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Differences in community composition of endophytic fungi between above- and below-ground tissues of *Aristolochia chilensis* in an arid ecosystem

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Abstract

Background: Endophytic fungi are diverse and ubiquitous in nature, yet studies simultaneously comparing endophyte communities in above- and below-ground plant tissues are relatively scarce. The main goal of our study was to compare the diversity and community composition of endophytic fungi associated with above- and below-ground tissues of the plant *Aristolochia chilensis* in an arid ecosystem. Endophytic fungi were isolated from healthy leaves and roots of *A. chilensis*, and the internal transcribed spacer (ITS) region was sequenced for phylogenetic and taxonomic analysis.

Results: A combined total of 457 fungal isolates were cultured from leaf and root tissues, belonging to 54 operational taxonomic units (OTUs). The genera *Fusarium*, *Penicillium*, *Phialemonium* and *Trichoderma* were the most representative endophyte taxa identified in *A. chilensis* tissues; nevertheless, *Fusarium* was significantly more dominant in the below-ground community, while foliar endophyte community was dominated by *Penicillium*. Whereas OTU richness and diversity were not different between below-ground and above-ground tissues, endophyte abundance was on average twice as high in below-ground tissue than in above-ground tissue. Fungal endophyte communities in the two tissue types were significantly dissimilar.

Conclusions: Results from this study indicate that *A. chilensis* harbors a similar diversity of endophytic fungi in above- and below-ground tissues. Dominant endophytic fungi were found to be dependent on tissue type, which potentially resulted in marked differences in community structure between above- and below-ground tissues. Ecological processes potentially affecting this pattern are discussed.

Keywords: Endophytic fungi, Diversity, Community composition, *Aristolochia chilensis*

Background

Fungal endophytes frequently occur in a variety of plant structures, living intercellularly in roots, stems and leaves [1] for at least part of their life cycle without causing any apparent sign of disease in hosts [2]. They are ubiquitous in nature, and have been isolated from every organ of nearly all plant species [3]. Fungal endophytes

can be transmitted either vertically, as in the case of 'type I' endophytic fungi of the Clavicipitaceae family that colonize grasses exclusively, or horizontally, as in the case of non-clavicipitaceous 'type II' endophyte, which colonize a wide range of hosts through air- and soil-borne spores [4]. Type II endophyte communities are highly phylogenetically diverse [5–7], and members of different classes and orders can frequently co-occur in the same tissue [5]. Fungal endophytes may confer diverse benefits to host plants by improving growth,

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resistance to different abiotic stresses, and by protecting them from herbivores and pathogens [4].

Type II endophyte community composition has been demonstrated to be strongly influenced by both biotic and abiotic factors, such as host species, plant tissue, plant chemistry, soil nutrient availability and local environmental conditions [8–11]. Above- and below-ground tissues potentially represent contrasting habitats for endophytic fungi, which might differentially affect their ability to disperse and colonize a given host. Studies have consistently reported large dissimilarities in endophyte community composition between different tissues of the same host plant, and it has been suggested that these communities display a high degree of organ specificity within plants [12, 13]. Some studies have reported higher endophyte diversity in leaf than in root tissues [14, 15], although the opposite pattern has also been shown to be true [12], or even similar [16]. Studies on the diversity and distribution of endophytic fungi for a given plant species is relevant in order to understand how these symbionts may confer fitness benefits and ecological adaptations to plants. This is particularly true when host plants grow under extreme environmental conditions such as arid habitats.

Here we examined, using a culture-dependent method, the diversity and community composition of endophytic fungi associated with above- and below-ground tissues of the native plant species *Aristolochia chilensis*, growing naturally in an arid population in Northern Chile. Despite the widespread occurrence of endophytic fungi in arid environments [9, 17–19], in Chile, there is a lack of information about endophytic fungi associated with arid plants. The aims of the study were to 1) isolate and molecularly identify fungal endophytes associated with above- and below-ground tissues of *A. chilensis*, 2) compare richness and diversity of above- and below-ground fungal endophyte communities, 3) determine the degree of structural similarity between communities of endophytic fungi in both above- and below-ground tissues. This knowledge will advance current understanding of colonization dynamics of endophytic fungi associated with different plant tissues in Chilean arid plants.

