INTERNATIONAL
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The role of endophytes in agriculture: Abiotic and biotic factors affecting their communities

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A thesis submitted for the degree of

Master of Science (MSc) in Sustainable Agriculture and Business

November 2018

Thessaloniki – Greece

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November 2018
Thessaloniki - Greece

Abstract

The dissertation was written as part of the MSc in Sustainable Agriculture and Business at the International Hellenic University.

As the need for more food is growing combined with the continuously increasing global population, special interest is given to research on the sustainability of agricultural production. The last decade, novel strategies and practices, new substances and organisms, have been introduced in Agriculture. Among these are endophytes too, acting as simulators and promoters of plant growth, as protectors of plants from stresses or pests, even as BCAs. These characteristics make endophytes promising, more-eco-friendly and economically sustainable tools of agriculture. 35 studies of the last 5-year period were selected to review the factors influencing endophytic communities (host, tissue type and abiotic environment) and to discuss whether the type of tissue has greater effect on endophyte community, irrespective of the host species. Additionally, to investigate if there is an effect on endophytic community when environmental conditions change in small or large scale.

The study revealed that host plant may be the main factor, affected directly by abiotic environment, while the type of tissue shapes further the existing endophytic community that has been recruited by host into specific plant compartments. Abiotic environment influences endophytes, too. Endophytic communities present a global homogeneity, with no significant differences in the composition of their communities at the phylum level. However, this does not mean that there are no differences among the individuals of each group at the family, genus and species level shaped by local environmental factors. Thus, there is a general/global pattern of maintenance of endophytic community structure, regardless of the study area, which is influenced at the lower taxonomic levels by local abiotic environmental parameters on the one hand, and by biotic on the other.

At this point I would like to acknowledge and thank cordially my supervisor and the people who contributed to complete this thesis.

Keywords: (endophytes, endophytic community, host effect, tissue type, abiotic environment)

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29-Nov-18

Preface

The present thesis was conducted as part of the MSc in Sustainable Agriculture and Business at the International Hellenic University, Thessaloniki, Greece.

Through this thesis we tried to summarize the roles of endophytes in agriculture and so regarding plants, as well as to study the influence of biotic and abiotic factors affecting endophytic community. The fact that there are not so many studies in this field of science could be a marker for future research prospects. Additionally, much more scientific information is needed in the field of endophytic communities, in order the humanity to be able to use it in applications of agriculture improvement, following the continuously increasing engaging of young people with the agricultural sector in our country and abroad.

I am very grateful and cordially thankful to my supervisor Prof. Dr. Efimia Papatheodorou, as well as Dr. Nikolaos Monokrousos, for their valuable comments and corrections on this thesis. In addition to these people, I would like to acknowledge Dr. Dimitris Schizas. Their help and continuous guidance throughout my MSc courses were particularly important and I am really gratefully indebted to them. Thank you very much for all that you have offered me in the field of knowledge!

Last but not least, I must express my very profound gratitude to my family, who offered me all kinds of support, as well as to all my own people, who shared the joys, the excitement and the sorrows and disappointments I met along the way.

Contents

Introduction

The term "endophytes"

The term "endophyte" can be literally explained as "inside the plant" (endon Gr.=inside, phyton=plant). Endophytes are living organisms which exist, at least, during one part of their lifecycle inside a host plant (Arora and Ramawat, 2017). "Endophyte" was introduced as a term by De Bary (1866) in order to distinguish and describe the "inside-the-plant living" organisms from the epiphytic organisms of a plant surface. Initially, the term was referred to fungi invading the stems and leaves of plants without causing any symptoms or disease (Carroll, 1988; Clay, 1988; Wilson, 1993); nevertheless, today it is widely known that endophytes are able to colonize any organ of the host (Schulz and Boyle, 2006). After several years, Hallmann et al. (1997) gave the most common definition of endophytes, suggesting that endophytes are "...those (bacteria) that can be isolated from surface-disinfested plant tissue or extracted from within the plant, and that do not visibly harm the plant". Nowadays, the term "endophytes" is broad enough, equal to the spectrum of potential hosts and inhabitants, i.e. bacteria (Kobayashi and Palumbo, 2000), fungi (Stone et al., 2000), plants (Marler et al., 1999) and insects in plants (Feller, 1995), but also algae within algae (Peters, 1991), even archaea (Ma et al., 2013; Shi et al., 2015). According to Stone et al. (2000), we can recognize endophytes as (1) endophytic *Clavicipitaceae*; (2) fungal endophytes of dicots; (3) endophytic fungi; (4) other systemic fungal endophytes; (5) fungal endophytes of lichens; (6) endophytic fungi of bryophytes and ferns; (7) endophytic fungi of tree bark; (8) fungal endophytes of xylem; (9) fungal endophytes of root; (10) fungal endophytes of galls and cysts; (11) prokaryotic endophytes of plants (including both endophytic bacteria and actinomycetes, as well as archaea). It is true that there were authors who used to determine mycorrhizal fungi interactions with plant roots as being endophytic interactions (Sieber, 2002), although, a couple of years later this issue was clarified and mycorrhizal interactions were distinguished from endophytic ones, eventhough it is not always clear-cut to discriminate them (Schulz and Boyle, 2006).

The association with plants, evolution and origin

Our present knowledge on diversity and distribution of endophytes' hosts, leads to the fact that plant-endophyte association must be since the ancient times (Clay, 1993). This is also noticed by Arora and Ramawat (2017), who stated that endophytes have been combined with plants since the early beginning stages of their evolution resulting in mutualism in diverse plant categories e.g. monocots, dicots, trees, gymnosperms and bryophytes. The starting point of this evolutionary path is the association of the early terrestrial plants with mycorrhizal fungi; this fact helped plants during evolution (Arora and Ramawat, 2017). There are also records showing the existence of this association for >400 years ago (Krings et al., 2007). In the initial stages of plant evolution, plants moved from aquatic environments to the terrestrial ones. As a result, they had to come up against the conditions of the terrestrial environment (e.g. CO_2, temperature and water availability fluctuations, limited nutrient availability in soil etc.) (Bonfante and Selosse, 2010), something that was attained in combination with endophytes' help. Endophytes adapted themselves into the plants' microenvironment while genetic variation was taking place (e.g. plant DNA uptake). As a result during evolution endophytes started producing metabolites or precursors assisting their hosts and undertaking a very important role in the ecosystem (Arora and Ramawat, 2017).

As it concerns the origin and the entry point of endophytic microorganisms, Sturz and Nowak (2000) stated that this may be from rhizosphere and phyllosphere microflora that penetrated through roots to xylem. Thin-walled cells (e.g. of the apical root zone) or basal root zone (e.g. through cuts, wounds or natural openings) are preferred for enter-points, while endophytes are able to produce cell wall lytic enzymes to dissolve it, such as cellulases and pectinases. Endophytes are also able for two different kinds of transfer; the vertical one (transmission from generation to generation) and the horizontal (transmission to allied species through soil, plant part decay or even through air) (Arora and Ramawat, 2017).

Co-existence and a complicated relationship

During the years and the long period of co-existence, different relationships have been established between endophytes and plants. The host-endophyte interaction can be recognized as mutualism (positive), antagonism (negative) or even neutralism (neutral).

Despite the fact that there are the pre-referred types of interaction, according to Saikkonen et al. (2004) the term “endophyte” has become synonymous with the term “mutualism” in literature. The factors that put pressure on the population and community structure of endophytes is considered to be the eco-habitat, the nutrient level as well as the genetic background of the host. In turn endophytes offer some benefits, such as disease, pest or herbivore resistance, induced host growth, increased nutrient uptake or the production of some kinds of bioactive compounds (Hardoim et al., 2015; Jia et al., 2016). The relationship between plants and endophytes is complicated. Mutualism as a characteristic is addressed in most cases, due to a degree of protection of the host that is afforded (Chanway, 1996). More specifically, the host plants provide nutrients and protection to the endophytes, while the microorganisms facilitate nutrient uptake and provide protection to the plant from possible biotic and abiotic stresses or even pests. In addition to the influence on plant growth, development, fitness and diversity, it has been reported that the presence of an endophyte may affect plant community diversity, population dynamics and functioning of the ecosystem (Saikkonen et al., 1998; Hardoim et al., 2015).

Endophytic diversity

Regarding their diversity, endophytes can be separated in different categories. First of all, they can be divided in prokaryotic (bacterial and archaeal endophytes) and eukaryotic (fungal endophytes). Among prokaryotes the presence of archaeal endophytes has been noticed in several plants, such as coffee cherries (Oliveira et al., 2013), rice (Sun et al., 2008) and maize roots (Chelius and Triplett, 2001), as well as in the arctic tundra rush *Juncus trifidus* (Nissinen et al., 2012). Archaea are represented by two phyla; Euryarchaeota and Thaumarchaeota. Althouh there is a large diversity among endophytic Bacteria (21 phyla), not all phyla are equally distributed. The majority (>96%) of bacterial endophytes are categorized in the 4 phyla; Proteobacteria (54%), Actinobacteria (20%), Firmicutes (16%) and Bacteriodetes (6%), existing in every plant environment (Hardoim et al., 2015; Arora and Ramawat, 2017).

A large number of Proteobacteria belong to Gammaproteobacteria (26% of prokaryotic endophytes) with many of them known as phytopathogens. In the group of Gammaproteobacteria are included *Pseudomonas*, *Enterobacter*, *Pantoea*,

Stenotrophomonas, *Acinetobacter* and *Serratia*. The interactions of Gammaproteobacteria that have been described vary from pathogenicity to mutualism (Hardoim et al., 2015). Alphaproteobacteria (18% of prokaryotic endophytes) is also a group of Proteobacteria endophytes, most of which belong to *Rhizobium* and *Bradyrhizobium* genera (N_2-fixing in legumes) as well as to *Methylobacterium* and *Sphingomonas*. Last, Betaproteobacteria (10% of prokaryotic endophytes) include genera such as *Burkholderia*, *Massilia*, *Variovorax* and *Collimonas* (Hardoim et al., 2015). Apart from the pre-referred categories of Proteobacteria, there are also Deltaproteobacteria and Epsilonproteobacteria in lower proportions (Williams and Kelly, 2013), as well as a sixth class, the "Zetaproteobacteria", although the name is not validly published yet (Emerson et al., 2007; McAllister et al., 2011).

The second largest phylum of bacterial endophytes, Actinobacteria, consists of diverse genera such as *Streptomyces* (known for antibiotic synthesis) (Liu et al., 2013), *Microbacterium, Mycobacterium, Arthrobacter* and *Curtobacterium*, while the phylum Firmicutes includes the two genera *Bacilli* and *Clostridia*. Part of this group is also *Bacillus thurigiensis*, that is known for the parasporal crystal protein production (pesticidal properties) (Schnepf et al., 1998; Hardoim et al., 2015).

As it concerns eukaryotic (or fungal) endophytes, the main phyla (according to their abundance) are Glomeromycota (40%), Ascomycota (31%), Basidiomycota (20%), unidentified phyla (8%) and Zygomycota (0.1%) (Hardoim et al., 2015). Most of the fungal endophytes belong to Glomeromycetes, a class of microorganisms which are endosymbionts with most land plants, a fact of great ecological and economic importance (Smith and Read, 2008). Endophytic Ascomycota include Dothideomycetes, many members of which are necrotrophic, producing host specific phytotoxic metabolites and peptides, while regarding endophytic Basidiomycota, many of them belong to Agaricomycetes (mushroom-forming mainly), but also saprotrophs or EMC symbionts (Hardoim et al., 2015).

Roles of endophytes related to the plant

Phytostimulation, Nutrient Cycling, Enzyme Production and Bioremediation

Endophytes play major role in the uptake of important nutrients (essential elements), like C, N, P, O etc. (Arachevaleta et al., 1989; Malinowski et al., 2000), while among others endophytes are able to produce a wide range of phytohormones e.g. auxins, cytokinins and gibberellic acids (Nair and Padmavathy, 2014; Arora and Ramawat, 2017). There are also cases in which indole-3 acetic acid (IAA - a phytohormone of the auxin class) is produced as an endophytic originated promoter of plant growth, leading to induced plant cell elongation and cell division (Xin et al., 2009). Apart from, their role in nutrient uptake of plants, endophytes possess another role, that of balancing the nutrients in plant's environment and making them available to the whole ecosystem. Microorganisms, among others, produce several vital enzymes, like cellulases, proteases, pectinases, xylanases (Bezerra et al., 2012) and hemicellulases (Bischoff et al., 2009). Such enzymes are studied for their possible application in bioconversion of lignocellulosic biomass into sugars, able to be fermented easier. For example, saprophytic organisms help in biodegradation, by degrading and decomposing organic components (litter of their hosts) e.g. lignin, cellulose, hemicellulose (Kumaresan and Suryanarayanan, 2002; Korkama-Rajala et al., 2008; Promputtha et al., 2010; He et al., 2011).

The ability of endophytes to break down complexes can also be expanded to bioremediation, the process of removing wastes or pollutants from the environment e.g. Cadmium (Mastretta et al., 2009) and other toxic metals (Nair and Padmavathy, 2014) or even plastic (PUR) (Russell et al., 2011), due to the great microbial diversity. It is fact that there is an interaction between above- and belowground communities and has been shown that regulation of soil by plants containing endophytic microbes, affects soil catabolic profiles e.g. endophytes modify host rhizo-depositions in the conditioning phase, and increase soil fungal activity, too (Malinowski et al., 1998; Van Hecke et al., 2005).

Antimicrobial Activity, Volatile Organic Compound, Bioactive and novel compounds production

A very important role of most endophytes is the antimicrobial activity (Nair and Padmavathy, 2014) which protects plants from pathogens by reducing pathogen's

severity (Zabalgogeazcoa, 2008). Pathogen control in plants, animals or human is a major effect of endophytes. For example, there is a wide spectrum of pathogenic microorganisms, in which several medicinal plant-evolved with endophytes have shown bioactivity effect (Nair and Padmavathy, 2014). This usually happens because endophytes produce inhibitors (Chareprasert et al., 2005; Kumar et al., 2010) antibiotics and antifungal compounds (Istifadah and McGee, 2006). Endophytes have been referred to synthesize bioactive compounds, used by hosts against pathogens e.g. alkaloids, terpenoids, flavonoids and steroids. Several such compounds are useful tools in novel drug discovery due to their multiple types of function, such as antibiotics, immunosuppressants, anticancer agents, biocontrol agents etc. (e.g. taxol, hyperzine A and brefeldin A) (Zhang et al., 2006; Liu et al., 2009; Joseph and Priya, 2011; Nair and Padmavathy, 2014). Siderophores (iron chelators) are also biologically active compounds, which are produced by endophytic microorganisms in many cases and found extensive application in the field of agriculture and medicine (Nair and Padmavathy, 2014). It has been proved, endophytes are a virulence tool of pathogenic microbes regarding plants, animals and humans, too (Neilands, 1993). It has also been proved that endophytes produce a wide variety of volatile organic compounds (VOCs) with antimicrobial activity (most of them unidentified), which highlights their possible application in medicine, industry or energy production (Nair and Padmavathy, 2014).

Endophytes as Bio-Control Agents (BCAs)

Endophytes have been used, due to their toxic substance production, as alternative to the chemical way, in order to control insect herbivory (Gehring and Whitham, 1994; Arora and Ramawat, 2017) and other entomopathogens (Posada and Vega, 2006), or even against poplar canker (Ren et al., 2011). It has been also noticed by Schouten (2016) that plants colonized by fungal endophytic microorganisms are better protected against plant nematodes. As it concerns biotechnology, endophytes are possible to be genetically engineered and express e.g. antipest proteins like lectins against plant pests (Fokkema, 1991; Nair and Padmavathy, 2014). Moreover, there are couple of cases in which endophytes seem to have a more complicated role concerning their hosts. For example, there have been found endophytic microbes with both herbicidal and antimicrobial activity (Li et al., 2012), or even others which display heavy metal and antibiotic

resistances, while on the other hand induce IAA, siderophore production and deaminase production (Luo et al., 2012).

Parameters describe biocommunities

There are various ecological parameters that can be used to study communities (and so endophytic communities as well), such as abundance, community composition, diversity (richness and evenness) as well as structure, stability and dominance. Abundance, is the relative representation of a species in a particular ecosystem. The measurement includes the number of individuals of a species per sample. The way that abundances of different species are distributed within a specific ecosystem is called relative abundance, and practically is referred to the evenness of distribution of individuals among different community species. Evenness is actually a diversity index quantifying the similarity in species relative abundance within a community. More detailed, evenness determines the diversity as a standardized index of species relative abundance. The number of different species in an ecological community is called richness, and it is the simples measure of diversity. It is a simple count of the species existing and does not count neither for the abundance of each species, nor the relative abundance distribution (Krebs, 1999). Diversity is a very important attribute regarding communities, that determines stability, productivity and migration (Zhang et al., 2012). It includes the two pre-referred terms; species richness and evenness, presuming the importance of richness in comparison to relative abundance (Stirling and Wilsey, 2001). Thus, species diversity consists of three components; richness, evenness of species and phylogenetic diversity (the genetic relationship between different groups of species). Most of studies with regard to diversity, have used structure as a diversity representative. This is based on the simplicity that its measurement has, compared to richness, but there are also many investigations which notice richness as the common cause of variation in relative abundance and diversity (Zhang et al., 2012).

