et al. 2017). A recent meta-analysis of data on different mycorrhi-

zal types shows that orchids tend to display greater specialization towards their fungal partners (Põlme et al. 2018). Often MH orchids associate only with a narrow range of closely related fungal taxa (e.g. Ogura-Tsujita & Yukawa 2008; Barrett et al. 2010; Kennedy et al. 2011; Okayama et al. 2012), with some exceptions (Martos et al. 2009; Roy et al. 2009). However, in general, mycorrhizal specificity is unrelated to orchid rarity (McCormick & Jacquemyn 2014). Taken together, we are starting to realize that an effective protection of orchids must focus not only on conserving their populations *per se*, but must also consider the ecological requirements of the organisms interacting with the orchids. Such a focus on the relationship of orchids with other organisms is exemplified in Australia where it has been shown that the presence of pollinator and OrM fungi determines the survival and persistence of orchids in re-introductions (Reiter et al. 2016). A deepened understanding of the relationship of orchids with other organisms in turn paves the way for improving the preservation of orchids in the wild.

In this thesis, we focus on putative OrM fungal taxa from the Ceratobasidiaceae, Tulasnellaceae and Sebacinales and their association with photosynthetic orchids in different habitats. The main aims of this thesis were the following:

- How does the community composition of putative OrM fungal taxa change over the vegetation period in relation to the developmental phases of host orchid species (paper **I**)?
- How does the community composition of putative OrM fungal taxa vary across different habitats (paper **I**) and within the same habitat (paper **II**)?
- How does the richness of putative OrM fungi change with the increasing distance from the orchid patches (paper **II**)?
- Do putative OrM fungi form spatial patterns along the distance from the orchid patches (paper **II**)?

In addition, our aim was:

- To extend annotations of publicly available OrM fungal ITS sequences (paper **III**)

2. MATERIALS AND METHODS

2.1. Studied species and their mycorrhizal associations

In total, four orchid species: *Cypripedium calceolus* L., *Neottia ovata* (L.) Bluff & Fingerh. (formerly known as *Listera ovata*), *Orchis militaris* L. and *Platanthera chlorantha* (Custer) Rchb were used as focal host species to study temporal and spatial patterns of OrM fungal communities (Fig. 2; papers **I** and **II**). The first three species were studied in paper **I** and the third and fourth species in paper **II**. All these orchids grow preferably on calcareous soil but in different habitat types. *C. calceolus* has 1–2(3) large flowers with yellow, shoe-shaped labellum (Fig. 2A). It grows most commonly in woodlands, less frequently in open habitats. The distribution of *C. calceolus* ranges from Great Britain to Japan, and from Spain to Scandinavia (Kull 1999). *N. ovata* has 15–30(100), small, green or yellowish-green flowers within inflorescence (Fig. 2B). This species occurs in a wide range of habitats in Euro-Siberia, mostly in shaded places (Kotilínek et al. 2015). The plants of *O. militaris* have a conical inflorescence with 7–42 purple flowers that morphologically resemble a human figure, a soldier (Fig. 2C). They are widely distributed across Eurasia, growing mostly in grasslands and open woodlands (Farrell 1985). *P. chlorantha* has inflorescence with 8–40 white-green flowers with a slender, long nectar-filled spur (Fig. 2D). It occurs preferably in the same habitats as *O. militaris* throughout Europe and adjacent parts of Africa and Asia (Hultén & Fries 1986). *C. calceolus* and *N. ovata* are both rhizomatous orchid species with long lasting roots, whereas tuberous orchids *O. militaris* and *P. chlorantha* have short-lived and annually renewed roots (Rasmussen 1995).

Multiple studies have investigated OrM fungal species of *C. calceolus* and *O. militaris*, whereas until very recently little was known about OrM fungal species of *N. ovata* and *P. chlorantha*. Investigations of mycorrhizal fungi in both *C. calceolus* and *O. militaris* have revealed their preferential association with members of *Tulasnella* (Shefferson et al. 2005, 2007, 2008; Jacquemyn et al. 2010, 2011a, 2012a; Lievens et al. 2010). A few previous studies of *N. ovata* and *P. chlorantha* have described associations with Ceratobasidiaceae and Tulasnellaceae (Rasmussen 1995; Bidartondo et al. 2004). Most recent studies show that *N. ovata* and *P. chlorantha* associate predominantly with Sebacinales and Ceratobasidiaceae, respectively (Jacquemyn et al. 2015; Těšitelová et al. 2015; Esposito et al. 2016). Besides the dominant OrM fungal taxa, other fungal species have been detected in the root samples of all the studied orchid species, except *C. calceolus* (Illyes et al. 2009; Jacquemyn et al. 2010, 2011a,b, 2015; Těšitelová et al. 2015, Esposito et al. 2016). For example, EcM fungi from different lineages (Jacquemyn et al. 2011b, 2015; Těšitelová et al. 2015; Esposito et al. 2016) and some non-mycorrhizal fungal taxa have been reported (Bidartondo et al. 2004; Jacquemyn et al. 2015; Těšitelová et al. 2015; Esposito et al. 2016).