Methods

Study species

Aristolochia chilensis (Bridges ex Lindl.), endemic to Chile, is a perennial creeping herb with a distribution ranging from a Mediterranean-type climate in central Chile (33° 29' S) to an arid climate (27° 30' S) in the Atacama Desert in the north of the country [20]. It has dark green reniform leaves and purple-brownish protogynous flowers [21]. This study was carried out between October and November 2015 in a population of *A. chilensis* in the Coquimbo Region in Northern Chile

(29° 58' S; 71° 22' W). Climate at the study site is classified as arid [22], with an average annual rainfall of approximately 80 mm [23].

Isolation and molecular identification of fungal endophytes

Ten adult *Aristolochia chilensis* plants of similar size and phenological stage were randomly selected in the field for leaf and root collection in October 2015. In each plant we collected three mature asymptomatic leaves and three primary healthy roots. These samples were then pooled in order to maximize fungal endophyte isolation from each individual plant. Once in the lab leaf and root material were surface-sterilized with ethanol (70%) for 3 min, sodium hypochlorite (1%) for 1 min, followed by three rinses in sterile distilled water for 3 min each [24]. The absence of any microbial growth from the water wash on PDA plates (potato-dextrose-agar, Phyto Technology Laboratories) confirmed the success of surface sterilization. We subsequently cultivated small sections of sterilized leaves and roots (0.5–1.0 cm) on PDA petri dishes plates. Plates were then incubated at room temperature (23 °C) for 3–4 weeks. After that time, emerging colonies were subcultured (this procedure was repeated three times) to obtain pure isolates. Pure isolates of endophytic fungi were grown on PDA plates (Phyto Technology Laboratories) at room temperature for 5–6 weeks for further DNA extraction and molecular identification. We extracted genomic DNA from the mycelial mat using a modified method described by [25]. Fresh mycelium was ground on Mini-BeadBeater-16 (BioSpec, USA). 100 mg of ground mycelium were suspended in extraction buffer (10 mM Tris buffer pH 8.0, 10 mM EDTA, 0.5% SDS, NaCl 250 mM). To this aqueous solution, phenol:chloroform:isoamyl alcohol (25:24:1) was added and mixed slowly for 3 min. The phases were separated by centrifugation at 13,000 rpm for 10 min at room temperature. Traces of phenol were removed by treating the aqueous layer with chloroform:isoamyl alcohol (24:1). DNA was precipitated from the aqueous phase with 2.0 volumes of isopropanol. DNA was recovered by centrifugation at 10,000 rpm for 15 min at 4 °C. The pellet was then washed with 70% ethanol and resuspended in molecular biology grade water (Mo Bio Laboratories, Inc). Species identification of endophytic fungi was performed using the primers ITS1-F-KYO1 (CTHGGTCATTTAGAGGAATAA) and ITS4 (TCCTCCGCTTATTGATATGC). Amplification of target region (around 680 bp) was conducted with 50 µL of PCR reaction mixtures, each containing 7 µL of total genomic DNA, 1 µL of each primer (10 µM), 27.5 µL of SapphireAmp Fast PCR Master Mix (Takara) and 14.5 µL of sterilized water. PCRs was performed in a Techne TC-5000 Thermal Cycler (Fisher

Table 1 Identified fungal endophyte species for leaf and root tissues of *Aristolochia chilensis*. The total number of isolates (considering the total individuals) for each OTU is indicated