As it concerns diversity, we can discriminate two types, alpha-diversity and beta-diversity. Whittaker (1972) described alpha-diversity as the species richness in a specific place, but later it was redefined on the basis of community structure and was linked on the number of species and the proportion by which each species is represented in the community. If there is a high number of species with similar abundances in a community

(high evenness), then it should be a community with high alpha-diversity. Some indices that are commonly used to describe alpha diversity include Shannon's index (H), Simpson's index (D) and Renyi entropy. Whittaker (1972) described beta-diversity, too, as the extent of species replacement or biotic change along environmental gradients. It measures the turnover of species between two sites in terms of gain or loss of species. Actually, beta-diversity means the dissimilarity between communities of two sampling sites (or even two samples). The higher the beta-diversity, the more dissimilar the two communities are. Some commonly used beta-diversity indices are Bray-Curtis dissimilarity, PSI (percent similarity index) and Jaccard's index (qualitative).

Next, species composition is referred to the contribution of each species to the total number of individuals in a community. It is generally expressed as a percentage, so that all species add up to 100%, defining in parallel from one perspective which species grow together. Additionally, community structure describes, in the words of networking, the occurrence of groups of organisms that act as nodes in a network, being more densely connected with the rest network organisms (Girvan and Newman, 2002). Another term is that of community stability, which can be defined as the ability of a community to defy changes or rebound from changes (resilience). Last, regarding terms which have to do with community, dominance is an ecology term describing the degree to which a taxon is more numerous than others in an ecological community (or makes up more of the biomass). The dominant species of a community are those that define the community.

There are several factors influencing plant microbial communities

Microorganisms are able to colonize any habitat in plants forming their own microbial communities, in different plant compartments (either on or within the plant) (Andreote et al., 2014). Thus, as different microbial microhabitats are found along a plant, the microbial community composition of each microhabitat could be different due to changes in the microenvironment conditions (Andreote and Pereira, 2017). In the literature, there are various factors that affect plant microbial communities, e.g. host species, type of tissue, surrounding environment (including its subfactors biotic and abiotic) in a small or even in a larger geographical scale. Microbial communities, and thus endophytic communities too, are affected (their structure and function) by host species (Berg and Smalla, 2009), and as McInroy and Kloepper (1995) have stated, even bacterial species

of different plant species growing side-by-side are different. Host species also affect some plant species-specific factors such as root architecture, surface structure, size of intracellular space, nutrient composition or even types of root exudates and consequently host's response to endophytic colonization. In turn, these factors determine the plant hosted endophytic community. Tissue type, is another attribute that affects the community of endophytes colonizing plants. Each plant tissue (i.e. root, stem/twig or leaf) creates a unique microenvironment including different conditions (e.g. plant-produced compounds, temperature or pH changes etc.) that influences epiphytic and endophytic microorganisms living on and within, respectively. For example, root endophytic communities are different in abundance and composition compared to phyllosphere ones and usually richer as suggested by Robinson et al. (2015).

Abiotic environmental conditions also exert a major influence on microbial endophytic community. It is remarkable the fact that even within the same plant species, endophytic population not only varies from region to region but many times differs in a local scale due to change of climatic conditions (Nair and Padmavathy, 2014). Environmental conditions, e.g. temperature, humidity, salinity, soil texture, pH and nutrient provision (naturally or through fertilization) are able to affect both directly or indirectly the population of endophytes (Jia et al., 2016). Temperature, is a factor that affects different groups of microorganisms, by enhancing or suppressing their growth. In general, an increase in temperature increases enzyme activity and the growth of microorganisms (Farrell and Rose, 1967), however, when temperatures get too high (above the optimum) enzymes denature and protein activity reduces (Daniel, 1996). Every microorganism has its own growth temperature spectrum (usually according to its enzyme temperature requirements) and thus there are groups of microorganisms benefiting from e.g. temperature increase or others that are suffering. Apart from temperature, moisture is another significant factor that affects microbial growth, either by damaging (negative relationship) some microorganisms or by benefiting others (positive relationship). Also, it is fact that both temperature and moisture are factors that depend on seasonal (e.g. spring is usually drier and warmer than autumn, etc.) or altitude changes (e.g. usually as altitude increases temperature and moisture elevate). Physicochemical variables of soil are also accounted as factors that influence microbial communities, and so plant endophytic communities. Such variables are salinity, pH or texture of soil, as well as soil

nutrients, which may increase or decrease microbial growth, induce shift in diversity patterns or even change the composition of microbial communities (Faoro et al., 2010; Stomeo et al., 2012).

Endophytes in Sustainable Agriculture

Increasing global population and its continuously growing needs for food are issues that are depended on agricultural production. Agriculture tries to get a more sustainable way during the last decade, including novel strategies and practices, new substances (mainly bio-originated) as well as organisms, too. The roles of endophytes as simulators and promoters of plant growth, as protectors of plants from stresses or pests, even as BCAs, are promising tools in a more eco-friendly and economically sustainable way of agriculture. It is true that sustainable agriculture needs self-contained actions and functions, as well as low-cost and eco-friendly inputs at the same time, which will lead to yield maximization and productivity intensification. Thus, as endophytes affect plant's survival, diversity and conservation (Busby et al., 2016), they are very important parts of agroecosystems. Although the most common approach of application is their inoculation either in soil or seeds (seed dressings), the best strategy for their application in agricultural ecosystems is not yet known (Le Cocq et al., 2017). Due to the above, there is an emerging need endophytes to be studied extensively regarding physiology and functioning, full lifecycles and genome plasticity (Redman et al., 2001), in order to be used as tools in sustainable ways of modern agriculture applications.

Research on endophytic biocommunities and on the factors affecting them

As it concerns endophytes in total, or even specific endophytic species which are studied in literature, they are studied in order to help the increase of production in agriculture, or to improve a plant's characteristic, which are both purely agronomic reasons of research. A literature search using the search engine PubMed, and the keyword "endophytes" resulted in more than 2,000 papers during the last 5 years, while in the case of the phrase "endophytic community", the search resulted in more than 300 papers. However, the number of studies that we have found, including studies on endophytic biocommunities, factors affecting these communities, as well as how beneficial these factors are on endophytic communities, was very small (i.e. 35) (details about the basic

search are presented in following chapter). Regarding temperature effect on endophytic communities only six studies have been found (Table 9), despite the fact that it is a very common factor studied in scientific research on biocommunities. On the other hand, in the last five-year period, there were more than 5,800 studies in literature referred on both “temperature” and “soil” keywords, almost 150 about “temperature” and “rhizosphere” and nearly 20 including “temperature” and “phyllosphere”. The same trend was also followed in the case of archaeal endophytic communities, where we found only one study in the last five years, in contrast with the general search using the term “archaea” that revealed more than 7,600 studies. We conclude that there are only a few studies on endophytes and the factors affecting their communities, in relation to the volume of work that have been done in the other fields at the same time-period, and thus, there is a need and we must emphasize more on the research on endophytic communities.

Additionally, as it is previously referred, in large scale there are not significant differences. Nevertheless, in small scale differences are detected at the genus and the species level. Therefore, it makes sense to study further and deeper the endophytes and their communities, as well as the influence of factors (biotic and abiotic) of their environment on them at the community level.

Objectives of the study

The objectives of this study were to review the factors that influence endophytic communities, to discuss whether the type of tissue has greater effect on endophyte community, irrespective of the host species. Additionally, to be investigated if there is an effect on the community of endophytes by changing the environmental conditions in two cases (scenarios). The first one is when local environmental changes occur without any abrupt changes in biocommunity or seasonality, while the second one when environmental conditions in a greater scale (global conditions) differ, including biocommunities, environmental characteristics, seasonality etc.

Methods

This thesis presents a review of the factors affecting endophytic (bacterial and fungal) communities, the changes of endophytic community structure and the importance of each factor. Many studies have demonstrated the effect of different factors (biotic or abiotic) on endophytic communities over the years; however, this thesis focuses on the last 5-year period of research on endophytic communities. The chosen studies, are referred mainly to the abundance and the diversity of endophytic communities. The aim was to review studies which had focused on the relative abundance of endophytic phyla, in order quantitative results to be provided. The search was based on studies on endophytic communities (both bacterial and fungal), and not on individual species of endophytic microorganisms, and the effect of each factor on these. We wanted to study the way that abiotic environmental factors influence the endophyte communities, and thus the main factors affecting endophytic communities e.g. temperature, moisture, type of tissue, soil, pH, were chosen to be included in the searching procedure. Although there are a couple more factors, such as growth stage of host, biotic stress via other microorganisms, or even abiotic factors like cultivation techniques and rhizosphere soil contamination e.g. contaminate the soil and every compound is a totally different case, and finally it would be too complicated to extract a result. Additionally, we did not include literature studies which try just to record and describe the endophytic microbial community of a certain host species. We tried to include only comparative studies, either within the same plant species, under different abiotic conditions, e.g. rice plants under different temperatures, or between different plant species under the same abiotic environmental conditions. Thus, the searching procedure was conducted by using two keywords each time. The first part included the word “endophytes” or the phrase “endophytic community”, while the second one was represented by one of the following; “sunlight”, “temperature”, “soil”, “pH”, “water”, “moisture”, “humidity” or “tissue type”. The search was filtered for studies of the last 5 years, using the search engine PubMed with access primarily in the MEDLINE database, and the studies chosen, were accessed from 18/07/2018 to 15/09/2018. The studies selected are presented in Table 1.

Table 1. List of the studies that selected and used in the present thesis

Author	Year	Method	Parameter of measurement	Factor of influence
Agler et al	2016	16S rRNA	abundance	sampling time and location
Rua et al	2016	16S rRNA	abundance (Chao1 and Shanon indexes)	silt, sand, clay and soil water content
Johnston-Monje et al	2014	16S rDNA	abundance	soil (Mexican, Canadian and sterilized sand)
Glynou et al	2016	rDNA sequencing (OUTs)	number of OTUs (Bootstrap analysis and Chao estimator)	climate (temperature, precipitation), soil (Mg, pH) spatial (latitude)
Massimo et al	2015	ITSrDNA (PCR)	diversity (OUT) (Fisher's alpha and ANOSIM)	tissue type
				host species
			community composition	host species
Hardoim et al	2012	PCR-DGGE	abundance (PCR-DGGE bands identification)	soil pH
Gomes et al	2018	ITSrDNA (PCR)	OTUs	season (spring/autumn)
				tissue type
				latitude (north/south)
Grau et al	2017	DNA metabarcoding	OTUSs	Soil N and P
				Soil C:N and pH
Mitter et al	2017	16S rRNA amplicon sequencing	diversity and community structure (OTUs)	host species (barley/clover)
				soil physical and chemical properties
Blain et al	2017	high-throughput sequencing (quantitative real-time PCR)	abundance and community structure	host species
				sampling location
Gottel et al	2011	bacterial 16S rRNA and fungal 28S rRNA 454 pyrosequencing	abundance (OTUs)	location (upland vs botomland)
Beckers et al	2017	16S rRNA amplicon pyrosequencing	relative abundance (OTUs)	plant tissue
Desgarennes et al	2014	16S rRNA	abundance	host species, season, tissue type (root/leaf endosphere)
Hong et al	2015	Illumina paired-end sequencing technique	abundance and diversity	plant species (*S.alterniflora, K.obovata*)
Bowman and Arnold	2018	SSUrDNA sequencing	abundance and diversity (OTU)	elevation
				climate
				soil chemistry
				host communities

(continued)

Table 1. (continued)

Asemaninejad et al	2016	Illumina MiSeq sequencing of ribosomal DNA (rDNA)	abundance (OTU)	temperature moisture
Yang et al	2016	sequencing of ribosomal DNA (rDNA)	abundance and diversity (OTU)	elevation
Campisano et al	2017		abundance and diversity	season altitude location (greenhouse/field) tissue type (roots/stems) temperature
Lee et al	2014	18S rDNA ITS	abundance and diversity	water stress *Cenangium ferruginosum* inoculation
Rangjaroen et al	2014	16S rRNA	abundance and diversity index	tissue type host cultivar
Szyma´nska et al	2016	PLFA analysis, culture-dependent techniques, 16S rRNA	abundance	salinity
Ma et al	2013	16S rRNA	diversity	salinity and tissue type
Yaish et al	2016	16S rRNA	abundance and diversity (OTUs)	salinity
Carrell et al	2016	16S rRNA	abundance and diversity (OTUs)	location host species
Geml et al	2015	DNA sequencing	abundance (OTUs)	warming treatment
Walitang et al	2018	T-RFLP analysis	community structure and diversity	host salinity
Balint et al	2015	rDNA metabarcoding	diverisity (OTUs)	host latidude
Pietro-Souza et al	2017	ITSrDNA (PCR)	diversity and abundance	Hg contamination
Huang et al	2016	ITSrDNA (PCR)	abundance and diversity (OTUs)	sampling location fire
Silva et al	2016	16S rDNA	community structure	host variety
Li et al	2018	high throughput sequencinng	abundance and diversity (OTUs)	biotic (*T.matsutake*)
Ren et al	2015	454 pyrosequencing	community structure	eCO2 (under low N and high N fertilization)
Bourdel et al	2016	ITSrDNA (PCR)	abundance and diversity (OTUs)	petroleum hydrocarbons host
Robinson et al	2015	PCR amplification 16S rRNA genes	abundance and diversity (OTUs)	tissue type

Results and Discussion

Factors studied and their influence on endophytic communities

The factors that affect endophytic microbial communities, in our study, were categorized into four main categories: host species, tissue type, abiotic environmental conditions in small scale (local), environmental conditions in large scale (global). After literature searching based on the criteria that have been previously described, 35 studies were sorted out according to the above-mentioned factors that affect endophytic community. There were several studies where more than one factor was examined. 12/35 (34%) studies focused on the effect of the host species, while the type of plant tissue was studied in 8/35 (23%) studies. The effect of environmental factors in small scale was examined in a large number of studies (25/35; 71%), while on the other hand, the effect of large scale environmental factors on endophytic communities was referred only in 3/35 (9%) studies (Table 2). Another type of sorting distinguished the 35 studies according to the biotic or abiotic nature of the aspect studied. 14/35 (40%) studies concerned abiotic factors and 7/35 (20%) studies referred to biotic ones, while there were also 14/35 (40%) studies including both biotic and abiotic (Table 3). Studies were also divided according to the type of organisms that they were referring, either on bacterial endophytic communities (15/35; 43%), or on fungal endophytic communities (14/35; 40%). Finally, the studies including both fungi and bacteria were only 5/35 (14%). Additionally, there was a unique study (3%) that had to do with endophytic archaea (Table 4).

Table 2. Different types of factors and the percentage distribution of studies in each category

Category	Amount	Total %
host species	12	34%
tissue type	8	23%
small scale	25	71%
large scale	3	9%

**Amount - the number of times that each factor was studied in the 35 studies; Total % - the percentage of studies found*

Table 3. Distribution of studies according to the biotic or abiotic nature of the factors studied

Category	Amount	Total %
Abiotic	14	40%
Biotic	7	20%
Abiotic+Biotic	14	40%
Total	35	100%

**Amount - the number of studies out of the 35 in total;*

Total % - the percentage of studies found

Table 4. Distribution of the 35 studies according to the type of microorganism/-s studied

Category	Amount	Total %
Bacteria	15	43%
Fungi	14	40%
Bacteria+Fungi	5	14%
Bacteria+Archaea	1	3%
Total	35	100%

**Amount - the number of studies out of the 35 in total;*

Total % - the percentage of studies found

Tissue type effect on endophyte communities

Eight out of thirty-five studies that were included in our work, have studied the plant tissue type effect as it is referred in Table 1. However, there are differences between these studies based on the plant compartment that was studied e.g. either above- or below-ground tissue, or even both above- and below-ground plant parts. In Table 5 it is shown that 2/8 (25%) studies were purely on above-ground tissues (e.g. stems or leaves), while 6/8 (75%) studies referred on both above- and below-ground tissues (e.g. roots, stems, or leaves).

Table 5. Number of studies focused on the effect of tissue type on the community of endophytes

Plant tisuue studied	Number of studies	Percentage %
above ground	2	25%
above and below ground	6	75%

As it concerns the plant tissue type effect (Table 6) on the abundance and genetic diversity of bacterial endophytic communities, (as this was described by OTUs; Operational Taxonomic Units), there is a continuous decrease in diversity and abundance along the axis root-stem/twig-leaf. We estimated that the same pattern was also followed in case of fungi, despite the fact that there were not so many studies on endophytic fungal communities, and the majority of fungi-focused studies relied on mycorrhizal fungi. The suggestion about higher diversity and abundance in root tissues, compared with stems and leaves, for both bacterial and fungal endophytes was also supported by Li et al. (2018). In contrast to bacterial and fungal communities, archaeal endophytic community diversity seems not to be affected by plant tissue type, maintaining the same pattern (Ma et al., 2013). However, this information on stability of archaeal endophytic diversity among different tissue types, was referred in just one study (Ma et al., 2013), and can be used only as an indication. Thus, as there are not enough studies on archaeal endophytic communities, future research should focus on them, as more information needs to be provided.