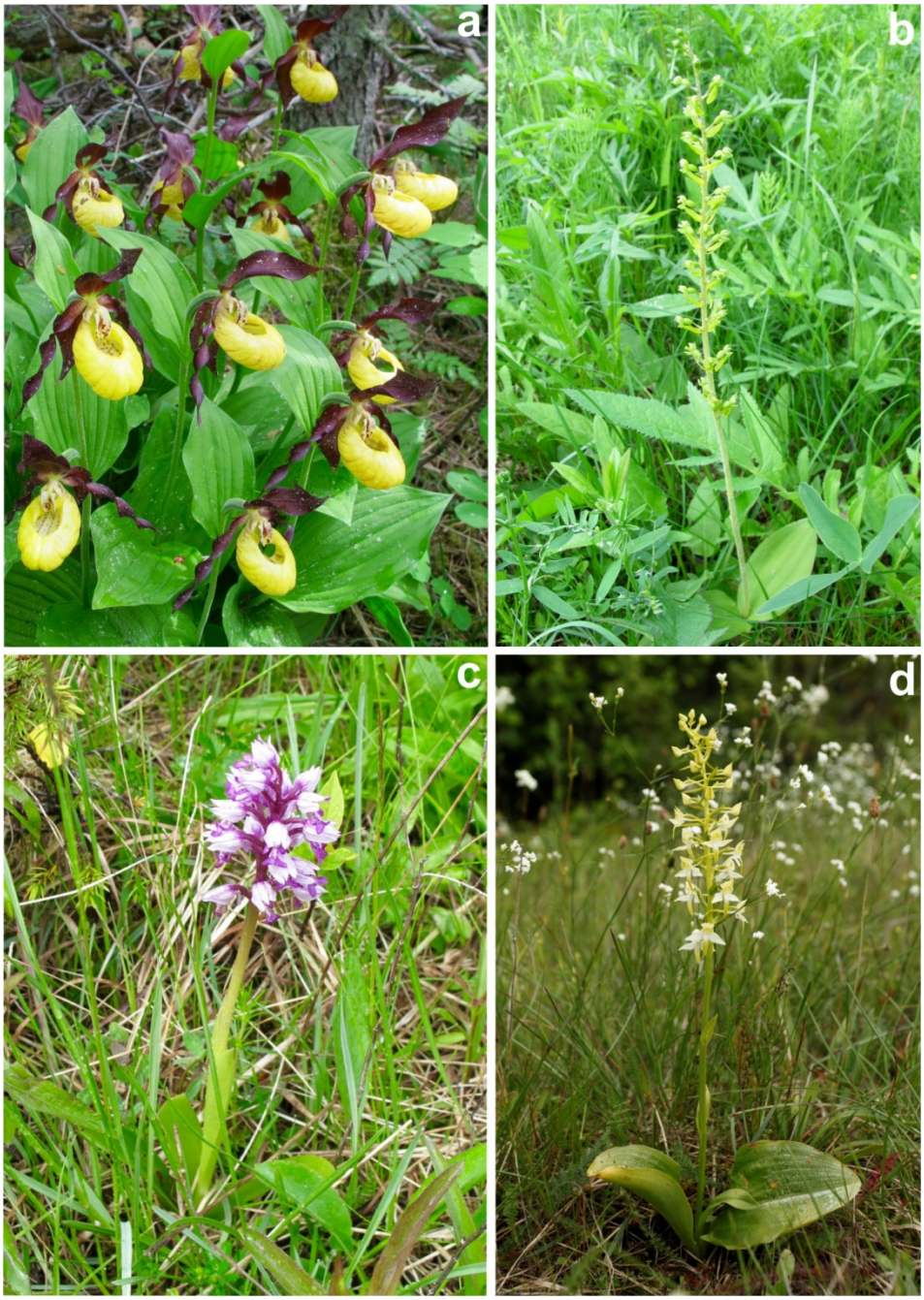

Figure 2. Photos of studied orchid species a) *Cypripedium calceolus* b) *Neottia ovata* c) *Orchis militaris*, and d) *Platanthera chlorantha*. Photos by J. Oja (a,b,c) and A.-R. Servet (d).

2.2. Study sites and sampling

Sampling was conducted in forest and grassland ecosystems throughout the western part of Estonia, mainly on the islands of Saaremaa and Muhu (Fig. 3). For paper **I**, we sampled *C. calceolus* and *N. ovata* from two forest sites, and *N. ovata* and *O. militaris* from two meadow sites (Table 1 in paper **I**). Samples were collected three times (June, July and August) at four week intervals during the vegetation period in 2011. At each sampling time, we collected roots from three different orchid individuals per species and adjacent soil in each site. The collected plants were characteristic to each collecting time (pre-flowering, full bloom and post-flowering). In total we sampled 72 orchid plants and 72 soil samples.

For paper **II**, we collected root samples of *O. militaris* and *P. chlorantha* from 21 semi-natural calcareous grasslands in July 2012. Additionally, at each site we established one transect with increasing distance from the outermost plant individual of a population of either focal plant species. In several sites, we collected additional orchid individuals of both focal orchid species from other parts of the population to provide additional material for identification of putative OrM fungal species (Table S1, in **II**). Altogether, we sampled 56 orchid plants and 287 soil samples from 21 transects. In the vicinity of focal plants and along the transect, we assessed four environmental variables: i) the level of grazing; ii) overgrowth by trees and shrubs; iii) the severity of periodical drought and waterlogging; and iv) the abundance of the host orchids (for detailed information see Table S2, in **II**).

All root and soil samples were collected by using either a knife (**I**) or polyvinyl chloride (PVC) tubes (**II**). For both studies, we collected five to seven root fragments per plant individual and approximately the same amount of soil. For paper **I,** we sampled soil surrounding the roots of orchid plants, whereas for paper **II** soil samples were collected using a nested design with base-2-logarithmically increasing distance commonly starting from beneath the orchid and reaching up to 32 m (Table S1 in **II**). All root and soil samples were placed immediately into plastic bags and processed on the same day. Orchid roots were carefully cleaned from adhering soil, followed by surface sterilisation in a 10% solution of commercial bleach for 1 min, and rinsed in water. Surface-sterilized roots were cut into 5 mm fragments with a sterilized razor blade and air-dried. Soil samples were either air-dried and stored in zip-lock plastic bags (**I**) or frozen for one month at -20 °C and then crushed and air-dried at 30 °C for 24 hours (**II**). For molecular analyses (papers **I** and **II**), we powdered 0.02 g of randomly selected root fragments and 0.2 g of the finest soil particles in 2-ml tubes using two 3-mm tungsten carbide beads in Mixer Mill MM400 (Retsch GmbH, Haan, Germany).