Closest relative from Genbank	Identity (%)	Cover (%)	Genbank Accession Number	Tissue	Number of isolates
<i>Alternaria alternata</i>	99	100	KX516025.1	Leaf	5
<i>Alternaria sp 1</i>	99	100	MH029120.1	Leaf	6
<i>Alternaria sp 2</i>	96	99	FN868462.1	Leaf	2
<i>Aspergillus niger</i>	100	100	MT074422.1	Leaf	3
<i>Cladosporium ramotenellum 1</i>	99	100	MK388045.1	Leaf	2
<i>Cladosporium ramotenellum 2</i>	99	99	MF473247.1	Root	1
<i>Clonostachys sp.</i>	99	99	KU556490.1	Root	14
<i>Epicoccum nigrum</i>	100	100	MK388043.1	Root	1
<i>Fungal sp.1</i>	99	99	KU839501.1	Root	15
<i>Fungal sp. 2</i>	98	92	KU838627.1	Root	1
<i>Fusarium decemcellulare</i>	99	100	MF076589.1	Root	3
<i>Fusarium equiseti</i>	100	100	MN133053.1	Leaf	1
<i>Fusarium oxysporum 1</i>	100	100	MK336584.1	Leaf	3
<i>Fusarium oxysporum 1</i>	99	100	MK336584.1	Root	115
<i>Fusarium oxysporum 2</i>	100	100	MK336615.1	Leaf	1
<i>Fusarium oxysporum 3</i>	100	100	MK336521.1	Root	8
<i>Fusarium sp.</i>	88	83	KP191630.1	Root	34
<i>Fusarium sambucinum</i>	99	100	KM231813.1	Root	9
<i>Hypocrea lixii</i>	100	100	JF923807.1	Root	1
<i>Hypocrea viridescens</i>	97	77	KF381075.1	Root	2
<i>Meyerozyma caribbica</i>	100	100	MH545919.1	Root	1
<i>Meyerozyma guilliermondii 1</i>	100	86	KY104257.1	Leaf	6
<i>Meyerozyma guilliermondii 2</i>	100	100	MN592978.1	Root	14
<i>Neostagonospora sp.</i>	98	86	MH399526.1	Leaf	2
<i>Penicillium corylophilum</i>	99	96	MF475922.1	Leaf	1
<i>Penicillium crustosum</i>	85	100	MN511336.1	Root	1
<i>Penicillium expansum</i>	99	100	MH879249.1	Leaf	1
<i>Penicillium glabrum 1</i>	100	100	MK910051.1	Leaf	33
<i>Penicillium glabrum 1</i>	100	100	MK910051.1	Root	5
<i>Penicillium italicum</i>	100	91	NR_163528.1	Leaf	6
<i>Penicillium murcianum</i>	100	100	KP016842.1	Root	3
<i>Penicillium sp. 1</i>	97	100	MN096594.1	Leaf	4
<i>Penicillium sp. 2</i>	98	53	MN704702.1	Leaf	2
<i>Penicillium sp. 3</i>	96	100	MK226541.1	Root	14
<i>Phialemoniopsis cornearis</i>	100	100	HQ719230.1	Root	8
<i>Phialemoniopsis sp.</i>	97	96	MH268053.1	Leaf	42
<i>Phomopsis columnaris</i>	99	98	LT821462.1	Root	2
<i>Pleosporales sp.</i>	95	82	KX611040.1	Leaf	1
<i>Preussia australis 1</i>	99	100	KX611039.1	Leaf	4
<i>Preussia australis 2</i>	98	83	KX710240.1	Root	1
<i>Sarocladium spinificis</i>	100	100	MK336486.1	Root	1
<i>Sordaria fimicola</i>	99	100	MK432735.1	Leaf	2
<i>Stemphylium eturminum</i>	100	100	MN401375.1	Leaf	3

Table 1 Identified fungal endophyte species for leaf and root tissues of *Aristolochia chilensis*. The total number of isolates (considering the total individuals) for each OTU is indicated (*Continued*)

Closest relative from Genbank	Identity (%)	Cover (%)	Genbank Accession Number	Tissue	Number of isolates
<i>Stemphylium vesicarium</i> 1	99	92	MN401397.1	Leaf	2
<i>Stemphylium vesicarium</i> 2	99	98	MN534849.1	Leaf	10
<i>Stemphylium vesicarium</i> 3	98	81	MH084268.1	Leaf	12
<i>Stemphylium vesicarium</i> 4	96	85	MN328386.1	Leaf	1
<i>Talaromyces amestolkiae</i> 1	100	100	MN086355.1	Leaf	11
<i>Talaromyces amestolkiae</i> 1	100	100	MN086355.1	Root	9
<i>Talaromyces minioluteus</i>	96	100	KY951916.1	Root	16
<i>Trichoderma atroviride</i> 1	99	100	MK460812.1	Leaf	1
<i>Trichoderma atroviride</i> 1	99	99	MK460812.1	Root	1
<i>Trichoderma breve</i>	99	97	MN400089.1	Root	1
<i>Trichoderma</i> sp.	99	100	MT035967.1	Root	9