Table 6. Tissue type effect on diversity, abundance and composition of endophytic communities in cultivated and wild plant

Plant species	Tissue	Relative abundance				OTUs	Shannon index	Archaea/Bacteria/Fungi	Reference
Phragmites australis	leaf	-	-	-	-	-	1.20	A	Ma et al 2013
Phragmites australis	stem	-	-	-	-	-	1.10	A	Ma et al 2013
Phragmites australis	root	-	-	-	-	-	1.20	A	Ma et al 2013
Agave salmiana	leaf	Actinobacteria	γ-Proteobacteria	Acidobacteria	α-Proteobacteria	34	3.53	B	Desgarennes et al 2014
Agave tequilana	leaf	Actinobacteria	Acidobacteria	γ-Proteobacteria	α-Proteobacteria	16	2.77	B	Desgarennes et al 2014
Oryza sativa	leaf	*β-Proteobacteria*	*γ-Proteobacteria*	*α-Proteobacteria*	*Spirochetes*	-	2.41	B	Rangjaroen et al 2014
Phragmites australis	leaf	-	-	-	-	-	1.20	B	Ma et al 2013
Populus tremula × Populus alba	leaf	α-Proteobacteria	γ-Proteobacteria	Actinobacteria	β-Proteobacteria	50-150	2.93	B	Beckers et al 2017
Triticum aestivum	leaf	Actinobacteria	**Firmicutes**	γ-Proteobacteria	α-Proteobacteria	21	-	B	Robinson et al 2015
Oryza sativa	stem	*β-Proteobacteria*	*γ-Proteobacteria*	*α-Proteobacteria*	*Spirochetes*	-	2.48	B	Rangjaroen et al 2014
Phragmites australis	stem	-	-	-	-	-	2.50	B	Ma et al 2013
Populus tremula × Populus alba	stem	α-Proteobacteria	γ-Proteobacteria	Actinobacteria	TM7	50-150	3.58	B	Beckers et al 2017
Vitis vinifera	stem	β-Proteobacteria	γ-Proteobacteria	α-Proteobacteria	Firmicutes	156	2.60	B	Campisano et al 2017
Agave salmiana	root	α-Proteobacteria	Actinobacteria	γ-Proteobacteria	Acidobacteria	35	3.56	B	Desgarennes et al 2014
Agave tequilana	root	γ-Proteobacteria	Actinobacteria	α-Proteobacteria	Acidobacteria	31	3.43	B	Desgarennes et al 2014
Oryza sativa	root	*β-Proteobacteria*	*γ-Proteobacteria*	*α-Proteobacteria*	*Spirochetes*	-	2.75	B	Rangjaroen et al 2014
Phragmites australis	root	-	-	-	-	-	3.40	B	Ma et al 2013
Populus tremula × Populus alba	root	α-Proteobacteria	β-Proteobacteria	TM7	Actinobacteria	250-300	3.83	B	Beckers et al 2017
Triticum aestivum	root	*γ-Proteobacteria*	Actinobacteria	*α-Proteobacteria*	-	28	-	B	Robinson et al 2015
Vitis vinifera	root	γ-Proteobacteria	α-Proteobacteria	Actinobacteria	β-Proteobacteria	290	3.70	B	Campisano et al 2017
Oryza sativa	grain	*β-Proteobacteria*	*γ-Proteobacteria*	*α-Proteobacteria*	-	-	2.38	B	Rangjaroen et al 2014
Larrea tridentata, Simmondsia chinensis, Parkinsonia microphylla	leaf	-	-	-	-	-	-	F	Massimo et al 2015
Olea europaea	leaf	*Dothideomycetes*	-	-	-	71	0.50	F	Gomes et al 2018
Larrea tridentata, Simmondsia chinensis, Parkinsonia microphylla	stem	*Dothideomycetes*	*Eurotiomycetes*	*Sordariomycetes*	-	-	-	F	Massimo et al 2015
Olea europaea	twig	*Perzizomycetes*	*Ascomycetes*	*Eurotiomycetes*	-	102	0.90	F	Gomes et al 2018

**Tissue – refers to the plant tissue type studied; Relative abundance – depicts the most abundant endophytic groups in decreasing row; Archaea/Bacteria/Fungi – the type of microorganisms studied in each case (A – for archaea; B – for bacteria; F – for fungi); "-" – no data The present table is colored with different shades to indicate the below- and above-ground plant tissues studied (reddish shades - roots or grain; yellow - stem and twig tissues; green – leaves)*

The fact that greater diversity and abundance occurs in roots rather than in stems and leaves, may be due to the roots' ability to act as sinks of photosynthetic products (Robinson et al., 2015), the carbon provider for endophytic microorganisms. Additionally, the upper part of the plant is more exposed to abrupt changes and stress factors compared to the below ground part, thus roots rather than leaves or stem provide a more protected environment from extreme fluctuations of temperature, moisture or even solar radiation (Ma et al., 2013; Robinson et al., 2015). Based on all the aforementioned, roots are considered to be more suitable and stable habitats for endophyte community establishment, which consequently results in greater diversity and abundance (Hong et al., 2015). Even in the upper part of the plant, the pattern remains similar, with a uniform being absent between e.g. stems and leaves. This opinion has also been supported by Gomes et al. (2018), who stated that leaves are affected more than twigs by climatic factors resulting in lower fungal endophyte richness in leaves. Moreover, Campisano et al. (2017) noticed that root endophytes' response to temperature changes is slower than that of stems' ones, due to protection of the below-ground plant part and so conditions for endophyte growth are more favorable in roots. Another explanation of the higher diversity and abundance of root endophytic communities in contrast with that of the above-ground plant parts, may be the fact that endophytic microorganisms originate mainly from rhizosphere; they enter into roots by colonizing lateral roots. However, there are other sources they can derive from, such as spermosphere, anthosphere, caulosphere, as well as via aerosols, and they colonize phyllosphere, stomata, wounds or lenticels and then the endosphere as depicted in Figure 1 (Cocking, 2003; Mano and Morisaki, 2008; Compant et al., 2012; Johnston-Monje et al., 2014; Ren et al., 2015; Beckers et al., 2017). Thus, roots tend to have higher diversity and abundance being closer to the main source of origin of endophytic microorganisms. The opinion that endophytic bacteria of roots constitute a subset of rhizosphere soil bacteria able to colonize the root, is also supported by Blain et al. (2017), who further noticed that there is an active influence of root in endophytic bacterial recruitment through plant exudates.

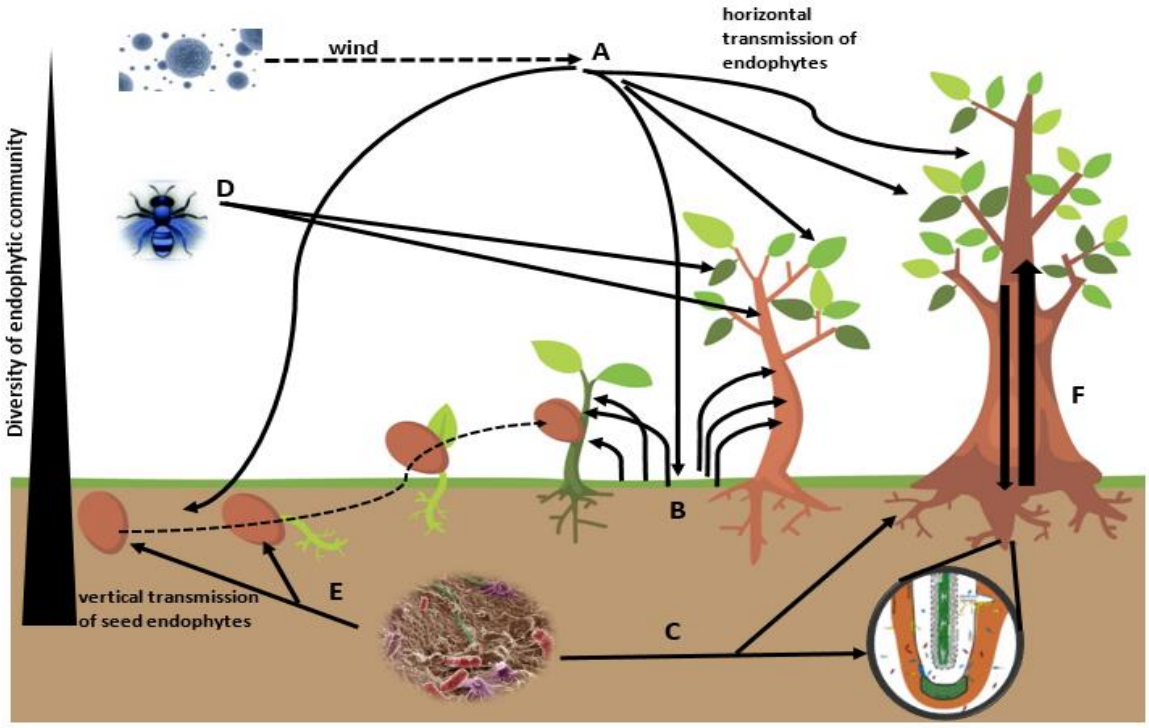

Figure 1. Transmission ways, sources of origin and entry points of endophytes, diversity in endophytic community and translocation within the plant. Endophyte horizontal transmission A. via bioaerosols through phyllosphere entry points e.g. wounds, stomata, shoot apical meristems, flowers, lenticels and hydathodes, B. via rain splash to soil and infection of the plant, C. via soil to roots and cracks, D. via insects (e.g. herbivores, predators of other plant associated organisms, sap-feeders) and pollinators (insects and animals), E. vertical transmission of endophytes via soil to seed or through colonization of the spermosphere. F. Translocation of endophytes within the plant. (Adapted and modified from nl.depositphotos.com)

In order to be valid, the opinion that "the higher on the plant axis the endophytic community is, the less abundant and diverse will be", it presupposes that endophytic microorganisms are able to translocate within plant immediately after they enter e.g. from roots to stems and leaves. This has been noticed by Chi et al. (2005) who found that endophytic *Rhizobia* which had been *gfp*-tagged, migrated from roots to leaves in rice plant. In addition, Hardoim et al. (2008) stated that endophytes may spread systemically inside the plant and colonize stems and leaves, while Compant et al. (2010) suggested that endophytes use xylem vessels to travel within plant tissues and reach

vegetative parts of the plant. Moreover, a study by Sturz et al. (1997) supported the scenario of endophyte translocation within plants. Sturz et al. found in their study that the amount (87%) of lower foliage endophytes originated from roots and root nodules, is much higher than that (57%) of root endophytes originated from foliage on red clover. Thus, root-to-leaves endophyte migration is more frequent than leaves-to-root, without excluding the last.

According to the pre-referred, we may conclude that root endophytic communities will be more similar to the rhizosphere soil community compared to the stem or leaf endophytic communities, as the longer the distance from the source, the higher dissimilarity among communities. This has been proved by Roesch et al. (2007) who showed in their study that diazotrophic endophytes in maize roots were more related to soil communities than shoot endophytes were, enhancing the idea that the closer to the root an endophytic community is, the more similar to the soil communities and more abundant will be.

Comparing the values of diversity indexes, we observed that in case of fungal endophytic communities Shannon index was lower than that of bacterial ones, which was expected as not only in endophytic communities but also in general, bacteria exhibit higher diversity than fungi (Figure 2), due to the fact that through evolution prokaryotes were pushed to be adapted into several different styles of life, as well as the phenomenon of horizontal gene transfer is easier in prokaryotes than in eukaryotes and consequently the production of new strains (Fitzpatrick, 2012; Gray and Archibald, 2012). Thus, we expect lower number of phyla in fungal endophytic compared to bacterial endophytic communities. Among bacterial phyla, Proteobacteria were dominant in every plant tissue, followed mostly by Actinobacteria, while Bacteroidetes were present only in root tissues and Firmicutes only in leaves. Generally, Proteobacteria is the most abundant bacterial phylum of endophytes in every type of tissue (Santoyo et al., 2016; Liu et al., 2017), in contrast with Actinobacteria and Firmicutes which are mainly found in high abundances in shoot and leaf tissues (Costa et al., 2012; Robinson et al., 2015). More specifically, Actinobacteria was the dominant phylum in leaves where they present higher abundance compared to the other phyla. This could be attribute to the fact that many Actinobacteria species have the ability to form endospores and thus may be better adapted in the harsh fluctuations of environmental conditions in leaf tissue (Robinson

et al., 2015; Ortega et al., 2016). Finally, Bacteroidetes is a representative phylum of root tissues where these bacteria are more active, due to their ability to degrade complex polymers (Perez-Jaramillo et al., 2018), e.g. chitin, cellulose, pectin and xylan (Thomas et al., 2011; Berlemont and Martiny, 2015) together with Proteobacteria and Actinobacteria (Bulgarelli et al., 2012; Gkarmiri et al., 2017). The members of Firmicutes are adapted to more harsh environments as their metabolism allows them to tolerate hot and dry weather conditions, thus they have been found to be the dominant phylum on plant phyllospheres in the Mediterranean region (Koeberl et al., 2011; Turner et al., 2013; Ortega et al., 2016).

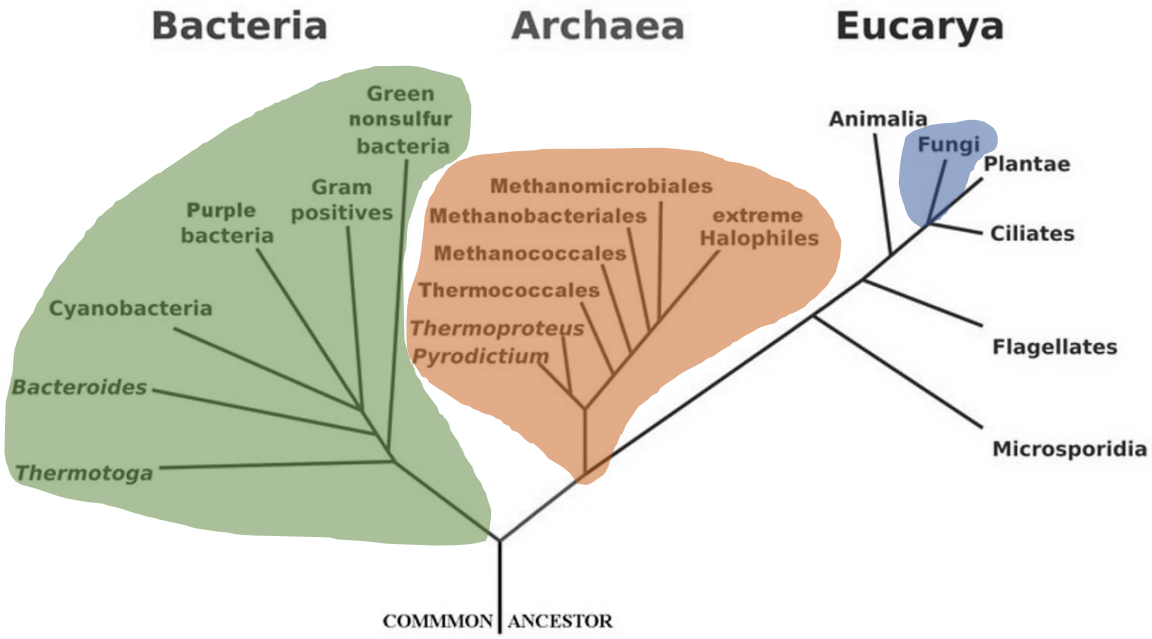

Figure 2 Phylogenetic Tree of Life (Adapted and modified from NASA Astrobiology Institute)

Fungal endophytic communities in both stem and leaf compartments seem to be dominated by the class Dothideomycetes (Ascomycota), with the exception of *Olea europeae*; its twigs were dominated by the class Perzizomycetes (Ascomycota). Among fungal endophytes, the major phyla were Ascomycota, while Basidiomycota and Zygomycota contributed with lower percentage (Sun and Guo, 2012). There are cases in which Ascomycota proportion is referred really high (99%) and Basidiomycota are presented in minor proportion (1%) (Potshangbam et al., 2017). Within the phylum

Ascomycota, the class of Dothideomycetes dominates the fungal endophytic communities (Sun and Guo, 2012; Pawlowska et al., 2014; Zhang and Yao, 2015; Ofek-Lalzar et al., 2016). This class contains most of the fungal endophytic species in total.

Host effect on endophytic communities; Cultivated and wild plant species

12 out of the 35 studies (34%) focused on cultivated plant species (Table 7), such as *Zea mays, Hordeum vulgare, Melilotus albus, Triticum aestivum, Olea europaea, Vitis vinifera, Oryza sativa* and *Agave tequilana* (Hardoim et al., 2012; Desgarennes et al., 2014; Johnston-Monje et al., 2014; Rangjaroen et al., 2014; Ren et al., 2015; Robinson et al., 2015; da Silva et al., 2016; Campisano et al., 2017; Mitter et al., 2017; Gomes et al., 2018; Walitang et al., 2018). Moreover, there were 25/35 (71%) studies regarding endophytes on wild plant species (Table 6) e.g. *Aeschynomene fluminensis, Agave salmiana, Agropyron trachycaulum, Arabidopsis thaliana, Betula ermanii, Betula nana, Bromus inermis, Dryas octopetala, Eleocharis erythropoda, Equisetum* spp.*, Eriophorum vaginatum, Fabaceae, Fragaria virginiana, Juniperus deppeana, Kandelia obovate, Larrea tridentate, Medicago truncatula, Parkinsonia microphylla, Phragmites australis, Pinus contorta, Pinus flexilis, Pinus koraiensis, Pinus ponderosa, Pinus radiata, Poa pratensis, Polygonum acuminatum, Populus alba, Populus balsamifera, Populus deltoids, Populus tremula, Quercus aquifolioides, Quercus* spp.*, Salicornia europaea, Salix arctica, Salix polaris, Salix pulchra, Simmondsia chinensis, Spartina alterniflora, Sphagnum* spp. and *Vaccinium* spp. (Gottel et al., 2011; Ma et al., 2013; Desgarennes et al., 2014; Lee et al., 2014; Balint et al., 2015; Geml et al., 2015; Hong et al., 2015; Massimo et al., 2015; Agler et al., 2016; Asemaninejad et al., 2016; Bourdel et al., 2016; Carrell et al., 2016; Glynou et al., 2016; Huang et al., 2016; Rua et al., 2016; Szymanska et al., 2016; Yaish et al., 2016; Yang et al., 2016; Beckers et al., 2017; Blain et al., 2017; Grau et al., 2017; Pietro-Souza et al., 2017; Bowman and Arnold, 2018; Li et al., 2018).