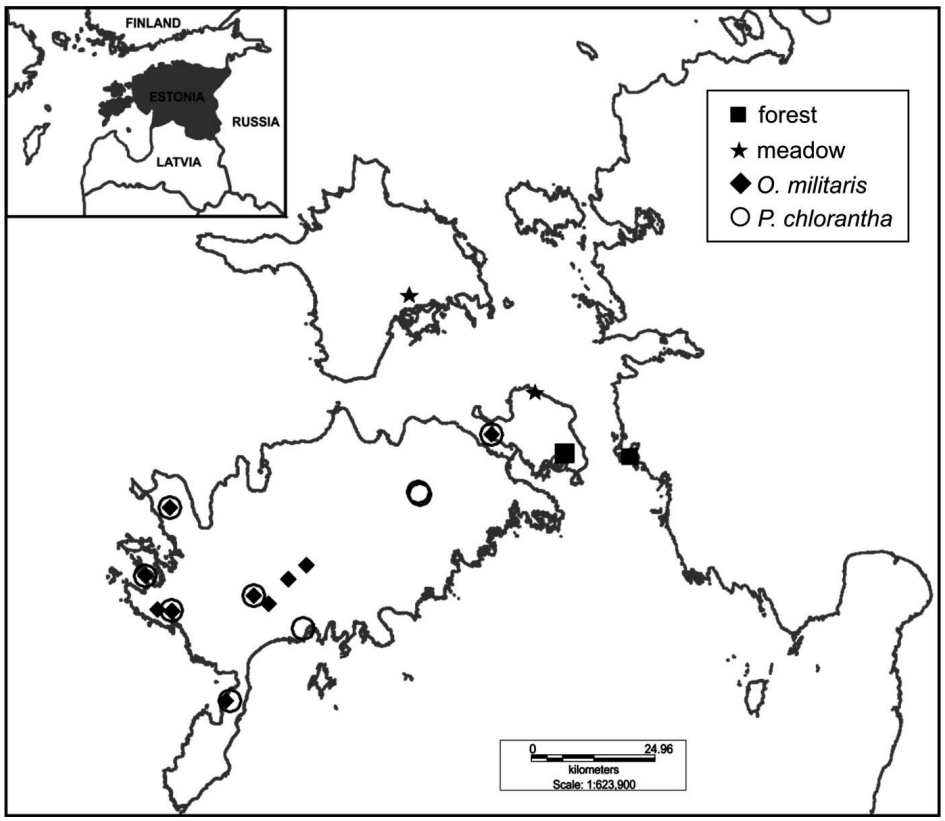

Figure 3. Locations of the study sites (**I–II**). Symbols indicate forest and meadow sites where different orchid species were sampled (**I**) and two orchid species studied in semi-natural grasslands (**II**). Due to the close spacing of some study sites, the symbols overlap (for coordinates of each site see Table S1 in paper **II**).

2.3. Molecular analyses

For papers **I** and **II**, the total DNA was extracted from powdered root and soil samples as well as from two positive (*viz* fruit-bodies of *Peziza* sp. and *Hydnoplicata whitei* from Australia) and negative controls using a PowerSoil DNA Isolation Kit (MoBio, Carlsbad, CA, USA) according to the manufacturer's instructions. Positive and negative controls were included to reduce as much noise (e.g. contaminant sequences, inaccurate clusters) from the datasets as possible (Nguyen et al. 2015). To identify a wide variety of fungal species including Tulasnellaceae, the full internal transcribed spacer (ITS) region was amplified with primer pairs ITS1ngs-ITS4ngs and ITS1Fngs-ITS4ngs (paper **I**; Tedersoo et al. 2014, 2015a). Each of the primers was tagged with a unique barcode (MID, 10-12 bases) that was modified according to the recommendations by Roche. A detailed description of PCR protocols and preparation for

pyrosequencing can be found in paper **I** and **II**. The PCR products were pyrosequenced using the Roche GS FLX+ platform and Titanium chemistry. For paper **II**, samples that originally retrieved <20 sequences were re-run in the same platform. Sequencing datasets with metadata are available in UNITE repository in raw quality-filtered formats in order to enable further analysis of high-throughput sequencing datasets (Tedersoo et al. 2015b). To our knowledge, this is the first PhD thesis at the University of Tartu which includes datasets with Digital Object Identifier (DOI) besides publications (dataset IV and V). In addition to pyrosequencing in both papers, DNA extracts from root samples were re-amplified with primer ITS1 in combination with ITS4-Tul2 (5′-TTCTTTTCCTCCGCTGAWTA-3′) to identify *Tulasnella* species that are not captured with universal and other fungal-specific primers. Sequencing was performed in Macrogen Inc. (Amsterdam, The Netherlands).