Table 7. Number of studies focused on cultivated and wild plant species

Plants studied	Number of studies	% (in 35 studies)
Wild	24	69%
Cultivated	11	31%

All the studies on cultivated plants but one regarding bacterial endophytes, showed that Proteobacteria were the dominant phylum, followed by Actinobacteria, Firmicutes and Bacteroidetes in decreasing order of abundance, while there were also phyla such as Acidobacteria, Tenericutes and Spirochetes to a lesser extent (Table 8a). The dominance of Proteobacteria, including α-, β-, γ- and δ-Proteobacteria, has been previously referred in cultivated plant species, such as in wheat by Robinson et al. (2015), and rice (Johnston-Monje and Raizada, 2011; Diaz Herrera et al., 2016; Walitang et al., 2017; Correa-Galeote et al., 2018), or even in agricultural important grass species (Wemheuer et al., 2017). The next phylum in abundance was Actinobacteria in the vast majority of cultivated plant species, as one of the largest groups of endophytic bacteria (Govindasamy et al., 2014; Wang et al., 2016) and usually the second phylum in decreasing dominance order among the endophytic bacterial phyla (Wemheuer et al., 2017). As it concerns Firmicutes, Mitter et al. (2017) referred that this group of endophytic bacteria occurred in specific plant species. In our table we present only the first four phyla in decreasing relative abundance, and thus, we cannot state that Firmicutes did not exist in general, but only that they were not in high relative abundance (usually the phylum was third in decreasing dominance order). Moreover, there were endophytic phyla e.g. Tenericutes and Spirochetes, that were present only in cultivated plant species in the first four most abundant phyla. Finally, there was just one study among the 35 studies, regarding fungal endophytes in cultivated plant species. It concerned to olive tree (*Olea europaea*) and showed that the dominant phylum was Ascomycota, as the major one (Sun and Guo, 2012), represented by the classes Dothideomycetes, Eurotiomycetes and Pezizomycetes.

Diversity indices (Shannon index; H') exhibited also a great variation among the different cultivated plant species, ranging from 0.7 to 4.9, while the abundance values (OTUs) ranged from 16 to 3302 (Table 8a). Endophytic microbial populations may be affected by different plant root exudates and rhizodeposition of the host -the means of endophyte selection- which lead to the formation of distinctive, rich and diverse microbial communities (Phillips et al., 2012; Beckers et al., 2017). One of the plant species with low diversity and abundance in bacterial endophytes was clover (*Melilotus albus*), presenting diversity equal to 1.91 (Shannon) and abundance equal to 2525 (OTUs), lower enough in comparison with other plant species e.g. barley (*Hordeum vulgare*).

According to Mitter et al. (2017) this may be due to the fact that selectivity among different plants varies and clover is a more selective plant than barley.

A great difference in diversity index was recorded even within the same species e.g. *Oryza sativa*, in which diversity index varied from 1.2 to 4.9. Despite the fact that host species is a major factor influencing endophytic diversity (and abundance) and similar plants usually exhibit high similarities on bacterial community composition (Blain et al., 2017), there are cases in which differences are presented within the same plant species regarding endophyte community. The statement that plant genotype plays the most important role in shaping the endophytic population (Johnston-Monje et al., 2014), has been also highlighted by Rangjaroen et al. (2014) who found dissimilarities in endophytic bacterial community structure of rice, related to the variety of rice landraces. However, in a more recent study coming from Walitang et al. (2018) on different rice cultivars, it was referred that only under stress conditions each cultivar presented different endophytic bacterial diversity, while major core-groups of endophytic bacteria occured, which seem to follow a general trend even along the different rice cultivars. Apart from the rice plant, cultivar effect on endophytic community has been noticed in kiwi fruits (*Actinidia* spp.) (Cho et al., 2018), in maize (*Zea mays*) (da Silva et al., 2016), in sweet pepper (*Capsicum anuum L.*) (Rasche et al., 2006), as well as in pea (*Pisum sativum L.*) (Elvira-Recuenco and Vuurde, 2000).

Table 8. Diversity, abundance and composition of endophytic communities

a. in cultivated plant species

Cultivated spp	Relative abundance (bacterial Phylum/fungal Family)				OTUs	Shannon index	Tissue type	Archaea/Bacteria/Fungi	Reference
Zea mays	-	-	-	-	124	-	root/stem	B	Johnston-Monje et al 2014
Zea mays	-	-	-	-	-	-	leaf	B	Silva et al 2016
Melilotus albus	*Proteobacteria*	*Actinobacteria*	*Bacteroidetes*	*Firmicutes*	2525	1.91	root	B	Mitter et al 2017
Hordeum vulgare	*Proteobacteria*	*Actinobacteria*	*Tenericutes*	*Bacteroidetes*	3302	3.00	root	B	Mitter et al 2017
Triticum aestivum	*Proteobacteria*	*Actinobacteria*	*Firmicutes*	*Bacteroidetes*	28	-	root/leaf	B	Robinson et al 2015
Olea europaea	*Dothideomycetes*	*Eurotiomycetes*	*Pezizomycetes*	-	125	0.70	twig/leaf	F	Gomes et al 2018
Vitis vinifera	*Proteobacteria*	*Actinobacteria*	*Firmicutes*	*Bacteroidetes*	290/156	3.700/2.600	root/stem	B	Campisano et al 2017
Oryza sativa	*Proteobacteria*	*Bacteroidetes*	*Firmicutes*	*Actinobacteria*	16	-	seed	B	Hardoim et al 2012
Oryza sativa	*β-Proteobacteria*	*γ-Proteobacteria*	*α-Proteobacteria*	*Spirochetes*	-	2.75/2.48/2.40/2.38	root/stem/leaf/grain	B	Rangjaroen et al 2014
Oryza sativa	*Proteobacteria*	*Actinobacteria*	*Firmicutes*	-	-	1.40	seed	B	Walitang et al 2018
Oryza sativa	*Proteobacteria*	*Firmicutes*	*Bacteroidetes*	*Actinobacteria*	490	4.90	leaf	B	Ren et al 2015
Agave tequilana	*γ-Proteobacteria*	*Actinobacteria*	*Acidobacteria*	*α-Proteobacteria*	31/16	3.43/2.77	root/leaf	B	Desgarennes et al 2014

**Relative abundance – depicts the most abundant endophytic groups in decreasing row; Archaea/Bacteria/Fungi – the type of microorganisms studied in each case (A – for archaea; B – for bacteria; F – for fungi); "-" for no data; Tissue type – shows the type of tissue used in the study. The different colors depict different bacterial phyla or fungal families; blue shades – Proteobacteria; red – Actinobacteria; green – Bacteroidetes; yellow – Firmicutes; no color – less common endophyte groups.*

b. in wild plant species

Wild spp	Relative abundance				OTUs	Shannon index	Tissue type	Archaea/Bacteria/Fungi	Reference
Phragmites australis	-	-	-	-	22	1.00 to 1.50	root/stem/leaf	A	Ma et al 2013
A. thaliana	*Proteobacteria*	*Deinococcus*	*Bacteroidetes*	-	-	-	leaf	B	Agler et al 2016
Agave salmiana	*α-Proteobacteria*	*Actinobacteria*	*γ-Proteobacteria*	*Acidobacteria*	35/34	3.55/3.53	root/leaf	B	Desgarennes et al 2014
Bromus inermis, Equisetum spp., Agropyron trachycaulum, Poa pratensis, Fabaceae, Fragaria virginiana	*Actinobacteria*	*α-Proteobacteria*	*γ-Proteobacteria*	-	-	-	root	B	Blain et al 2017
Kandelia obovata	*Cyanobacteria*	*γ-Proteobacteria*	*α-Proteobacteria*	*Firmicutes*	2142	3.50	root	B	Hong et al 2015
Medicago truncatula	*Proteobacteria*	*Actinobacteria*	*Bacteroidetes*	-	41	0.30	root	B	Yaish et al 2016
Phragmites australis	-	-	-	-	126	2.10 to 3.40	root/stem/leaf	B	Ma et al 2013
Pinus flexilis Pinus contorta	*α-Proteobacteria*	*Bacteroidetes*	*Acidobacteria*	*Firmicutes*	350	-	needles	B	Carrell et al 2016
Pinus radiata	*γ-Proteobacteria*	*β-Proteobacteria*	*α-Proteobacteria*	-	83	0.92/1.47/1.36	needles	B	Rua et al 2016
Populus deltoides	*Proteobacteria*	*Acidobacteria*	*Firmicutes*	-	76	-	root	B	Gottel et al 2011
Populus tremula × Populus alba	*α-Proteobacteria*	*γ-Proteobacteria*	*β-Proteobacteria*	*Actinobacteria*	50/300	3.83/3.58/2.93	root/stem/leaf	B	Beckers et al 2017
Quercus aquifolioides	*Proteobacteria*	*Cyanobacteria*	*Bacteroidetes*	*Firmicutes*	3980	5.18/4.93/4.58	root/stem/leaf	B	Li et al 2018
Salicornia europaea	*Firmicutes*	*Actinobacteria*	*Proteobacteria*	-	8	-	root	B	Szyma´nska et al 2016
Spartina alterniflora	*Cyanobacteria*	*δ-Proteobacteria*	*γ-Proteobacteria*	*Bacteroidetes*	4213	5.80	root	B	Hong et al 2015

(continued)

b. (continued)

Betula nana, Salix pulchra species, Eriophorum vaginatum, Sphagnum spp.	*Ascomycota*	*Basidiomycota*	*Glomeromycota*	-	3534	5.30	root	F	Geml et al 2015
Aeschynomene fluminens	*Ascomycota*	-	-	-	34	0.60	root	F	Pietro-Souza et al 2017
Betula ermanii	*Ascomycota*	*Basidiomycota*	-	-	1762	2.50	leaves	F	Yang et al 2015
Dryas octopetala, Salix polaris, Vaccinium species,	*Ascomycota*	*Basidiomycota*	*Glomeromycota*	-	3543	5.10	root	F	Geml et al 2015
Eleocharis erythropoda Populus balsamifera	*Ascomycota*	*Basidiomycota*	*Glomeromycota*	-	592	-	root	F	Bourdel et al 2016
Juniperus deppeana Quercus spp.	*Ascomycota*	*Basidiomycota*	-	-	95	*24.30	leaf	F	Huang et al 2016
Larrea tridentata, Simmondsia chinensis, Parkinsonia microphylla	*Dothideomycetes*	*Eurotiomycetes*	*Sordariomycetes*	-	89	*31.80	stm/leaf	F	Massimo et al 2015
Microthlaspi	*Dothideomycetes*	*Sordariomycetes*	*Leotiomycetes*	-	296	0.70 to 3.20	root	F	Glynou et al 2016
Pinus koraiensis	*Leotiomycetes*	*Dothideomycetes*	-	-	81	0.82	needles	F	Lee et al 2014
Pinus ponderosa	*Leotiomycetes*	*Eurotiomycetes*	*Dothideomycetes*	*Sordariomycetes*	40	0.73	root/leaf	F	Bowman and Arnold 2018
Polygonum acuminatum	*Ascomycota*	-	-	-	38	0.80	root	F	Pietro-Souza et al 2017
Populus balsamifera	*Ascomycota*	*Basidiomycota*	-	-	2022	-	leaf	F	Balint et al 2014
Populus deltoides	*Ascomycota*	*Zygomycota*	*Basidiomycota*	-	72	-	root	F	Gottel et al 2011
Quercus aquifolioides	*Ascomycota*	*Basidiomycota*	-	-	457	3.02/1.78/1.83	root/stem/leaf	F	Li et al 2018
Sphagnum	*Leotiomycetes*	*Sordariomycetes*	*Eurotiomycetes*	-	171.7	3.24	peat	F	Asemaninejad et al 2016
Dryas octapetalla	-	-	-	-	413	-	root	F	Grau et al 2017
Salix arctica	-	-	-	-	403	-	root	F	Grau et al 2017

**Relative abundance – depicts the most abundant endophytic groups in decreasing row; Archaea/Bacteria/Fungi – the type of microorganisms studied in each case (A – for archaea; B – for bacteria; F – for fungi); "-" for no data; * - Fisher's alpha (not Shannon index) Tissue type – shows the type of tissue used in the study. The different colors depict different bacterial phyla or fungal families; blue shades – Proteobacteria; red – Actinobacteria; green – Bacteroidetes; yellow – Firmicutes; mauve – Cyanobacteria; grey – Acidobacteria; no color – less common bacterial endophyte groups. For endophytic fungi: blue shades – Ascomycota; red – Basidiomycota; green – Basidiomycota; yellow – Zygomycota.*

Proteobacteria have been found to be the dominant phylum in the majority of wild plant species, followed by Actinobacteria, Bacteroidetes and Acidobacteria (Table 8b). Despite the fact that the dominance pattern was similar to that presented in cultivated plant species, there were phyla which were unique in wild plant species, or even more common. Specifically, Cyanobacteria and Deinococcus are phyla that were not included in cultivated species, while others e.g. Acidobacteria were more common in wild plant species. Moreover, there were some cases in which Cyanobacteria, Firmicutes or Actinobacteria and not Proteobacteria were the dominant phylum. Cyanobacteria, a phylum presented in wild plant species, mainly includes diazotrophic bacteria that may provide N to the plant system in order to increase its biomass and usually are present in endophytic forms in roots (Hong et al., 2015). Thus, the reason why they dominated in some cases may be related to a possible need of plants in N, as in cultivated species N is provided by fertilizers while in wild species the plants must trap N. Another endophytic bacterial phylum presented only in wild plant species is Deinococcus that is often found in organic rich environments (soils with high amount of organic matter) (Battista, 1997), while Acidobacteria, a group which was more abundant in wild plant species rather than in cultivated (Table 8a and 8b), are linked with nutrient-poor soils (Gottel et al., 2011; Beckers et al., 2017). Regarding the fungal dominant phyla, Ascomycota was the most abundant, followed by Basidiomycota, as well as by Glomeromycota and Zygomycota in lower relative abundances, a pattern similar to that described by Sun and Guo (2012).

Wild plant species also showed a great variety of diversity (Shannon index) and abundance (OTUs) values ranging from 0.3 to 5.8 and from 8 to 4213 respectively. The high variation in values did not allow us to reveal a pattern of diversity changes among species. However, looking at diversity values of *Pinus* spp., in a couple of studies, we observed that diversity and abundance of endophytes in this genus were relatively low (compared to the rest) ranged from 0.73 to 1.47 and from 83 to 350 respectively. Similar values were also reported in other studies concerning endophytes of *Pinus* species (Oono et al., 2015; Prihatini et al., 2015).

Except for bacteria and fungi, there was a case that endophytic archaeal community was detected in common reed tissues (*Phragmites australis*). Although *Archaea* represent a significant part of the endophytic plant microbiome, their potential role still remains unclear and much less is known about the so-called third domain of life, a group

of microorganisms which have been described only in a few publications as internal plant tissue colonizers (Oliveira et al., 2013; Ma et al., 2013; Chelius and Triplett, 2001; Sun et al., 2008). Archaeal endophytes may act as plant growth promoters, nutrient suppliers or even protectors against abiotic stress (Taffner et al., 2018). The diversity index of archaeal endophyte community in the common reed (Ma et al., 2013) varied from 1.0 to 1.5, indicating lower diversity compared to fungal and bacterial endophytes. The low diversity and abundance of archaeal endophytic communities has also been mentioned in maize roots (Chelius and Triplett, 2001), in northern peatlands (Galand et al., 2005), in rice (Sun et al., 2008), in coffee cherries (Oliveira et al., 2013), as well as in alpine peat bog vegetation (Taffner et al., 2018), where both abundance and diversity of archaea endophytes were usually lower than the bacterial ones. Taking into account the aforementioned and the fact that *Archaea* are not as diverse as *Bacteria* (Aller and Kemp, 2008), including a lower number of genera and species, we can only speculate the possibility for archaeal endophytes to be less diverse and abundant than bacterial ones, however further studies are needed to support this opinion.

Abiotic factor's effect on endophytic communities

Temperature effect

Except from biotic factors including the type of plant tissue and the host species, endophytic communities are also influenced by abiotic factors (Martín-García et al., 2011), such as temperature, moisture, pH level, salinity, fertilizer presence as well as soil texture. Regarding temperature effect on endophytic communities (Table 9), it has been showed that diversity and abundance increase with temperature, in the case of bacteria. It has also been observed that changes are more abrupt in stems rather than in root tissues, which probably results from the more protected environment that roots provide (Ma et al., 2013; Robinson et al., 2015). Fluctuations of temperature in the below-ground plant part are not so wide as in the upper part (Ortega et al., 2016), providing more stable environment for endophytic communities establishment. Thus, they respond slower to temperature changes and present greater diversity and abundance (Hong et al., 2015; Campisano et al., 2017). More studies on bacterial communities are needed in order to extract a pattern of endophyte community composition changes in

relation to temperature. Here we have only the syndication of one study that there are no composition changes relating to temperature.

Table 9. Temperature effect on diversity, abundance and composition of endophytic communities in cultivated and wild plant species

Temperature	Relative abundance (bacterial Phylum/fungal Family)				Shannon	OTUs	Tissue	Authors	Bacteria/Fungi
low (15°C)	*Proteobacteria*	*Actinobacteria*	*Firmicutes*	*Bacteroidetes*	3.60/4.10	290/156	root/stem	Campisano et al 2017	B
high (35°C)	*Proteobacteria*	*Actinobacteria*	*Firmicutes*	*Bacteroidetes*	4.20/4.90	350/480	root/stem	Campisano et al 2017	B
low (2076m)	*Dothideomycetes*	*Tremellomycetes*	*Leotiomycetes*	*Sordariomycetes*	4.20	-	leaves	Yang et al 2016	F
high (1630m)	*Sordariomycetes*	*Dothideomycetes*	*Leotiomycetes*	*Tremellomycetes*	2.50	-	leaves	Yang et al 2016	F
low (9 to 12°C)	-	-	-	-	5.30	3534	root	Geml et al 2015	F
high (increased by 2°C)	-	-	-	-	5.05	-	*root*	Geml et al 2015	F
low (9 to 12°C)	-	-	-	-	5.10	3543	root	Geml et al 2015	F
high (increased by 2°C)	-	-	-	-	5.20	-	*root*	Geml et al 2015	F
low (autumn~8.1°C)	*Dothideomycetes*	*Eurotiomycetes*	*Pezizomycetes*		0.60	2.5	twig/leaf	Gomes et al 2018	F
high (spring~14.4°C)	*Pezizomycetes*	*Dothideomycetes*	*Sordariomycetes*		0.90	3.2	twig/leaf	Gomes et al 2018	F
low (3.5°C to 16.2°C)	*Leotiomycetes*	*Eurotiomycetes*	*Dothideomycetes*	*Sordariomycetes*	1.91	-	root/leaf	Bowman and Arnold 2018	F
high (6.3°C to 19.9°C)	*Leotiomycetes*	*Dothideomycetes*	*Sordariomycetes*		0.61	-	root/leaf	Bowman and Arnold 2018	F
low (ambient)	*Leotiomycetes*	*Sordariomycetes*	*Eurotiomycetes*		3.24	171.7	peat	Asemaninejad et al 2016	F
high (+8°C)	*Leotiomycetes*	*Sordariomycetes*	*Eurotiomycetes*		3.24	-	peat	Asemaninejad et al 2016	F

**Relative abundance – depicts the most abundant endophytic groups in decreasing row; Bacteria/Fungi – the type of microorganisms studied in each case (B – for bacteria; F – for fungi); "-" for no data; Tissue – shows the type of tissue used in the study.*

Contrarily with bacterial communities, the main pattern in fungal endophytic communities showed that diversity decreases as temperature increases; nevertheless, there were some cases in which diversity and abundance slightly increased with temperature elevation (Geml et al., 2015; Gomes et al., 2018). In the fungal communities presented in Table 9, there is a variety of changes with temperature elevation in class level e.g. Sordariomycetes increase, Eurotiomycetes decrease, etc., however Ascomycota remain the dominant phylum, as the most abundant among fungal phyla. In general, there are fungal endophytic taxa known as psychrophiles with growth temperature ≤15°C and a maximum one ≤20°C and others named psychrotrophs with optimum growth temperature between 15-20°C and a maximum temperature for growth >20°C. However, endophytic microorganisms can also be mesophiles, with an optimum growth temperature above 20°C (Zhang et al., 2013). So, it is possible that the negative correlation of fungal endophytic communities with temperature increase (Randriamanana et al., 2015; Asemaninejad et al., 2016) is a result of non-optimal temperatures for growth

e.g. higher than 15°C is not an optimum temperature for psychrophilic endophytic fungi. Respectively, in the case of a mesophile endophytic fungal community, an increase in temperature close to the optimum temperature for growth, may be beneficial for the endophytic fungi. Thus, we could speculate that it is possible for Table 9 to be referred in a variety of fungal communities (psychrophiles, psychrotrophs or mesophiles), thus explaining the variation in diversity and abundance changes in relation to temperature. Except for the overall changes observed in Table 9, Geml et al. (2015) showed that the fungal endophytic community response differed between moist and dry tundra i.e. diversity decreased with temperature elevation when tundra was moist while increased when tundra was dry. In moist tundra soils were generally cooler even throughout the summer season, which means that less temperature fluctuations occur than in dry tundra (Geml et al., 2015). This may be the reason why the fungal endophytic communities of plans cover moist and dry tundra respond differently.

Moreover, there are different explanations about temperature effects on endophytes. According to Yang et al. (2016), temperature change may also be a result of altitude change, which also affects leaf carbon. Leaf carbon increases sharply with elevation and may broaden the habitat space associated with microorganisms (mainly in foliar environment) (Yang et al., 2016). This has as result more microbial organisms to be hosted and thus endophytes, too. On the other hand, it is fact that endophytes originated from rhizosphere soil (Beckers et al., 2017), that warming affects positively root exudation (Vančura, 1967) and that root exudates play key role in microorganisms recruitment (Broeckling et al., 2008) and endophytes as well. Thus, it could be suggested that temperature increase benefits endophytic communities to increase. Finally, temperature is usually linked with the moisture of the environment e.g. due to seasonal and altitude changes, or even due to climatic fluctuations, the increase of temperature is accompanied by the decrease of humidity and vice versa. This explains why there are studies that take into account the effect of both factors (temperature and moisture), on endophytic community simultaneously. Zimmerman and Vitousek (2012) and Gomes et al. (2018) stated that these two abiotic factors strongly affect the fungal endophytic microbiome, thus it may be better to be studied jointly.

Moisture effect

With the increase of moisture, bacterial diversity decreased (Shannon index, H') in contrast to what happened in fungal endophytic communities. The diversity of the latter increased with moisture elevation (Table 10). Soil moisture influences bacterial motility, and specifically their chemotactic behavior (Bashan, 1999). Proper condition regarding moisture is an important factor for microbial growth, as water is responsible for the transfer of nutrients and waste products in and out of bacterial cells. At high moisture content endophytic bacterial population in maize roots is lower than in low moisture (Adejumo and Orole, 2010). However, Adejumo and Orole noticed in their study that the differences in bacterial endophytic population at various moisture levels were not significant, indicating that moisture is a factor that should be taken into account in combination with others such as temperature, salinity, pH etc. The increase of fungal endophyte abundance and diversity due to moisture increase has been also observed in other cases, and it is usually linked with precipitation increase (U'Ren et al., 2012; Lau et al., 2013). This is probably due to the fact that rainfall is an important factor for endophytic fungi dispersion and colonization (Gomes et al., 2018).

Additionally, although the number of studies was not large enough, there was an indication that changes in diversity (Shannon index) of fungal and bacterial endophytic communities in *Pinus* spp. (*P.koraiensis* and *P.ponderosa*) due to moisture elevation may be not as abrupt as in other species. However more studies are needed in order to ascertain this. In both bacterial and fungal communities, the pattern of composition remained the same in relation to moisture increase, e.g. Proteobacteria and especially *γ*-Proteobacteria dominated in bacterial communities, and Ascomycota was the dominant phylum in fungal ones. Nevertheless, there was a case of fungal community (*Populus deltoides*) in which *Basidiomycota* dominated when moisture elevated.

Table 10. Moisture effect on diversity, abundance and composition of endophytic communities

Plant species	Moisture	Relative abundance (bacterial Phylum/fungal Family)				Shannon	OTUs	Tissue	Comments	Authors	Bacteria/Fungi
Pinus radiata	high	*γ-Proteobacteria*	-	-	-	0.95	-	needles	1.2 soil water content	Rua et al 2016	B
Pinus radiata	low	*γ-Proteobacteria*	β-Proteobaccteria	-	-	1.45	-	needles	1.0 soil water content	Rua et al 2016	B
Populus deltoides	high	γ-Proteobacteria	α-Proteobacteria	Acidobacteria	-	-	-	root	35 to 40% moisture	Gottel et al 2011	B
Populus deltoides	low	γ-Proteobacteria	α-Proteobacteria	β-Proteobacteria	-	-	-	root	22.2 to 29.6 % moisture	Gottel et al 2011	B
Betula ermanii	high	*Dothideomycetes*	*Tremellomycetes*	*Leotiomycetes*	*Sordariomycetes*	4.20	-	leaves	2076m altitude	Yang et al 2016	F
Betula ermanii	low	*Sordariomycetes*	*Dothideomycetes*	*Leotiomycetes*	*Tremellomycetes*	2.50	-	leaves	1630m altitude	Yang et al 2016	F
Pinus koraiensis	high	Dothideomycetes	Leotiomycetes	Eurotiomycetes	-	1.13	-	needles	−18.3 ± 9.5 MPa	Lee et al 2014	F
Pinus koraiensis	low	Dothideomycetes	Sordariomycetes	-	-	0.81	-	needles	−54.3 ± 14.5 MPa	Lee et al 2014	F
Pinus ponderosa	high	*Leotiomycetes*	*Eurotiomycetes*	*Dothideomycetes*	*Sordariomycetes*	1.91	-	root/leaf	74.6cm preclpitation	Bowman and Arnold 2018	F
Pinus ponderosa	low	*Leotiomycetes*	*Dothideomycetes*	*Sordariomycetes*	-	0.61	-	root/leaf	61.2cm precipitation	Bowman and Arnold 2018	F
Populus deltoides	high	Basidiomycota	Ascomycota	-	-	-	-	root	35 to 40% moisture	Gottel et al 2011	F
Populus deltoides	low	Ascomycota	Basidiomycota	-	-	-	-	root	22.2 to 29.6 % moisture	Gottel et al 2011	F

**Relative abundance – depicts the most abundant endophytic groups in decreasing row; Bacteria/Fungi – the type of microorganisms studied in each case (B – for bacteria; F – for fungi); Tissue – shows the type of tissue used in the study; "-" for no data.*

Salinity effect

Changes in salinity can also affect endophytic communities. Studies that examined the effect of salinity were all focused on bacterial endophytic communities and showed that both diversity and abundance increased as salinity increased (Table 11). As it concerns community composition, the most abundant phyla were Proteobacteria and Actinobacteria, a pattern which did not change with changes in salinity in two out of three cases. There is one study (Szymanska et al., 2016), where the dominant phylum was Firmicutes and the community was dominated by Proteobacteria due to salinity increase. Although Proteobacteria are usually found in nutrient rich soils (Gottel et al., 2011; Beckers et al., 2017), their abundance was higher in more saline sites (Szymanska et al., 2018). Specifically, there was a category of these, δ-Proteobacteria, that are considered to be halophilic, along with Acidobacteria *(Szymanska et al., 2018)*. According to Foesel et al. (2014), the latter are linked with higher salinity level, as they are able to grow in saline and poor-in-nutrients environment (halophilic or halotolerant). Regarding the group of endophytic Actinobacteria, there is the opinion that they exhibit low salt stress tolerance, being a phylum, which is usually present in lower salinity level environments (Szymanska et al., 2016; Szymanska et al., 2018). However there is an opposite opinion that Actinobacteria shift in dominance in terms of abundance under salinity increase (Walitang et al., 2018) (Table 11). The difference in these cases may be due to the different salinity spectrum presented in the two cases e.g. from 55 to 112 dSm in case of *Salicornia europaea* and from 0 to 4 and 8 dSm in case of *Oryza sativa* (Table 11). As the

amount of increase was higher in the first case we may could speculate that the specific case is representative of an abrupt salinity change for Actinobacteria.

In general, differences at the dominant phylum of endophytic communities between different saline sites can be associated with differences related to rhizosphere soil and more specifically to its physico-chemical properties. Based on the aforementioned, endophytes are able to enter the root tissues through wound at the point of lateral root emergence and since the lateral root development is decreased by salt stress (Ma et al., 2013), the invasion in higher salinity levels may be suppressed. Nevertheless, there were studies where no significant difference in endophyte diversity due to salinity changes was recorded (Ma et al., 2013), and others where significant differences occured (Szymanska et al., 2016). Specifically, Szymanska et al. (2016) found higher microbial diversity at the high salinity site, due to the fact that it was a naturally saline site, in contrast to the anthropogenic less saline and more recent site that was also examined. Such differences occur as salt stress affects negatively populations of microorganisms, while halophilic or halotolerant microbes can easily survive and increase in abundance. Finally, there was also the category of archaeal endophytes which were also influenced by salinity. Ma et al. (2013) noticed in their study that salinity had a significant effect in endophytic archaeal community, and that diversity decreased along with salinity decrease. This may be because of the more tolerant nature of archaeal prokaryotes in comparison with bacterial ones, but it is only an indication and has to be further studied.

Table 11. The effect of salinity on diversity, abundance and composition of endophytic communities

Plant species	Salinity	Relative abundance (bacterial Phylum/fungal Family)				Shannon	OTUs	Tissue	Comments	Authors
Salicornia europaea	low	Firmicutes	Actinobacteria	Proteobacteria	-	-	8	root	55 dSm	Szyma´nska et al 2016
Salicornia europaea	high	Proteobacteria	Firmicutes	Actinobacteria	-	-	12	root	112 dSm	Szyma´nska et al 2016
Medicago truncatula	low	γ-Proteobacteria	α-Proteobacteria	β-Proteobacteria	Bacteroidetes	0.30	29.33	root	EC:1.23	Yaish et al 2016
Medicago truncatula	high	γ-Proteobacteria	α-Proteobacteria	β-Proteobacteria	Bacteroidetes	3.15	34.33	root	EC:14.40	Yaish et al 2016
Oryza sativa	low	γ-Proteobacteria	Actinobacteria	-	-	1.40	-	seed	0 dSm	Walitang et al 2018
Oryza sativa	mid	Actinobacteria	γ-Proteobacteria	Bacteroidetes	Sphingomonas	1.37	-	seed	4dSm	Walitang et al 2018
Oryza sativa	high	Actinobacteria	γ-Proteobacteria	Bacteroidetes	α-Proteobacteria	1.37	-	seed	8dSm	Walitang et al 2018

**Relative abundance – depicts the most abundant endophytic groups in decreasing row; Bacteria/Fungi – the type of microorganisms studied in each case (B – for bacteria; F – for fungi); Tissue – shows the type of tissue used in the study; "-" for no data.*

Fertilizer application effect

Robinson et al. (2015), observed that in the case of manure application the community composition pattern changed and Proteobacteria dominated over Actinobacteria (Table 12a). It has been suggested that Proteobacteria are linked with nutrient-rich environment, while Actinobacteria is a group of endophytes adapted in harsh fluctuations of abiotic conditions better than Proteobacteria (Gottel et al., 2011; Robinson et al., 2015; Beckers et al., 2017). This is depicted in the Table 12a, in which the relative abundance of Proteobacteria was higher than that of Actinobacteria when manure was applied as fertilizer and soil became more fertile. An increased number of endophytes has been recorded when no fertilizer was applied, while in cases where inorganic fertilizers or manure were incorporated, the abundance decreased. This may be probably due to the fact that the release of organic acids occurs into the rhizosphere of nutrient stressed plants, which may attract higher numbers of endophytic microorganisms (Robinson et al., 2015). The higher abundance of endophytes in such cases (Robinson et al., 2015) may be a result of the long-term interaction of endophytes and plants under low nutrient conditions, a scenario that is also supported by the evolutionary theory. It has been suggested that under poor quality environmental conditions, exist higher chances for mutually beneficial symbiotic relationships to be developed since the involved species cannot survive without this mutualistic relationship (Ellison et al., 1996). In general, such changes in the community composition due to fertilization may occur because of two reasons. Firstly, fertilizers may directly alter the soil bacterial community, consequently changing the available pool of colonizing bacteria, and secondly, fertilizers may shift plant growth and/or result in plant exudates changes which consequently alter the endophytic community and influence the recruitment of endophytes (Robinson et al., 2015).

Table 12. a. Fertilization, b. soil texture and c. soil pH effect on diversity, abundance and composition of endophytic communities

Plant species	N fertilizer	Relative abundance (bacterial Phylum/fungal Family)				Abundance (logCFU)	Tissue	Authors
Triticum aestivum	No	Actinobacteria	γ-Proteobacteria	α-Proteobacteria	β-Proteobacteria	2.25	root/leaf	Robinson et al 2015
Triticum aestivum	Manure	β-Proteobacteria	γ-Proteobacteria	Actinobacteria	α-Proteobacteria	1.40		
Triticum aestivum	Manure + N (96)	γ-Proteobacteria	α-Proteobacteria	Actinobacteria	β-Proteobacteria	1.30		
Triticum aestivum	N (144)	Actinobacteria	α-Proteobacteria	Bacteroidetes	γ-Proteobacteria	1.50		
Triticum aestivum	N (288)	Actinobacteria	γ-Proteobacteria	α-Proteobacteria	β-Proteobacteria	1.25		

Plant species	Soil texture	Relative abundance				Shannon	Tissue	Authors
Pinus radiata	silt	γ-Proteobacteria	β-Proteobacteria	-	-	1.40	needles	Rua et al 2016
Pinus radiata	clay	γ-Proteobacteria	β-Proteobacteria	-	-	1.30	needles	
Pinus radiata	sand	γ-Proteobacteria	-	-	-	0.90	needles	
Populus deltoides	clay	Basidiomycota	Ascomycota	-	-	-	root	Gottel et al 2011
Populus deltoides	sandy loam	Ascomycota	Basidiomycota	-	-	-	root	

Plant species	pH	Relative abundance				Comments	Tissue	Authors
Populus deltoides	high	Basidiomycota	Ascomycota	-	-	7.70-7.90	root	Gottel et al 2011
Populus deltoides	low	Ascomycota	Basidiomycota	-	-	6.60-6.80	root	

**Relative abundance – depicts the most abundant endophytic groups in decreasing row; Tissue – shows the type of tissue used in the study; "-" for no data.*

Soil texture effect

Among the other environmental factors referred in the 35 studies selected, soil texture was also included. The effect of soil texture on endophytic communities was studied in two tree plant species studies (*Pinus radiata* and *Populus deltoides)* (Table 12b), in which bacterial and fungal communities respectively, were examined. In the case of *Pinus radiata* it was observed an increase of diversity across the axis sand-clay-silt, and domination of *γ*-Proteobacteria, in all three cases (silt, clay and sand). However, Rua et al. (2016) stated that there was no strong correlation between bacteria and soil texture although some specific OTUs recorded in this study related to specific soil characteristics. Regarding *Populus deltoides,* the fungal phylum Ascomycota dominated in sandy loam, while Basidiomycota dominated when soil texture was clay.