2.4. Bioinformatics and statistical analyses

The pyrosequencing data was processed using a combination of ACACIA 1.52 (Bragg et al. 2012) and MOTHUR 1.30.2 (Schloss et al. 2009). In brief, after quality filtering aberrant, short or low quality sequences were excluded (more details in paper **I** and **II**). High-quality sequences were clustered into Operational Taxonomic Units (OTUs) at 97% similarity using CROP 1.33 (Hao et al. 2011). Thereafter, all singletons were omitted and remaining OTUs were taxonomically assigned based on the 10 best BLAST results of their representative sequences using the International Nucleotide Sequence Databases Collaboration (INSDC) and UNITE (Abarenkov et al. 2010) databases. Identified OTUs were manually screened for putative OrM fungal taxa. Only OTUs from the main OrM fungal groups (Tulasnellaceae, Ceratobasidiaceae and Sebacinales) were considered potential mycorrhizal partners, because of the information from the roots of these focal orchid species or their congeners that was available at the time, and used for further analyses. For paper **II**, we additionally conducted indicator species analysis (Dufrene & Legendre 1997) to detect characteristic fungal taxa associated with studied orchid species, *O. militaris* and *P. chlorantha*.

Multiple statistical analyses, i.e., different versions of analysis of variance (ANOVA), regression, were used to test the main determinants of putative OrM fungal richness in soil and roots (papers **I** and **II)**. In both studies, we calculated residuals of OTU richness in relation to the square root of sequencing depth to account for the unequal sequencing depth across samples (Tedersoo et al. 2014). In addition, we analysed the relationship between the richness of putative OrM fungal taxa and the distance from host plant for each transect individually and across study sites with linear regression (paper **II**). This potential relationship was explored at two distances of transect, e.g. up to 1m and maximum distance of the transect.

Multivariate permutational analysis of variance (PERMANOVA) was performed to identify the main determinants of the putative OrM fungal commu-

nity composition in soil and roots as implemented in adonis routine of the Vegan package of R (Oksanen et al. 2013; R Core Team 2014; papers **I** and **II**). Raup-Crick and Bray-Curtis indices were used to generate distance matrices for community composition for paper **I** and **II**, respectively. Patterns of community composition and the effects of significant variables were visualized using a Non-metric Multidimensional Scaling (NMDS) using the R software package Ecodist (**I**) or Vegan (**II**).

For paper **II,** the community variation for putative OrM fungal taxa among each soil transect sample points was analysed with Mantel tests as implemented in Ecodist package of R (Goslee & Urban 2007). To test the spatial autocorrelation in OrM fungal community composition across soil samples per transect we calculated Mantel correlograms at nine distance classes. Bray-Curtis and Euclidean indices were, respectively, used to generate distance matrices for community composition of putative OrM fungal taxa and geographical coordinates. For the study sites with significant spatial turnover, we calculated the slope of the relationship between the geographic distance matrix and community dissimilarity matrix (Bahram et al. 2013).

2.5. Sequence annotations

In paper **III**, we focused on all public OrM fungal ITS sequences of the INSDC as mirrored in the UNITE database, available as of January 18, 2011. Only short sequences (<200 bp in length) and sequences derived from NGS studies were excluded. The annotation of sequence quality and addition of metadata to the existing INSDC entries were performed in two steps. The first step was based on taxonomic group searches and the second on scientific study searches (Fig. 1 in paper **III**). In the first step, all OrM fungal taxonomic groups were retrieved using the names of the inclusive taxa as search strings in the organism field in the PlutoF workbench. In addition, several randomly selected representative sequences or fully identified species of OrM fungi were used as a query in BLASTn and emerencia searches against INSDC for retrieving potential OrM fungi among unnamed sequences. Subsequently, all of these sequences were aligned multiple times, followed by blast searches and Maximum Likelihood analyses. In this way, we could identify chimeras, reverse complementary sequences and sequences belonging to non-targeted taxa. In the second step, sequences of OrM fungi were downloaded by studies and provided with metadata on the isolation source, locality and interacting taxon (host). In addition, we added a remark whether or not fungus formed pelotons and/or stimulated germination or development of orchids. Both remarks provide considerable confidence to say that a fungus can form OrM.

3. RESULTS

3.1. Orchid mycorrhizal fungal richness

In total we detected 67 and 61 OTUs (species) of putative OrM fungi in temporal (**I**) and spatial (**II**) variation analyses, respectively. The number of OrM fungal OTUs was significantly higher in forest than in meadow soil (**I**). Most of the OrM fungi in forest were OTUs of Sebacinales. Overall, Sebacinales was the most OTU-rich OrM fungal taxon in the soil samples (paper **I** and **II**). In study **I**, we found 46 OTUs assigned as Sebacinales (average 0.64 OTUs per soil sample), whereas in study **II** the number of OTUs of Sebacinales was 34 (average 0.12 OTUs per soil sample). The number of OTUs of Ceratobasidiaceae and Tulasnellaceae in soil samples varied across studies, yet the range of OTUs for both was noticeably lower than OTUs of Sebacinales. In study **I**, Ceratobasidiaceae and Tulasnellaceae accounted for 10 and 5 OTUs, respectively. In study **II**, the respective families accounted for 9 and 13 OTUs. Across semi-natural grasslands, the number of OrM fungal OTUs remained unaffected by studied environmental variables (paper **II**). Similarly, the richness of putative OrM fungal OTUs was unaffected by the spatial proximity of the host plant. In only a few sites did we find that the richness of some OrM fungal OTUs declined with increasing distance from the host plants (paper **II**).

In roots, we found that the richness of putative OrM fungal OTUs studied in semi-natural grasslands was significantly affected by host species (paper **II**). In particular, the richness of OrM fungal OTUs was higher in the roots of *O. militaris* than in the roots of *P. chlorantha*. However, the number of OrM fungal OTUs in the roots of *O. militaris* did not differ substantially from the number of OrM fungal OTUs detected in the roots of *C. calceolus* and *N. ovata* (**I**).