Effect of pH

According to the literature search, pH effect on endophytic communities was studied only in a case of fungal endophytes in *Populus deltoides* (Table 12c)*,* in which Ascomycota was the dominant phylum followed by Basidiomycota when pH was low (neutral). On the other hand, when pH increased dominance of phyla was reversed, and Basidiomycota dominated. It has already been suggested that soil pH strongly affects the abundance and diversity of soil microbiota and therefore the endophytic microorganisms in

some proportion. By affecting the physiology of the host plant (e.g. soil pH alters mineral uptake), soil pH indirectly leads to the selection of different microbial groups (Johnston-Monje et al., 2014) or even changes part of the host's development (e.g. lateral root), resulting in decrease or differentiation of endophyte recruitment (Ma et al., 2013). pH is able to affect endophytic community even through the phenomenon of acid rain according to Helander et al. (1993), who stated that low rain pH (pH= 3) decreased almost 25% the endophytic community, nevertheless, the endophytic community composition of the host did not change.

Abiotic factors in large scale

Although many studies focus on the effect of abiotic environmental factors in a small scale to be studied, there are a few studies with regard to the effect of these factors in large scale. Balint et al. (2015) noticed that endophyte diversity varied with latitude, with poplar trees in the south exhibiting lower fungal endophyte diversity than trees in the north. Carrell et al. (2016) also stated that endophytic community composition of subalpine conifers differed due to large geographical distance, while on the other hand diversity and abundance had no differences at all. This could be explained by the existence of low dispersal barriers for canopy-associated endophytic bacteria, which has as a result the aerial surfaces of plants to be significant sources of aerosols, and microorganisms to be able to be dispersed across large distances via particulate matters (Carrell et al., 2016).

Additionally, Glynou et al. (2016) suggested that geographic distance did not affect similarities or dissimilarities among endophytic communities of *Microthlaspi* plants, supporting the idea of the strong influence of local environment in determining root endophytic communities. They supported that geographic distance of each location exhibits a negligible effect on endophytic community. More specifically, the latitude determines the composition but does not affect the diversity and the species richness, while climatic variables present higher correlation with community composition of endophytes, collinear with latitudinal gradient. Regarding factors related to moisture and temperature, Glynou et al. (2016) stated that these clearly differentiated root endophytic communities in southern areas (hot and dry summers and wet winters) compared to others found in northern areas (wetter and colder summers and winters).

It seems that large scale on its own, poorly affects community composition of endophytes. However, the environmental conditions of each region influence the composition of endophytic community, along with several other factors (both biotic and abiotic) and their interaction as well (Blain et al., 2017). Our suggestion is in agreement with Gomes et al. (2018) who stated that endophytic community is driven by both environmental and biotic factors. We suggest that endophytic communities present a global homogeneity, with no significant differences in the composition of their communities at the phylum level. Of course, this does not mean that there are no differences among the individuals of each group at the family, the genus and the species level shaped by local environmental factors, something which is expected and reasonable. It is very important to mention that the taxonomic level of grouping in each case study plays the key role. Undoubtedly, the more detailed the level of grouping, the more the differences will be. Thus, we can state that there is a general (global) pattern of maintenance of endophytic community structure, regardless of the study area, which is influenced at the lower taxonomic levels by local abiotic environmental parameters on the one hand, and by biotic on the other (Figure 3).

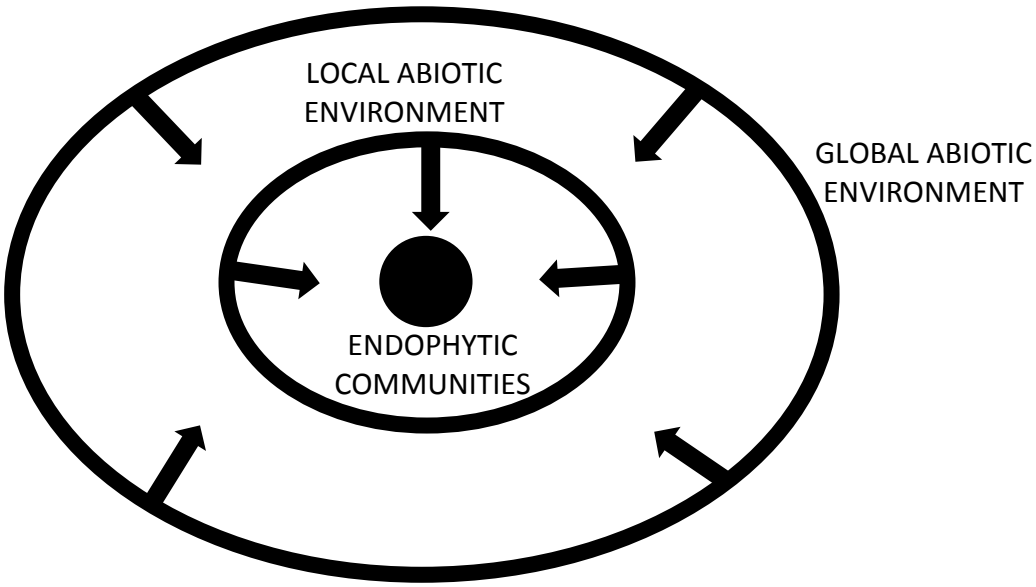

Figure 3 The influence of large scale environmental conditions (global) and small scale environmental conditions (local) on endophytic communities.

**The direction of the arrows indicates the direction of the effect of each factor on endophytic community. The bullet in the center depicts the endophytic communities, the middle ellipsis represents the local abiotic environment, and the outer ellipsis the global abiotic environment.*

Conclusions

To sum it up, there is an uncertainty on which factor (host, tissue type and abiotic environment) mainly affects the endophytic community, as there are several studies whose results vary, and plenty of subfactors (i.e. abiotic environmental factors) that affect the different microbial groups. Each factor affects the endophytic community on its own way, with a different level of influence (in case that the factor is studied separately). In our study, the plant host is the main biotic factor that affects endophytic community e.g. each plant species makes a selective recruitment of different endophytic microorganisms, compared to other plant species, while the type of tissue (root, stems/twigs or leaves) also plays a crucial role i.e. by compartmentalizing the already recruited endophytic microbial population. Despite the fact that the type of tissue is important, its effect remains lower than the effect of the plant host. On the other hand, abiotic environmental factors affect the plant host (different plant species usually grow under different environmental conditions), but also influence directly the endophytic community to some extent e.g. in case of acid rain, endophytic community composition does not change; nevertheless, the abundance of endophytes changes (Helander et al., 1993) and thus finally, the host is the main contributor to the endophytic community selection and composition. Our conclusion is that the host acts as the main factor affecting the endophytes, as it is directly affected by abiotic environmental factors, while the type of tissue shapes further the existing endophytic community that has been recruited by host, into specific plant compartments. (Figure 4).

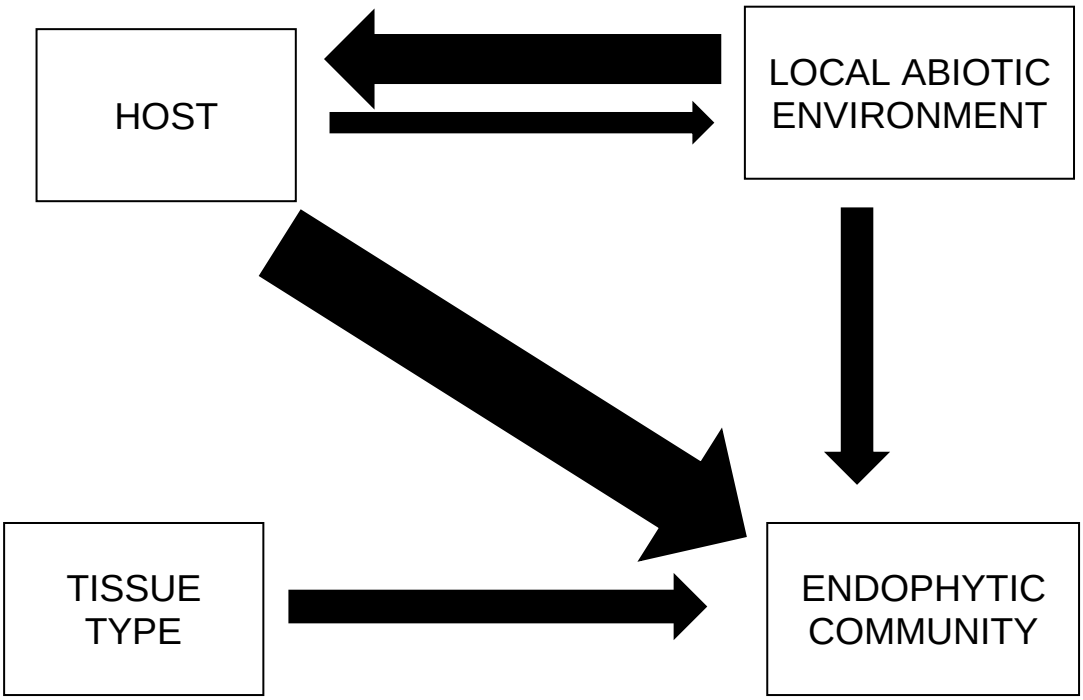

Figure 4 The abiotic and biotic interactions and their influence on endophytic community

**The width of the arrows indicates the level of each factor's influence on endophytic community. The wider the arrow, the higher the level of influence.*

Bibliography

ADEJUMO, T. O. & OROLE, O. O. 2010. Effect of pH and moisture content on endophytic colonization of maize roots. *Scientific Research and Essays,* 5**,** 1655-1661.

AGLER, M. T., RUHE, J., KROLL, S., MORHENN, C., KIM, S. T., WEIGEL, D. & KEMEN, E. M. 2016. Microbial Hub Taxa Link Host and Abiotic Factors to Plant Microbiome Variation. *PLoS Biol,* 14**,** e1002352.

ALLER, J. Y. & KEMP, P. F. 2008. Are Archaea inherently less diverse than Bacteria in the same environments? *FEMS Microbiol Ecol,* 65**,** 74-87.

ANDREOTE, F. D., GUMIERE, T. & DURRER, A. 2014. Exploring interactions of plant microbiomes. *Scientia Agricola,* 71**,** 528-539.

ANDREOTE, F. D. & PEREIRA, E. S. M. C. 2017. Microbial communities associated with plants: learning from nature to apply it in agriculture. *Curr Opin Microbiol,* 37**,** 29-34.

ARACHEVALETA, M., BACON, C. W., HOVELAND, C. S. & RADCLIFFE, D. E. 1989. Effect of the Tall Fescue Endophyte on Plant Response to Environmental Stress. *Agronomy Journal,* 81**,** 83-90.

ARORA, J. & RAMAWAT, K. G. 2017. *Endophytes: Biology and Biotechnology*.

ASEMANINEJAD, A., THORN, R. G. & LINDO, Z. 2016. Experimental Climate Change Modifies Degradative Succession in Boreal Peatland Fungal Communities. *Microbial Ecology,* 73**,** 521-531.

BALINT, M., BARTHA, L., O'HARA, R. B., OLSON, M. S., OTTE, J., PFENNINGER, M., ROBERTSON, A. L., TIFFIN, P. & SCHMITT, I. 2015. Relocation, high-latitude warming and host genetic identity shape the foliar fungal microbiome of poplars. *Mol Ecol,* 24**,** 235-48.

BASHAN, Y. 1999. Interactions of Azospirillum spp. in soils: a review. *Biol Fertil Soils,* 29**,** 246–256.

BATTISTA, J. R. 1997. AGAINST ALL ODDS: The Survival Strategies of Deinococcus radiodurans. *Annu. Rev. Microbiol.,* 51**,** 203–24.

BECKERS, B., OP DE BEECK, M., WEYENS, N., BOERJAN, W. & VANGRONSVELD, J. 2017. Structural variability and niche differentiation in the rhizosphere and endosphere bacterial microbiome of field-grown poplar trees. *Microbiome,* 5**,** 25.

BERG, G. & SMALLA, K. 2009. Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiol Ecol,* 68**,** 1-13.

BERLEMONT, R. & MARTINY, A. C. 2015. Genomic potential for polysaccharide deconstruction in bacteria. *Appl Environ Microbiol,* 81**,** 1513-19.

BEZERRA, J. D., SANTOS, M. G., SVEDESE, V. M., LIMA, D. M., FERNANDES, M. J., PAIVA, L. M. & SOUZA-MOTTA, C. M. 2012. Richness of endophytic fungi isolated from Opuntia ficus-indica Mill. (Cactaceae) and preliminary screening for enzyme production. *World J Microbiol Biotechnol,* 28**,** 1989-95.

BISCHOFF, K. M., WICKLOW, D. T., JORDAN, D. B., DE REZENDE, S. T., LIU, S., HUGHES, S. R. & RICH, J. O. 2009. Extracellular hemicellulolytic enzymes from the maize endophyte Acremonium zeae. *Curr Microbiol,* 58**,** 499-503.

BLAIN, N. P., HELGASON, B. L. & GERMIDA, J. J. 2017. Endophytic root bacteria associated with the natural vegetation growing at the hydrocarbon-

contaminated Bitumount Provincial Historic site. *Can. J. Microbiol.,* 63**,** 502-515.

BONFANTE, P. & SELOSSE, M.-A. 2010. A glimpse into the past of land plants and of their mycorrhizal affairs: from fossils to evo-devo *New Phytologist,* 186**,** 267-270.

BOURDEL, G., ROY-BOLDUC, A., ST-ARNAUD, M. & HIJRI, M. 2016. Concentration of Petroleum-Hydrocarbon Contamination Shapes Fungal Endophytic Community Structure in Plant Roots. *Front Microbiol,* 7**,** 685.

BOWMAN, E. A. & ARNOLD, A. E. 2018. Distributions of ectomycorrhizal and foliar endophytic fungal communities associated with Pinus ponderosa along a spatially constrained elevation gradient. *Am J Bot,* 105**,** 687-699.

BROECKLING, C. D., BROZ, A. K., BERGELSON, J., MANTER, D. K. & VIVANCO, J. M. 2008. Root exudates regulate soil fungal community composition and diversity. *Appl Environ Microbiol,* 74**,** 738-44.

BULGARELLI, D., ROTT, M., SCHLAEPPI, K., VER LOREN VAN THEMAAT, E., AHMADINEJAD, N., ASSENZA, F., RAUF, P., HUETTEL, B., REINHARDT, R., SCHMELZER, E., PEPLIES, J., GLOECKNER, F. O., AMANN, R., EICKHORST, T. & SCHULZE-LEFERT, P. 2012. Revealing structure and assembly cues for Arabidopsis root-inhabiting bacterial microbiota. *Nature,* 488**,** 91-5.

BUSBY, P. E., RIDOUT, M. & NEWCOMBE, G. 2016. Fungal endophytes: modifiers of plant disease. *Plant Mol Biol,* 90**,** 645-55.

CAMPISANO, A., ALBANESE, D., YOUSAF, S., PANCHER, M., DONATI, C. & PERTOT, I. 2017. Temperature drives the assembly of endophytic communities' seasonal succession. *Environ Microbiol,* 19**,** 3353-3364.

CARRELL, A. A., CARPER, D. L. & FRANK, A. C. 2016. Subalpine conifers in different geographical locations host highly similar foliar bacterial endophyte communities. *FEMS Microbiol Ecol,* 92.

CARROLL, G. 1988. Fungal Endophytes in Stems and Leaves: From Latent Pathogen to Mutualistic Symbiont. *Ecology,* 69**,** 2-9.

CHANWAY, C. P. 1996. Endophytes: they're not just fungi! *Can. J. Bot.,* 76.

CHAREPRASERT, S., PIAPUKIEW, J., THIENHIRUN, S., WHALLEY, A. J. S. & SIHANONTH, P. 2005. Endophytic fungi of teak leaves Tectona grandis L. and rain tree leaves Samanea saman Merr. *World Journal of Microbiology and Biotechnology,* 22**,** 481-486.

CHELIUS, M. K. & TRIPLETT, E. W. 2001. The Diversity of Archaea and Bacteria in Association with the Roots of Zea mays L. *Microb Ecol,* 41**,** 252-263.

CHI, F., SHEN, S. H., CHENG, H. P., JING, Y. X., YANNI, Y. G. & DAZZO, F. B. 2005. Ascending migration of endophytic rhizobia, from roots to leaves, inside rice plants and assessment of benefits to rice growth physiology. *Appl Environ Microbiol,* 71**,** 7271-8.

CHO, G., KIM, M. J., KWON, Y. & KWAK, Y. S. 2018. Comparison of Endophytic Microbial Community in Kiwifruit Plant Cultivars. *Plant Pathol J,* 34**,** 341-346.

CLAY, K. 1988. Fungal Endophytes of Grasses: A Defensive Mutualism between Plants and Fungi. *Ecology,* 69**,** 10-16.

CLAY, K. 1993. The ecology and evolution of endophytes. *Agriculture, Ecosystems and Environment,* 44**,** 39-64.

COCKING, E. C. 2003. Endophytic colonization of plant roots by nitrogen-fixing bacteria. *Plant and Soil,* 252**,** 169-175.

COMPANT, S., CLÉMENT, C. & SESSITSCH, A. 2010. Plant growth-promoting bacteria in the rhizo- and endosphere of plants: Their role, colonization, mechanisms

involved and prospects for utilization. *Soil Biology and Biochemistry,* 42**,** 669-678.

COMPANT, S., SESSITSCH, A. & MATHIEU, F. 2012. The 125th anniversary of the first postulation of the soil origin of endophytic bacteria – a tribute to M.L.V. Galippe. *Plant Soil* 356**,** 299–301.

CORREA-GALEOTE, D., BEDMAR, E. J. & ARONE, G. J. 2018. Maize Endophytic Bacterial Diversity as Affected by Soil Cultivation History. *Front Microbiol,* 9**,** 484.

COSTA, L. E. D. O., QUEIROZ, M. V. D., BORGES, A. C., MORAES, C. A. D. & ARAÚJO, E. F. D. 2012. ISOLATION AND CHARACTERIZATION OF ENDOPHYTIC BACTERIA ISOLATED FROM THE LEAVES OF THE COMMON BEAN (PHASEOLUS VULGARIS) *Brazilian Journal of Microbiology***,** 1562-1575.

DA SILVA, K. J., DE ARMAS, R. D., SOARES, C. R. & OGLIARI, J. B. 2016. Communities of endophytic microorganisms in different developmental stages from a local variety as well as transgenic and conventional isogenic hybrids of maize. *World J Microbiol Biotechnol,* 32**,** 189.

DANIEL, R. M. 1996. The denaturation and degradation of stable enzymes at high temperatures. *Biochem. J.,* 317**,** 1-11.

DE BARY, A. 1866. Morphologie und Physiologie Pilze, Flechten, und myxomyceten. *Hofmeister's Handbook of Physiological Botany.* Leipzig.

DESGARENNES, D., GARRIDO, E., TORRES-GOMEZ, M. J., PE˜NA-CABRIALES, J. J. & PARTIDA-MARTINEZ, L. P. 2014. Diazotrophic potential among bacterial communities associated with wild and cultivated Agave species. *FEMS Microbiol Ecol,* 90**,** 844-857.

DIAZ HERRERA, S., GROSSI, C., ZAWOZNIK, M. & GROPPA, M. D. 2016. Wheat seeds harbour bacterial endophytes with potential as plant growth promoters and biocontrol agents of Fusarium graminearum. *Microbiol Res,* 186-187**,** 37-43.

ELLISON, A. M., FARNSWORTH, E. J. & TWILLEY, R. R. 1996. Facultative Mutualism Between Red Mangroves and Root-Fouling Sponges in Belizean Mangal. *Ecology,* 77**,** 2431-2444.

ELVIRA-RECUENCO, M. & VUURDE, J. W. L. V. 2000. Natural incidence of endophytic bacteria in pea cultivars under field conditions. *Can. J. Microbiol.,* 46**,** 1036–1041.

EMERSON, D., RENTZ, J. A., LILBURN, T. G., DAVIS, R. E., ALDRICH, H., CHAN, C. & MOYE, C. L. 2007. A Novel Lineage of Proteobacteria Involved in Formation of Marine Fe-Oxidizing Microbial Mat Communities. *PLoS ONE,* 2.

FAORO, H., ALVES, A. C., SOUZA, E. M., RIGO, L. U., CRUZ, L. M., AL-JANABI, S. M., MONTEIRO, R. A., BAURA, V. A. & PEDROSA, F. O. 2010. Influence of soil characteristics on the diversity of bacteria in the Southern Brazilian Atlantic Forest. *Appl Environ Microbiol,* 76**,** 4744-9.

FARRELL, J. & ROSE, A. 1967. Temperature Effects on Microorganisms. *Annual Review of Microbiology,* 21**,** 101-120.

FELLER, I. C. 1995. EFFECTS OF NUTRIENT ENRICHMENT ON GROWTH AND HERBIVORY OF DWARF RED MANGROVE (RHIZOPHORA MANGLE)' *Ecological Monographs,* 65**,** 477-505.

FITZPATRICK, D. A. 2012. Horizontal gene transfer in fungi. *FEMS Microbiology Letters,* 329**,** 1-8.

FOESEL, B. U., NAGELE, V., NAETHER, A., WUST, P. K., WEINERT, J., BONKOWSKI, M., LOHAUS, G., POLLE, A., ALT, F., OELMANN, Y., FISCHER, M., FRIEDRICH, M. W. & OVERMANN, J. 2014. Determinants of Acidobacteria activity inferred from

the relative abundances of 16S rRNA transcripts in German grassland and forest soils. *Environ Microbiol,* 16**,** 658-75.

FOKKEMA, N. J. 1991. Genetically Engineered Endophytes as Biocontrol Agents: A Case Study from Industry. *In:* ANDREWS, J. H. & HIRANO, S. S. (eds.) *Microbial Ecology of Leaves*

1ed. New York: Springer.

GALAND, P. E., FRITZE, H., CONRAD, R. & YRJALA, K. 2005. Pathways for methanogenesis and diversity of methanogenic archaea in three boreal peatland ecosystems. *Appl Environ Microbiol,* 71**,** 2195-8.

GEHRING, C. A. & WHITHAM, T. G. 1994. Interactions between aboveground herbivores and the mycorrhizal mutualists of plants. *Trends in Ecology and Evolution,* 9**,** 251-255.

GEML, J., MORGADO, L. N., SEMENOVA, T. A., WELKER, J. M., WALKER, M. D. & SMETS, E. 2015. Long-term warming alters richness and composition of taxonomic and functional groups of arctic fungi. *FEMS Microbiology Ecology*.

GIRVAN, M. & NEWMAN, M. E. 2002. Community structure in social and biological networks. *Proc Natl Acad Sci U S A,* 99**,** 7821-6.

GKARMIRI, K., MAHMOOD, S., EKBLAD, A., ALSTROM, S., HOGBERG, N. & FINLAY, R. 2017. Identifying the Active Microbiome Associated with Roots and Rhizosphere Soil of Oilseed Rape. *Appl Environ Microbiol,* 83.

GLYNOU, K., ALI, T., BUCH, A. K., HAGHI KIA, S., PLOCH, S., XIA, X., CELIK, A., THINES, M. & MACIA-VICENTE, J. G. 2016. The local environment determines the assembly of root endophytic fungi at a continental scale. *Environ Microbiol,* 18**,** 2418-34.

GOMES, T., PEREIRA, J. A., BENHADI, J., LINO-NETO, T. & BAPTISTA, P. 2018. Endophytic and Epiphytic Phyllosphere Fungal Communities Are Shaped by Different Environmental Factors in a Mediterranean Ecosystem. *Microb Ecol,* 76**,** 668-679.

GOTTEL, N. R., CASTRO, H. F., KERLEY, M., YANG, Z., PELLETIER, D. A., PODAR, M., KARPINETS, T., UBERBACHER, E., TUSKAN, G. A., VILGALYS, R., DOKTYCZ, M. J. & SCHADT, C. W. 2011. Distinct microbial communities within the endosphere and rhizosphere of Populus deltoides roots across contrasting soil types. *Appl Environ Microbiol,* 77**,** 5934-44.

GOVINDASAMY, V., FRANCO, C. M. M. & GUPTA, V. V. S. R. 2014. Endophytic Actinobacteria: Diversity and Ecology. *In:* VERMA, V. C. & GANGE, A. C. (eds.) *Advances in Endophytic Research.* New Delhi: Springer India.

GRAU, O., GEML, J., PEREZ-HAASE, A., NINOT, J. M., SEMENOVA-NELSEN, T. A. & PENUELAS, J. 2017. Abrupt changes in the composition and function of fungal communities along an environmental gradient in the high Arctic. *Mol Ecol,* 26**,** 4798-4810.

GRAY, M. W. & ARCHIBALD, J. M. 2012. *Genomics of Chloroplasts and Mitochondria,* Dordrecht, Heidelberg, New York, London, Springer.

HALLMANN, J., QUADT-HALLMANN, A., MAHAFFEE, W. F. & KLOEPPER, J. W. 1997. Bacterial endophytes in agricultural crops *Can. J. Microbiol.,* 43.

HARDOIM, P. R., HARDOIM, C. C., VAN OVERBEEK, L. S. & VAN ELSAS, J. D. 2012. Dynamics of seed-borne rice endophytes on early plant growth stages. *PLoS One,* 7**,** e30438.

HARDOIM, P. R., VAN OVERBEEK, L. S., BERG, G., PIRTTILA, A. M., COMPANT, S., CAMPISANO, A., DORING, M. & SESSITSCH, A. 2015. The Hidden World within

Plants: Ecological and Evolutionary Considerations for Defining Functioning of Microbial Endophytes. *Microbiol Mol Biol Rev,* 79**,** 293-320.

HARDOIM, P. R., VAN OVERBEEK, L. S. & ELSAS, J. D. 2008. Properties of bacterial endophytes and their proposed role in plant growth. *Trends Microbiol,* 16**,** 463-71.

HE, X., HAN, G., LIN, Y., TIAN, X., XIANG, C., TIAN, Q., WANG, F. & HE, Z. 2011. Diversity and decomposition potential of endophytes in leaves of a Cinnamomum camphora plantation in China. *Ecological Research,* 27**,** 273-284.

HELANDER, M. L., NEUVONEN, S., SIEBER, T. & PETRINI, O. 1993. Simulated acid rain affects birch leaf endophyte populations. *Microb Ecol,* 26**,** 227-34.

HONG, Y., LIAO, D., HU, A., WANG, H., CHEN, J., KHAN, S., SU, J. & LI, H. 2015. Diversity of endophytic and rhizoplane bacterial communities associated with exotic Spartina alterniflora and native mangrove using Illumina amplicon sequencing. *Can. J. Microbiol.*

HUANG, Y. L., DEVAN, M. M., U'REN, J. M., FURR, S. H. & ARNOLD, A. E. 2016. Pervasive Effects of Wildfire on Foliar Endophyte Communities in Montane Forest Trees. *Microb Ecol,* 71**,** 452-68.

ISTIFADAH, N. & MCGEE, P. A. 2006. Endophytic Chaetomium globosum reduces development of tan spot in wheat caused by Pyrenophora tritici-repentis. *Australasian Plant Pathology,* 35**,** 411-418.

JIA, M., CHEN, L., XIN, H. L., ZHENG, C. J., RAHMAN, K., HAN, T. & QIN, L. P. 2016. A Friendly Relationship between Endophytic Fungi and Medicinal Plants: A Systematic Review. *Front Microbiol,* 7**,** 906.

JOHNSTON-MONJE, D., MOUSA, W. K., LAZAROVITS, G. & RAIZADA, M. N. 2014. Impact of swapping soils on the endophytic bacterial communities of pre-domesticated, ancient and modern maize. *BMC Plant Biol,* 14**,** 233.

JOHNSTON-MONJE, D. & RAIZADA, M. N. 2011. Conservation and diversity of seed associated endophytes in Zea across boundaries of evolution, ethnography and ecology. *PLoS One,* 6**,** e20396.

JOSEPH, B. & PRIYA, R. M. 2011. Bioactive Compounds from Endophytes and their Potential in Pharmaceutical Effect: A Review. *American Journal of Biochemistry and Molecular Biology,* 1**,** 291-309.

KOBAYASHI, D. & PALUMBO, J. 2000. Bacterial endophytes and their effects on plants and uses in agriculture. *In:* CW, B. & JF, W. (eds.) *Microbial endophytes.* New York: Dekker.

KOEBERL, M., MUELLER, H., RAMADAN, E. M. & BERG, G. 2011. Desert Farming Benefits from Microbial Potential in Arid Soils and Promotes Diversity and Plant Health. *PLoS One,* 6.

KORKAMA-RAJALA, T., MULLER, M. M. & PENNANEN, T. 2008. Decomposition and fungi of needle litter from slow- and fast-growing Norway spruce (Picea abies) clones. *Microb Ecol,* 56**,** 76-89.

KREBS, C. 1999. *Ecological methodology,* San Francisco, CA.

KRINGS, M., TAYLOR, T. N., HASS, H., KERP, H., DOTZLER, N. & HERMSEN, E. J. 2007. Fungal endophytes in a 400-million-yr-old land plant: infection pathways, spatial distribution, and host responses. *New Phytol,* 174**,** 648-57.

KUMAR, S., KAUSHIK, N., EDRADA-EBEL, R., EBEL, R. & PROKSCH, P. 2010. Isolation, characterization, and bioactivity of endophytic fungi of Tylophora indica. *World Journal of Microbiology and Biotechnology,* 27**,** 571-577.

KUMARESAN, V. & SURYANARAYANAN, T. S. 2002. Endophyte assemblages in young, mature and senescent leaves of Rh izoph ora apiculata: evidence for the role of endophytes in mangrove litter degradation. *Fungal Diversity,* 9**,** 81-91.

LAU, M. K., ARNOLD, A. E. & JOHNSON, N. C. 2013. Factors influencing communities of foliar fungal endophytes in riparian woody plants. *Fungal Ecology,* 6**,** 365-378.

LE COCQ, K., GURR, S. J., HIRSCH, P. R. & MAUCHLINE, T. H. 2017. Exploitation of endophytes for sustainable agricultural intensification. *Mol Plant Pathol,* 18**,** 469-473.

LEE, S. K., LEE, S. K., BAE, H., SEO, S. T. & LEE, J. K. 2014. Effects of Water Stress on the Endophytic Fungal Communities of Pinus koraiensis Needles Infected by Cenangium ferruginosum. *Mycobiology,* 42**,** 331-8.

LI, J., ZHAO, G. Z., HUANG, H. Y., QIN, S., ZHU, W. Y., ZHAO, L. X., XU, L. H., ZHANG, S., LI, W. J. & STROBEL, G. 2012. Isolation and characterization of culturable endophytic actinobacteria associated with Artemisia annua L. *Antonie Van Leeuwenhoek,* 101**,** 515-27.

LI, Q., XIONG, C., LI, X., JIN, X. & HUANG, W. 2018. Ectomycorrhization of Tricholoma matsutake with Quercus aquifolioides affects the endophytic microbial community of host plant. *J Basic Microbiol,* 58**,** 238-246.

LIU, G., CHATER, K. F., CHANDRA, G., NIU, G. & TAN, H. 2013. Molecular regulation of antibiotic biosynthesis in streptomyces. *Microbiol Mol Biol Rev,* 77**,** 112-43.

LIU, H., CARVALHAIS, L. C., CRAWFORD, M., SINGH, E., DENNIS, P. G., PIETERSE, C. M. J. & SCHENK, P. M. 2017. Inner Plant Values: Diversity, Colonization and Benefits from Endophytic Bacteria. *Front Microbiol,* 8**,** 2552.

LIU, K., DING, X., DENG, B. & CHEN, W. 2009. Isolation and characterization of endophytic taxol-producing fungi from Taxus chinensis. *J Ind Microbiol Biotechnol,* 36**,** 1171-7.

LUO, S., XU, T., CHEN, L., CHEN, J., RAO, C., XIAO, X., WAN, Y., ZENG, G., LONG, F., LIU, C. & LIU, Y. 2012. Endophyte-assisted promotion of biomass production and metal-uptake of energy crop sweet sorghum by plant-growth-promoting endophyte Bacillus sp. SLS18. *Applied Microbiology & Biotechnology,* 93**,** 1745-1753.

MA, B., LV, X., WARREN, A. & GONG, A. J. 2013. Shifts in diversity and community structure of endophytic bacteria and archaea across root, stem and leaf tissues in the common reed, Phragmites australis, along a salinity gradient in a marine tidal wetland of northern China. *Antonie Van Leeuwenhoek,* 104**,** 759-68.

MALINOWSKI, D. P., ALLOUSH, G. A. & BELESKY, D. P. 1998. Evidence for chemical changes on the root surface of tall fescue in response to infection with the fungal endophyte Neotyphodium coenophialum. *Plant and Soil,* 205**,** 1-12.

MALINOWSKI, D. P., ALLOUSH, G. A. & BELESKY, D. P. 2000. Leaf endophyte Neotyphodium coenophialum modifies mineral uptake in tall fescue. *Plant and Soil,* 227**,** 115-126.

MANO, H. & MORISAKI, H. 2008. Endophytic Bacteria in the Rice Plant. *Microbes and Environments,* 23**,** 109-117.

MARLER, M., PEDERSEN, D., MITCHELL-OLDS, T. & CALLAWAY, R. M. 1999. A polymerase chain reaction method for detecting dwarf mistletoe infection in Douglas-fir and western larch. *Can. J. For. Res.,* 29**,** 1317-1321.

MARTÍN-GARCÍA, J., ESPIGA, E., PANDO, V. & DIEZ, J. J. 2011. Factors Influencing Endophytic Communities in Poplar Plantations. *Silva Fennica,* 45**,** 169-180.

MASSIMO, N. C., NANDI DEVAN, M. M., ARENDT, K. R., WILCH, M. H., RIDDLE, J. M., FURR, S. H., STEEN, C., U'REN, J. M., SANDBERG, D. C. & ARNOLD, A. E. 2015.

Fungal endophytes in aboveground tissues of desert plants: infrequent in culture, but highly diverse and distinctive symbionts. *Microb Ecol,* 70**,** 61-76.

MASTRETTA, C., TAGHAVI, S., VAN DER LELIE, D., MENGONI, A., GALARDI, F., GONNELLI, C., BARAC, T., BOULET, J., WEYENS, N. & VANGRONSVELD, J. 2009. Endophytic Bacteria from Seeds Ofnicotiana Tabacumcan Reduce Cadmium Phytotoxicity. *International Journal of Phytoremediation,* 11**,** 251-267.

MCALLISTER, S. M., DAVIS, R. E., MCBETH, J. M., TEBO, B. M., EMERSON, D. & MOYER, C. L. 2011. Biodiversity and emerging biogeography of the neutrophilic iron-oxidizing Zetaproteobacteria. *Appl Environ Microbiol,* 77**,** 5445-57.