3.2. Orchid mycorrhizal fungal community composition

Overall, we found some factors driving the variation in the community composition of putative OrM fungi in soil. The community composition of putative OrM fungi in soil samples from semi-natural grasslands were affected by grazing and spatial factors (paper **II**), whereas habitat and time played a negligible role for OrM fungi in soil samples studied in meadow and forest sites (paper **I**).

In roots, the community composition of putative OrM fungi displayed more distinguishable patterns. The community composition of the OrM fungi in roots was primarily affected by the host (papers **I**, **II**). The roots of *O. militaris* and *C. calceolus* were predominately associated with Tulasnellaceae OTUs, whereas Sebacinales and Ceratobasidiaceae colonised most commonly the roots of *N. ovata* and *P. chlorantha*, respectively (Table 3 in **I** and Fig. 2 in paper **II**). In case of the mycobionts of *O. militaris*, the indicator species analysis revealed that in addition to Tulasnellaceae, OTUs of Sebacinales were also characteristic

partners (Table 2 in **II**). In addition to the host effect, we found that habitat and time also affected OrM fungal community composition (Fig. 3a in **I**). The effect of these factors was particularly evident in the OrM fungal community of *N. ovata.* The composition of OrM fungal community in roots sampled across semi-natural grasslands was not affected by local environmental conditions (paper **II**).

3.3. Orchid mycorrhizal fungal spatial structure

In paper **II**, Mantel tests indicated significant spatial turnover in a few study sites for putative OrM fungal taxa. The average slope of distance-decay of similarity for putative OrM fungi was low. In only a single site did Mantel correlograms reveal significant positive autocorrelation for putative OrM fungal taxa in soil at fine spatial scale.

3.4. Annotation of orchid mycorrhizal fungal sequences

As of January 18, 2011, INSDC comprised 183,208 fungal ITS sequences, of which 2,267 were recovered from the roots of orchids (**III**). Of these OrM fungal sequences, we identified and annotated 11 (0.5%) chimeric sequences and 121 (5.3%) sequences of potentially low quality. In the second step of annotation, we supplemented sequence entries with metadata retrieved from 93 OrM fungal studies. The availability of metadata varied greatly among mycorrhizal types. We found that OrM fungal sequences were most frequently equipped with information on host (1608 entries), isolation source (1335) and country (1150), whereas information on geocode (i.e. latitude and longitude, 91) was particularly scarce and no information on whether or not fungus formed pelotons and/or stimulated germination or development in orchids was available. Most of the missing information we retrieved and added to the sequence entries of OrM fungi was on country (903 entries), followed by information on isolation source (874), geocode (605) and host (557). In addition, we obtained 1,591 and 676 sequences originating directly from orchid roots and living cultures, respectively. The majority of experimentally tested isolates stimulated seed germination or growth of their host plants. These annotated sequences are publicly available via UNITE (http://unite.ut.ee/).

4. DISCUSSION

In general, our findings demonstrate that the community composition of OrM fungi in orchid roots is primarily host-dependent and only secondarily affected by other factors (I, II). All orchid species studied by us were associated with multiple OrM fungi, although distinctive preferences for fungal partners were present among species. In particular, *C. calceolus* and *O. militaris* associated preferentially with Tulasnellaceae, whereas *P. chlorantha* and *N. ovata* favoured Ceratobasidiaceae and Sebacinales, respectively. These results are consistent with the previous reports of respective orchid species (Shefferson et al. 2005, 2007, 2008; Jacquemyn et al. 2010, 2011a, 2012a, 2015; Lievens et al. 2010; Těšitelová et al. 2015; Esposito et al. 2016). To date, there is a large amount of evidence from high-throughput sequencing studies that multiple fungal species co-occur within orchid roots, however, one or two fungal taxa tend to dominate over others (e.g. Jacquemyn et al. 2015; Těšitelová et al. 2015; Esposito et al. 2016). It has even been shown that more than one fungus can colonise a single peloton (Kristiansen et al. 2001). Association of an orchid with several OrM fungal taxa provides a wider range of nutrients via mycorrhizal fungi (Nurfadilah et al. 2013) and the orchid can be expected to have better opportunities for survival in nature, yet a single widespread fungus could be sufficient for the distribution and abundance of orchids (McCormick & Jacquemyn 2014). Therefore, the low number of OTUs found in the roots of *C. calceolus* does not necessary mean that this species is facing extinction. It has been shown that widely distributed *C. calceolus* exhibits strikingly narrow mycorrhizal specificity (Shefferson et al. 2007). Many studies of photosynthetic orchids indicate that the decline of orchids species and rarity is not necessarily related to mycorrhizal specificity (Shefferson et al. 2007; Bailarote et al. 2012; Pandey et al. 2013). Besides the main OrM fungi in roots of autotrophic orchids, other fungi, such as EcM, saprotrophs, endophytes and pathogens, have been frequently recorded (Dearnaley et al. 2012; Kohout et al. 2013), although their functional importance remains unclear. So far, we only know that EcM fungi provide nutrients to PMH and MH orchids (Gebauer & Meyer 2003). A recent study of stable isotopes suggests that EcM fungi in photosynthetic orchids are not massively contributing to the carbon budget of orchids (Jacquemyn et al. 2017b).

The community composition of OrM fungi in roots was significantly distinct in different habitats (I). Local environmental factors showed no effect on OrM fungal communities of orchids across semi-natural grasslands (II). The effect of habitat was conspicuous in the community composition of OrM fungi of *N. ovata*. It was evident for *N. ovata* that the OTUs of Serendipitaceae occurred equally in root samples from forest and meadow sites, whereas OTUs of the EcM Sebacinaceae were more frequent in forest sites. Two other studies of *N. ovata* have also shown that the most common associating partners were from the fungal family Serendipitaceae (Jacquemyn et

al. 2015; Těšitelová et al. 2015). However, the composition and phylogenetic position of Sebacinales associated with *N. ovata* were only little influenced by the habitat type (Těšitelová et al. 2015). Our results seem to be in line with other studies that have shown noticeable differences in the OrM fungal communities of single orchid genus as well as of single orchid species (Pandey et al. 2013; Esposito et al. 2016; Jacquemyn et al. 2016; Waud et al. 2017). These findings suggest that habitat conditions can affect the occurrence of OrM fungi, hence the plant-fungus interaction. For example, the variation in OrM fungal communities can be driven by soil conditions, primarily moisture and pH (Jacquemyn et al. 2015). However, we found no evidence that the OrM fungal community composition in soil was affected by the habitat type. We can suggest that the plant-fungus interaction is driven by specific physiological needs of orchid species in the habitat. A somewhat similar conclusion can be drawn from stable isotope studies that have shown different carbon nutrition of *N. ovata* depending on the study site (Gebauer & Meyer 2003). Across semi-natural grasslands, we found that OrM fungal as well as total fungal community composition in soil were affected by the intensity of grazing. However, OrM fungal community composition in roots was not affected by the studied environmental factors.

The community composition of OrM fungi in roots changed significantly over time (I). However, when orchid species were analysed separately, only the OrM fungal communities of *N. ovata* showed a significant change in time, whereas the effect of time on OrM fungi in *C. calceolus* and *O. militaris* remained non-significant. This could be due to the fact that the latter orchid species were less intensively colonized. Ercole et al. (2015) showed a clear seasonal variation in the mycorrhizal associations of adult *Anacamptis morio* plants. It was shown that *Tulasnella* was more common in autumn and winter, whereas certain ascomycete from the pezizacean clade was very frequent in spring, and *Ceratobasidium* was more frequent in the summer (Ercole et al. 2015). A similar change of ecologically different fungal guilds has been shown for *P. albida* by Kohout et al. (2013). They found that OrM fungi (predominantly *Tulasnella* species) colonised orchids in the summer and endophytes colonised the roots in the autumn, suggesting that the OrM fungi are necessary at certain developmental stages of the adult plants. Huynh et al. (2009) were only able to isolate the main OrM fungi from prefruiting phases of *Caladenia formosa*. Throughout the vegetation period, the intensity of OrM colonisation may vary and lead to a minimum level at some point, i.e., at fruiting time (Rasmussen & Whigham 2002; Roy et al. 2013; Gonneau et al. 2014). Respectively, recent studies have found that the level of fungal C from OrM fungi decreases in above-ground organs towards the end of the growth season (Roy et al. 2013; Gonneau et al. 2014). We found no significant change in the richness of OrM fungi over the vegetative time, although the OTU richness of OrM fungal tended to be the lowest in August in *O. militaris* (annual roots), but not in *C. calceolus* and *N. ovata* (long-lived roots). It has been suggested that seasonal turnover of fungal symbionts occurs in orchids that have annual below-ground

structures rather than in those with perennial root systems (Taylor & Bruns 1999). Notably, the previously studied orchids, *A. morio, C. formosa* and *P. albida*, that had different fungal guilds, are all tuberous (Huynh et al. 2009; Kohout et al. 2013; Ercole et al. 2015). Indeed, the change of symbiotic fungi inside roots may be dependent on the life cycle of symbiotic fungi. On the other hand, the putative OrM fungal community remained relatively stable in soil and there was negligible turnover during the vegetation period. Such different patterns of OrM fungal communities suggest that host plants may choose different mycobionts from the soil species pool over time. At the same time, we cannot exclude the possibility that detected OrM fungal taxa are not physiologically active, and thus make our assessment debatable.

In soil, we found a few instances when the richness of OrM fungi declined with distance from the adult host and limited evidence for spatial structure of OrM fungi (II). We found that forest soil contained more OTUs of OrM fungi than meadow soil (I), whereas across semi-natural grasslands, the number of OrM fungi remained the same and was not affected by studied environmental variables (II). Of all OrM fungal taxa in soil, Sebacinales was the most OTU-rich. The predominance of sebacinoid fungi over other OrM fungi has also been detected in other habitats (Voyron et al. 2017; Egidi et al. 2018). Fungi in the order Sebacinales are commonly present in soil samples around roots, although there is too little information on their life and nutrition in soil (Weiss et al. 2016). More information on nutritional traits could be revealed from genome analyses (Kohler et al. 2015). So far, it has been demonstrated that not all OrM fungi have the same ability to access nutrient and carbon sources (Kohler et al. 2015). Our data show also that OrM fungi found in roots were comparably well recovered from the soil adjacent to orchid roots (I). However, when we studied OrM fungi along transects from host plants, we detected only a few cases when the number of OrM fungal OTUs declined with the distance from the adult orchids (II). A somewhat similar result was recently reported by two other studies of OrM fungi in soil (Voyron et al. 2017; Egidi et al. 2018). One of these studies, Voyron et al. (2017), found that OrM fungal read numbers did not correlate with distance from adult orchid plant and Egidi et al. (2018) reported extremely rare occurrences of OrM fungi in soil directly beneath and distant from adult orchids. However, other recent studies have found distance-dependent declines in the abundance of certain OrM fungal taxa (McCormick et al. 2016; Waud et al. 2016b). This suggests that the distribution of some OrM fungi is dependant on their orchid host, but not for all potential OrM fungi in soil. OrM fungi are commonly regarded as unspecialised saprotrophs with independent distribution of their host plant (McCormick et al. 2012). Distribution dependence on the host would be more expected for the partner for whom the association is obligatory, as it has been shown that the richness of obligately mutualistic EcM fungi declines with increasing distance from host trees (Dickie & Reich 2005). This again raises the question as to what kind of benefits the fungi gain from the orchids (Cameron et al. 2006, 2008) and whether orchids maintain the presence of OrM fungi in habitats (Selosse &