MCINROY, J. A. & KLOEPPER, J. W. 1995. Survey of indigenous bacterial endophytes from cotton and sweet corn. *Plant and Soil,* 173**,** 337-342.

MITTER, E. K., DE FREITAS, J. R. & GERMIDA, J. J. 2017. Bacterial Root Microbiome of Plants Growing in Oil Sands Reclamation Covers. *Front Microbiol,* 8**,** 849.

NAIR, D. N. & PADMAVATHY, S. 2014. Impact of endophytic microorganisms on plants, environment and humans. *ScientificWorldJournal,* 2014**,** 250693.

NEILANDS, J. B. 1993. "Siderophores". *Archives of Biochemistry and Biophysics,* 302**,** 1-3.

NISSINEN, R. M., MANNISTO, M. K. & ELSAS, J. D. V. 2012. Endophytic bacterial communities in three arctic plants fromlow arctic fell tundra are cold-adapted and host-plant specific. *FEMS Microbiology Ecology,* 82**,** 510-522.

OFEK-LALZAR, M., GUR, Y., BEN-MOSHE, S., SHARON, O., KOSMAN, E., MOCHLI, E. & SHARON, A. 2016. Diversity of fungal endophytes in recent and ancient wheat ancestors Triticum dicoccoides and Aegilops sharonensis *FEMS Microbiology Ecology,* 92.

OLIVEIRA, M. N., SANTOS, T. M., VALE, H. M., DELVAUX, J. C., CORDERO, A. P., FERREIRA, A. B., MIGUEL, P. S., TOTOLA, M. R., COSTA, M. D., MORAES, C. A. & BORGES, A. C. 2013. Endophytic microbial diversity in coffee cherries of Coffea arabica from southeastern Brazil. *Can J Microbiol,* 59**,** 221-30.

OONO, R., LEFEVRE, E., SIMHA, A. & LUTZONI, F. 2015. A comparison of the community diversity of foliar fungal endophytes between seedling and adult loblolly pines (Pinus taeda). *Fungal Biol,* 119**,** 917-928.

ORTEGA, R. A., MAHNERT, A., BERG, C., MÜLLER, H. & BERG, G. 2016. The plant is crucial: specific composition and function of the phyllosphere microbiome of indoor ornamentals. *FEMS Microbiology Ecology,* 92.

PAWLOWSKA, J., WILK, M., SLIWINSKA-WYRZYCHOWSKA, A., METRAK, M. & WRZOSEK, M. 2014. The diversity of endophytic fungi in the above-ground tissue of two Lycopodium species in Poland. *Symbiosis,* 63**,** 87-97.

PEREZ-JARAMILLO, J. E., CARRION, V. J., DE HOLLANDER, M. & RAAIJMAKERS, J. M. 2018. The wild side of plant microbiomes. *Microbiome,* 6**,** 143.

PETERS, A. F. 1991. Field and culture studies of Streblonema macrocystis sp. nov. (Ectocapales, Phaeophyceae) from Chile, a sexual endophyte of giant kelp *Phycologia,* 30**,** 365-377.

PHILLIPS, L. A., GREER, C. W., FARRELL, R. E. & GERMIDA, J. J. 2012. Plant root exudates impact the hydrocarbon degradation potential of a weathered-hydrocarbon contaminated soil. *Applied Soil Ecology,* 52**,** 56-64.

PIETRO-SOUZA, W., MELLO, I. S., VENDRUSCULLO, S. J., SILVA, G. F. D., CUNHA, C. N. D., WHITE, J. F. & SOARES, M. A. 2017. Endophytic fungal communities of Polygonum acuminatum and Aeschynomene fluminensis are influenced by soil mercury contamination. *PLoS One,* 12**,** e0182017.

POSADA, F. & VEGA, F. E. 2006. Inoculation and colonization of coffee seedlings (Coffea arabica L.) with the fungal entomopathogen Beauveria bassiana (Ascomycota: Hypocreales). *Mycoscience,* 47**,** 284-289.

POTSHANGBAM, M., DEVI, S. I., SAHOO, D. & STROBEL, G. A. 2017. Functional Characterization of Endophytic Fungal Community Associated with Oryza sativa L. and Zea mays L. *Front Microbiol,* 8**,** 325.

PRIHATINI, I., GLEN, M., WARDLAW, T. J. & MOHAMMED, C. L. 2015. Diversity and identification of fungi associated with needles ofPinus radiatain Tasmania. *Southern Forests: a Journal of Forest Science,* 78**,** 19-34.

PROMPUTTHA, I., HYDE, K. D., MCKENZIE, E. H. C., PEBERDY, J. F. & LUMYONG, S. 2010. Can leaf degrading enzymes provide evidence that endophytic fungi becoming saprobes? *Fungal Diversity,* 41**,** 89-99.

RANDRIAMANANA, T. R., LAVOLA, A. & JULKUNEN-TIITTO, R. 2015. Interactive effects of supplemental UV-B and temperature in European aspen seedlings: Implications for growth, leaf traits, phenolic defense and associated organisms. *Plant Physiol Biochem,* 93**,** 84-93.

RANGJAROEN, C., RERKASEM, B., TEAUMROONG, N., SUNGTHONG, R. & LUMYONG, S. 2014. Comparative study of endophytic and endophytic diazotrophic bacterial communities across rice landraces grown in the highlands of northern Thailand. *Arch Microbiol,* 196**,** 35-49.

RASCHE, F., TRONDL, R., NAGLREITER, C., REICHENAUER, T. G. & SESSITSCH, A. 2006. Chilling and cultivar type affect the diversity of bacterial endophytes colonizing sweet pepper (Capsicum anuum L.). *Can J Microbiol,* 52**,** 1036-45.

REDMAN, R. S., DUNIGAN, D. D. & RODRIGUEZ, R. J. 2001. Blackwell Science Ltd Fungal symbiosis from mutualism to parasitism: who controls the outcome, host or invader? *New Phytologist,* 151**,** 705-716.

REN, G., ZHANG, H., LIN, X., ZHU, J. & JIA, Z. 2015. Response of leaf endophytic bacterial community to elevated CO2 at different growth stages of rice plant. *Front Microbiol,* 6**,** 855.

REN, J. H., YE, J. R., LIU, H., XU, X. L. & WU, X. Q. 2011. Isolation and characterization of a new Burkholderia pyrrocinia strain JK-SH007 as a potential biocontrol agent. *World Journal of Microbiology and Biotechnology,* 27**,** 2203-2215.

ROBINSON, R. J., FRAAIJE, B. A., CLARK, I. M., JACKSON, R. W., HIRSCH, P. R. & MAUCHLINE, T. H. 2015. Endophytic bacterial community composition in wheat (Triticum aestivum) is determined by plant tissue type, developmental stage and soil nutrient availability. *Plant and Soil,* 405**,** 381-396.

ROESCH, L., PASSAGLIA, L., BENTO, F., TRIPLETT, E. & CAMARGO, F. 2007. Diversity of diazotrophic endophytic bacteria associated with maize plants. *Rev Bras Ciência Solo,* 31**,** 1367–1380.

RUA, M. A., WILSON, E. C., STEELE, S., MUNTERS, A. R., HOEKSEMA, J. D. & FRANK, A. C. 2016. Associations between Ectomycorrhizal Fungi and Bacterial Needle Endophytes in Pinus radiata: Implications for Biotic Selection of Microbial Communities. *Front Microbiol,* 7**,** 399.

RUSSELL, J. R., HUANG, J., ANAND, P., KUCERA, K., SANDOVAL, A. G., DANTZLER, K. W., HICKMAN, D., JEE, J., KIMOVEC, F. M., KOPPSTEIN, D., MARKS, D. H., MITTERMILLER, P. A., NUNEZ, S. J., SANTIAGO, M., TOWNES, M. A., VISHNEVETSKY, M., WILLIAMS, N. E., VARGAS, M. P., BOULANGER, L. A., BASCOM-SLACK, C. & STROBEL, S. A. 2011. Biodegradation of polyester polyurethane by endophytic fungi. *Appl Environ Microbiol,* 77**,** 6076-84.

SAIKKONEN, K., FAETH, S. H., HELANDER, M. & SULLIVAN, T. J. 1998. FUNGAL ENDOPHYTES: A Continuum of Interactions with Host Plants. *Annu. Rev. Ecol. Syst.,* 29**,** 319-43.

SAIKKONEN, K., WALI, P., HELANDER, M. & FAETH, S. H. 2004. Evolution of endophyte-plant symbioses. *Trends Plant Sci,* 9**,** 275-80.

SANTOYO, G., MORENO-HAGELSIEB, G., OROZCO-MOSQUEDA MDEL, C. & GLICK, B. R. 2016. Plant growth-promoting bacterial endophytes. *Microbiol Res,* 183**,** 92-9.

SCHNEPF, E., CRICKMORE, N., RIE, J. V., LERECLUS, D., BAUM, J., FEITELSON, J., ZEIGLER, D. R. & DEAN, D. H. 1998. Bacillus thuringiensis and Its Pesticidal Crystal Proteins. *MICROBIOLOGY AND MOLECULAR BIOLOGY REVIEWS,* 62**,** 775-806.

SCHOUTEN, A. 2016. Mechanisms Involved in Nematode Control by Endophytic Fungi. *Annu Rev Phytopathol,* 54**,** 121-42.

SCHULZ, B. & BOYLE, C. 2006. *Microbial Root Endophytes*, Springer.

SHI, Y., TAPA, M., LI, C., YANG, H., ZHANG, T., GAO, Y., SUN, J., ZENG, J., LIN, Q., CAO, Z., OUTI, K., LI, Y. & LOU, K. 2015. Diversity and space-time dynamics of endophytic archaea from sugar beet in the north slope of Tianshan Mountain revealed by 454 pyrosequencing and T-RFLP. *World J Microbiol Biotechnol,* 31**,** 1031-9.

SIEBER, T. 2002. Fungal root endophytes. *In:* Y, W., A, E. & U, K. (eds.) *The hidden half.* New York: Dekker.

SMITH, S. & READ, D. 2008. *Mycorrhizal Symbiosis,* London, United Kingdom, Elsevier Science.

STIRLING, G. & WILSEY, B. 2001. Empirical Relationships between Species Richness, Evenness, and Proportional Diversity. *The American Naturalist,* 158**,** 286-299.

STOMEO, F., MAKHALANYANE, T. P., VALVERDE, A., POINTING, S. B., STEVENS, M. I., CARY, C. S., TUFFIN, M. I. & COWAN, D. A. 2012. Abiotic factors influence microbial diversity in permanently cold soil horizons of a maritime-associated Antarctic Dry Valley. *FEMS Microbiol Ecol,* 82**,** 326-40.

STONE, J., BACON, C. & WHITE, J. 2000. An overview of endophytic microbes: Endophytism defined. *In:* CW, B. & JF, W. (eds.) *Microbial endophytes.* New York: M Dekker.

STURZ, A. V., CHRISTIE, B. R., MATHESON, B. G. & NOWAK, J. 1997. Biodiversity of endophytic bacteria which colonize red clover nodules, roots, stems and foliage and their influence on host growth. *Biol Fertil Soils,* 25**,** 13-19.

STURZ, A. V. & NOWAK, J. 2000. Endophytic communities of rhizobacteria and the strategies required to create yield enhancing associations with crops. *Applied Soil Ecology,* 15**,** 183-190.

SUN, L., QIU, F., ZHANG, X., DAI, X., DONG, X. & SONG, W. 2008. Endophytic bacterial diversity in rice (Oryza sativa L.) roots estimated by 16S rDNA sequence analysis. *Microb Ecol,* 55**,** 415-24.

SUN, X. & GUO, L.-D. 2012. Endophytic fungal diversity: review of traditional and molecular techniques. *Mycology,* 3**,** 65–76.

SZYMANSKA, S., BORRUSO, L., BRUSETTI, L., HULISZ, P., FURTADO, B. & HRYNKIEWICZ, K. 2018. Bacterial microbiome of root-associated endophytes of Salicornia europaea in correspondence to different levels of salinity. *Environ Sci Pollut Res Int,* 25**,** 25420-25431.

SZYMANSKA, S., PLOCINICZAK, T., PIOTROWSKA-SEGET, Z. & HRYNKIEWICZ, K. 2016. Endophytic and rhizosphere bacteria associated with the roots of the

halophyte Salicornia europaea L. - community structure and metabolic potential. *Microbiol Res,* 192**,** 37-51.

TAFFNER, J., ERLACHER, A., BRAGINA, A., BERG, C., MOISSL-EICHINGER, C. & BERG, G. 2018. What Is the Role of Archaea in Plants? New Insights from the Vegetation of Alpine Bogs. *mSphere,* 3.

THOMAS, F., HEHEMANN, J. H., REBUFFET, E., CZJZEK, M. & MICHEL, G. 2011. Environmental and gut bacteroidetes: the food connection. *Front Microbiol,* 2**,** 93.

TURNER, T. R., JAMES, E. K. & POOLE, P. S. 2013. The plant microbiome. *Genome Biol,* 14**,** 209.

U'REN, J. M., LUTZONI, F., MIADLIKOWSKA, J., LAETSCH, A. D. & ARNOLD, A. E. 2012. Host and geographic structure of endophytic and endolichenic fungi at a continental scale. *Am J Bot,* 99**,** 898-914.

VAN HECKE, M. M., TREONIS, A. M. & KAUFMAN, J. R. 2005. How does the Fungal Endophyte Neotyphodium coenophialum Affect Tall Fescue (Festuca arundinacea) Rhizodeposition and Soil Microorganisms? *Plant and Soil,* 275**,** 101-109.

VANČURA, V. 1967. Root exudates of plants. *Plant and Soil,* 27**,** 319-328.

WALITANG, D. I., KIM, C. G., KIM, K., KANG, Y., KIM, Y. K. & SA, T. 2018. The influence of host genotype and salt stress on the seed endophytic community of salt-sensitive and salt-tolerant rice cultivars. *BMC Plant Biol,* 18**,** 51.

WALITANG, D. I., KIM, K., MADHAIYAN, M., KIM, Y. K., KANG, Y. & SA, T. 2017. Characterizing endophytic competence and plant growth promotion of bacterial endophytes inhabiting the seed endosphere of Rice. *BMC Microbiology,* 17.

WANG, W., ZHAI, Y., CAO, L., TAN, H. & ZHANG, R. 2016. Illumina-based analysis of core actinobacteriome in roots, stems, and grains of rice. *Microbiol Res,* 190**,** 12-8.

WEMHEUER, F., KAISER, K., KARLOVSKY, P., DANIEL, R., VIDAL, S. & WEMHEUER, B. 2017. Bacterial endophyte communities of three agricultural important grass species differ in their response towards management regimes. *Sci Rep,* 7**,** 40914.

WHITTAKER, R. H. 1972. EVOLUTION AND MEASUREMENT OF SPECIES DIVERSITY. *Taxon,* 21**,** 213-251.

WILLIAMS, K. P. & KELLY, D. P. 2013. Proposal for a new class within the phylum Proteobacteria, Acidithiobacillia classis nov., with the type order Acidithiobacillales, and emended description of the class Gammaproteobacteria. *Int J Syst Evol Microbiol,* 63**,** 2901-6.

WILSON, D. 1993. Fungal Endophytes: Out of Sight but Should Not Be out of Mind. *Oikos,* 68**,** 379-384.

XIN, G., ZHANG, G., KANG, J. W., STALEY, J. T. & DOTY, S. L. 2009. A diazotrophic, indole-3-acetic acid-producing endophyte from wild cottonwood. *Biology and Fertility of Soils,* 45**,** 669-674.

YAISH, M. W., AL-LAWATI, A., JANA, G. A., VISHWAS PATANKAR, H. & GLICK, B. R. 2016. Impact of Soil Salinity on the Structure of the Bacterial Endophytic Community Identified from the Roots of Caliph Medic (Medicago truncatula). *PLoS One,* 11**,** e0159007.

YANG, T., WEISENHORN, P., GILBERT, J. A., NI, Y., SUN, R., SHI, Y. & CHU, H. 2016. Carbon constrains fungal endophyte assemblages along the timberline. *Environ Microbiol,* 18**,** 2455-69.

ZABALGOGEAZCOA, I. 2008. Review. Fungal endophytes and their interaction with plant pathogens. *Spanish Journal of Agricultural Research,* 6**,** 138-146.

ZHANG, H., JOHN, R., PENG, Z., YUAN, J., CHU, C., DU, G. & ZHOU, S. 2012. The Relationship between Species Richness and Evenness in Plant Communities along a Successional Gradient: A Study from Sub-Alpine Meadows of the Eastern Qinghai-Tibetan Plateau, China. *PLOS ONE* 7.

ZHANG, H. W., SONG, Y. C. & TAN, R. X. 2006. Biology and chemistry of endophytes. *Natural Product Reports,* 23**,** 753-771.

ZHANG, T. & YAO, Y. F. 2015. Endophytic Fungal Communities Associated with Vascular Plants in the High Arctic Zone Are Highly Diverse and Host-Plant Specific. *PLoS One,* 10**,** e0130051.

ZHANG, T., ZHANG, Y. Q., LIU, H. Y., WEI, Y. Z., LI, H. L., SU, J., ZHAO, L. X. & YU, L. Y. 2013. Diversity and cold adaptation of culturable endophytic fungi from bryophytes in the Fildes Region, King George Island, maritime Antarctica. *FEMS Microbiol Lett,* 341**,** 52-61.

ZIMMERMAN, N. B. & VITOUSEK, P. M. 2012. Fungal endophyte communities reflect environmental structuring across a Hawaiian landscape. *PNAS,* 109.