Martos 2014). Our spatial statistics revealed a weak spatial structuring for the communities of OrM fungi in soil, suggesting that they are randomly dispersed, like other saprotrophic fungi (Bahram et al. 2015). However, in orchid-rich Mediterranean grasslands in Italy, it has been shown that the distribution of OrM fungi in soil is similar to spatial patterns of other mycorrhizal fungi (Voyron et al. 2017). Some OrM fungi displayed higher frequency of spatial autocorrelation compared with others, which may reflect either different dispersal patterns or trophic strategies (Voyron et al. 2017). Taken together, it appears that OrM fungi regarded as saprotrophs display more complex and non-uniform distribution patterns. Different distribution mechanisms can be presumed for OrM fungi that associate with fully or partially mycoheterotrophic orchids and at the same time form EcM with autotrophic plants (McKendrick et al. 2002; Těšitelová et al. 2012).

Last but not least, we found that OrM fungal sequences deposited in public databases are poorly annotated with metadata and suffer from low read quality or chimeric sequences (III). Many other studies have claimed that a large proportion of fungal sequences in public databases are not fully identified or are misidentified, and additionally they may have technical artefacts or lack metadata (Ryberg et al. 2009; Kõljalg et al. 2013; Nilsson et al. 2018). Unfortunately, third-party annotations are still not allowed in public databases (Bidartondo et al. 2008). However, there are several quality-filtered, narrow-niche fungal sequence databases and prokaryote databases (DeSantis et al. 2006; Pruesse et al. 2007; Le Calvez et al. 2009; Abarenkov et al. 2010). One of the fungal sequence datasets has been jointly annotated many times by fungal taxonomists (Kõljalg et al. 2013; Nilsson et al. 2018). As a part of one joint annotation, we have provided annotation of sequences quality and addition of metadata to the available OrM fungal entries in public databases. In this way, the sequences are more reliable and can be used in automated species identifiers or for large-scale studies in mycorrhizal data mining, fungal biogeography and phylogenetic community composition.

5. CONCLUSIONS

In contrast to other mycorrhizal types, orchid mycorrhizal symbioses, which only include hosts from a single family, is unique anatomically, taxonomically as well as functionally. The main conclusions of this thesis are as follows:

- The community composition of OrM fungi in roots was primarily host-dependent (I, II). In some cases, the richness of OrM fungi was affected by host species (II). *Cypripedium calceolus* and *Orchis militaris* associated preferentially with the fungal family Tulasnellaceae, whereas *Platanthera chlorantha* and *Neottia ovata* favoured fungal taxa Ceratobasidiaceae and Sebacinales, respectively. In particular, as shown in (II) the richness of OrM fungi was higher in the roots of *O. militaris* compared with the OrM fungi in the roots of *P. chlorantha.*
- The community composition of OrM fungi in roots was significantly affected by habitat, whereas local environmental factors showed no effect on OrM fungal communities of orchids (I, II).
- The community composition of OrM fungi in roots was significantly affected by time (I). The effect of time and habitat was most clearly identified in the OrM fungal community of *N. ovata*.
- In semi-natural grasslands, OrM fungi were randomly distributed and showed little evidence of a distance-dependent decline from the adult orchids (II). However, the richness of OrM fungi was very high in the soil adjacent to orchid roots (I). Mostly, the richness of OrM fungi in soil was affected by habitat, being the highest in forest sites (I).
- Public databases deposited poorly annotated OrM fungal sequences and suffered from low read quality sequences or chimeras (III). However, to date, this can be overcome with the third-party annotations. During one joint third-party annotation, we provided annotation of sequences quality and addition of metadata to the available OrM fungal entries in public databases.

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SUMMARY IN ESTONIAN

Orhideede mükoriisa seenekoosluste ajalised ja ruumilised mustrid metsa ja niidu ökosüsteemides

Orhideelised ehk käpalised (sugukond Orchidaceae) on üks liigirikkamaid õistaimede sugukondi. Teadusele on kirjeldatud enam kui 28 000 liiki orhideesid, millest enamus levib troopikas ning lähistroopikas. Orhideed kasvavad väga erinevates elupaikades (v.a kõrbetes) ja kõikjal maailmas (v.a Antarktikas). Käpalised on tihedalt seotud nii putuktolmeldajate kui ka seenjuurt moodustavate seentega. Kuna käpaliste seemned on tolmpeened ning ilma idanemiseks piisavalt vajalike toitaineteta, siis sõltuvad nad idanemise faasis täielikult seene poolt transporditavatest toitainetest. Sellist toitumistüüpi nimetatakse mükoheterotroofiaks. Pärast edukat seemne idanemist ja nn protokormi staadiumit (idandi algarengu faas) arenevad enamikul käpalistel rohelised lehed ning fotosünteesivõime. Samas on ka fotosünteesivate orhideede juured koloniseeritud seensümbiontide poolt ning taim hangib jätkuvalt vähemalt osa toitainetest seene vahendusel. Mitmed eelnevad teadustööd on leidnud, et mükoriisaseente kooslused võivad muutuda orhideede erinevate arenguetappide jooksul ning täiskasvanud taimede juurtes mingil hetkel asenduda hoopis teist eluviisi seentega. Orhideede mükoriisaseened moodustavad taime juurerakkudes tihedaid seeneniitide kogumikke ehk pelotone (vt Foto 1, lk 8). Viimased esinevad samuti orhideede idanevate seemnete, protokormi ja idandi rakkudes. Orhideedel mükoriisat moodustavad seeneliigid kuuluvad fülogeneetiliselt üksteisest kaugel asetsevatesse taksonitesse. Tavaliselt on rohelised, s.o fotosünteesivad orhideed seotud mullas leiduvate saproobidega sugukondadest Tulasnellaceae ja Ceratobasidiaceae ning seltsist Sebacinales. Seevastu mükoheterotroofsed (mitte-fotosünteesivad) orhideed on vahetanud saproofsed seened biotroofsete vastu. Enamasti on tegu samal ajal puujuurtega ektomükoriisat moodustavate seentega sugukondadest Thelephoraceae ja Russulaceae. Tõenäoliselt on ektomükoriisa seened stabiilsemad ja pikaealisemad toitainetega „varustajad“ kui eelnimetatud saprotroofid. Viimased sõltuvad sobiva surnud orgaanilise aine olemasolust mullas, mis on ebastabiilsem ja lühiajalisem toitainete allikas kui puujuured. Mükoheterotroofsete orhideede puhul on selge, et orhideed parasiteeritavad oma seensümbiontidel. Selline parasitism esineb kõikidel orhideedel arengu algusetappidel, kui taime seeme idaneb. Fotosünteesivate orhideede puhul on aga siiani lahtine küsimus, mis kasu saab seensümbiont antud kooseluvormist, kuna tehniliselt on seda keeruline looduses uurida. Väheste tööde tulemused annavad alust arvata, et toitained võivad vähesel määral siiski liikuda ka orhideedelt seensümbiondile ning kooselu jooksul avalduvad geenid, mis viitavad mutualismile. Alternatiiviks toitainetele võib orhidee pakkuda seenele hoopis vitamiine või pakub seeneniitidele kaitset. Orhideede mükoriisaseened on looduses laialt levinud ning nende levikut orhideed ei mõjuta. Kuid orhidee jaoks mängib seenpartnerite olemasolu ja ohtrus kasvukohas olulist rolli. Seensümbiontide

levikut ning neid mõjutavaid, orhideedest mittesõltuvaid faktoreid on looduses vähe uuritud. Tänu molekulaarsetele meetoditele on võimalik neid seeni määrata otse mullast. Selleks on vajalik referentsandmebaasi, mis sisaldab ekspertide poolt määratud seente geenijärjestusi. Määramiseks võrreldakse neid siis mullast, taimejuurtest või teistest bioloogilistest proovidest saadud seente geenijärjestustega.

Antud doktoritöö käigus uuriti fotosünteesivate orhideeliikide mükoriisa seenekoosluste ajalisi ja ruumilisi mustreid. Töö eesmärgiks oli välja selgitada, 1) kuidas muutuvad ühe vegetatsiooniperioodi vältel täiskasvanud orhideede seensümbiontide kooslused; 2) kas seensümbiontide kooslused on mõjutatud kasvukohatüübist; 3) kas seensümbiontide rohkus on mõjutatud orhidee lähedusest; 4) millised on nende seenekoosluste ruumilised mustrid. Lisaks oli eesmärgiks arendada seente globaalse geenijärjestustel põhineva määraja UNITE referentsandmebaasi. Selle käigus töötati ja analüüsiti artikleid, mis kasutasid orhideede mükoriisaseente määramiseks molekulaarseid meetodeid. Saadud tulemuste põhjal annoteeriti ja täiendati rahvusvahelistes geenipankades olemasolevaid seente geenijärjestusi.

Doktoritöös selgus, et orhideede mükoriisaseente kooslused on esmalt mõjutatud orhidee liigist ning seejärel kasvukeskkonnast ning orhidee arenguetapist (I). Doktoritöös leiti, et kaunis kuldking (*Cypripedium calceolus*) ja hall käpp (*Orchis militaris*) eelistavad seenpartneritena põhiliselt saproobseid seeni sugukonnast Tulasnellaceae, samas rohekas käokeel (*Platanthera chlorantha*) eelistas saproobe sugukonnast Ceratobasidiaceae ning suur käopõll (*Neottia ovata*) seeni seltsist Sebacinales (I, II). Viimase kahe orhideeliigi seensümbionte ei olnud varem uuritud. Kasvukohatüübi ja orhidee arenguetapi mõjud orhideede mükoriisaseente kooslustele olid kõige paremini nähtavad suure käopõlle juurtes (I). Seevastu mullas nende seente kooslused ei olnud mõjutatud kasvukohatüübist ega proovide kogumise ajast (I). Sellest lähtuvalt võib eeldada, et orhidee valib seensümbiondid sõltuvalt oma füsioloogilistest vajadusest ja seeneliikide kättesaadavusest. Ühe kasvukohatüübi piires olid orhideede mükoriisaseened mullas levinud juhuslikult ning üldjuhul ei mõjutanud nende seente esinemist mullas kaugus peremeestaimest (II). Samal ajal esines orhideede mükoriisaseeni ohtralt orhideede juurte vahetus läheduses ning nende liigirikkus oli mõjutatud kasvukohatüübist (I). Kõige rohkem leiti orhideede mükoriisaseeni metsa proovidest (I). UNITE andmebaasi annoteerimisel selgus, et väga vähesed orhideede mükoriisaseente DNA järjestused avalikes andmebaasides sisaldavad metaandmeid, eelkõige proovialaga seonduvaid andmeid (III). Lisaks selgus, et andmebaasides oli mitmeid ebakvaliteetseid orhideede mükoriisaseente DNA järjestusi (III). Suurte andmemahtude analüüsimisel võib see osutuda tõsiseks probleemiks. Andmebaasi annoteerimise tulemused tehti avaandmetena kõigile kättesaadavaks.

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