Scientific) according to the following program: 94 °C for 3 min, followed by 35 cycles of denaturation at 94 °C for 1 min, annealing at 54 °C for 30 s and primer extension at 72 °C for 1 min, completed with a final extension at 72 °C for 7 min. Efficacy in the DNA extraction was verified by 1% agarose gel electrophoresis. PCR products were sent to Macrogen, South Korea, for further purification and sequencing. Sense and antisense sequences were assembled using SeqTrace software. Assembled sequences were aligned with the Codoncode Aligner software and screened using BLAST (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>). Sequences alignments and phylogenetic tree were constructed by using MEGA software, version 7.0 [26]. Alignments were performed with ClustalW [27], DNA weight matrix ClustalW 1.6 and default parameters. Phylogenetic reconstruction was performed by using neighbor-joining method [28], with p-distance substitution model and bootstrapping of 1000. Additional sequences from ITS1 and ITS2 regions for the phylogenetic tree were retrieved from NCBI. Fungal sequences have been deposited at the NCBI with accession numbers MT441588-MT441640.

Statistical analyses

Differences in relative abundance of the most prevalent fungal endophyte genera, fungal endophyte abundance (number of fungal isolates), species richness (number of OTUs), Chao-1 (richness estimator) index, and Shannon and Simpson diversity indices between above- and below-ground tissues were assessed using a nested ANOVA, where plant tissue (leaf and root) was considered a fixed factor, and nested on individual plants (N per tissue: 10 individuals); individual plants were considered random factors. An analysis of similarity (ANOSIM) was used to examine differences in community composition between tissues. ANOSIM was performed with Bray-Curtis similarities after 999 permutations using the vegan package in R [29]. Differences in fungal

endophyte communities between above- and below ground tissues were visualized using non-metric multidimensional scaling (NMDS) plots. Plots were constructed based on a Bray-Curtis coefficient of similarity of the incidence and abundance of taxa found in different tissues. In addition, the degree of structural similarity between above- and below-ground communities was assessed using similarity indices based on presence/absence data (Jaccard and Sorensen). All analyses were performed using the R statistical package [29].

Results

Total isolates were 167 for above-ground tissues and 290 for below-ground tissues, assigned to 27 and 27 OTUs, respectively (Table 1). OTUs were aligned and the phylogenetic tree shows different clades by taxonomic groups but shared between above- and below-ground tissues (Fig. 1). Phylogeny corroborates the species assignments done by the BLAST alignments. The most abundant taxa corresponded to the genera *Fusarium*, *Penicillium*, *Phialemoniopsis* and *Talaromyces* (Table 1, Fig. 2). Seven fungal genera, including *Cladosporium*, *Fusarium*, *Meyerozyma*, *Penicillium*, *Preussia*, *Talaromyces* and *Trichoderma* were present in both tissue types. Different endophyte taxa were found to dominate respective tissues: while the genus *Fusarium* was significantly more dominant in below-ground tissues ($F_{1,18} = 39.5$, $P < 0.001$, nested ANOVA) (Fig. 2), foliar endophytes were dominated by the *Penicillium* genus ($F_{1,18} = 5.12$, $P = 0.036$, nested ANOVA) (Fig. 2). Whereas fungal endophyte abundance was significantly higher in root than in leaf tissue ($F_{1,18} = 4.87$, $P = 0.040$, nested ANOVA) (Table 2), richness was not significantly affected by tissue type (richness: $F_{1,18} = 0.34$, $P = 0.564$, nested ANOVA) (Table 2). Neither Shannon diversity ($F_{1,18} = 2.39$, $P = 0.138$, nested ANOVA) nor Simpson

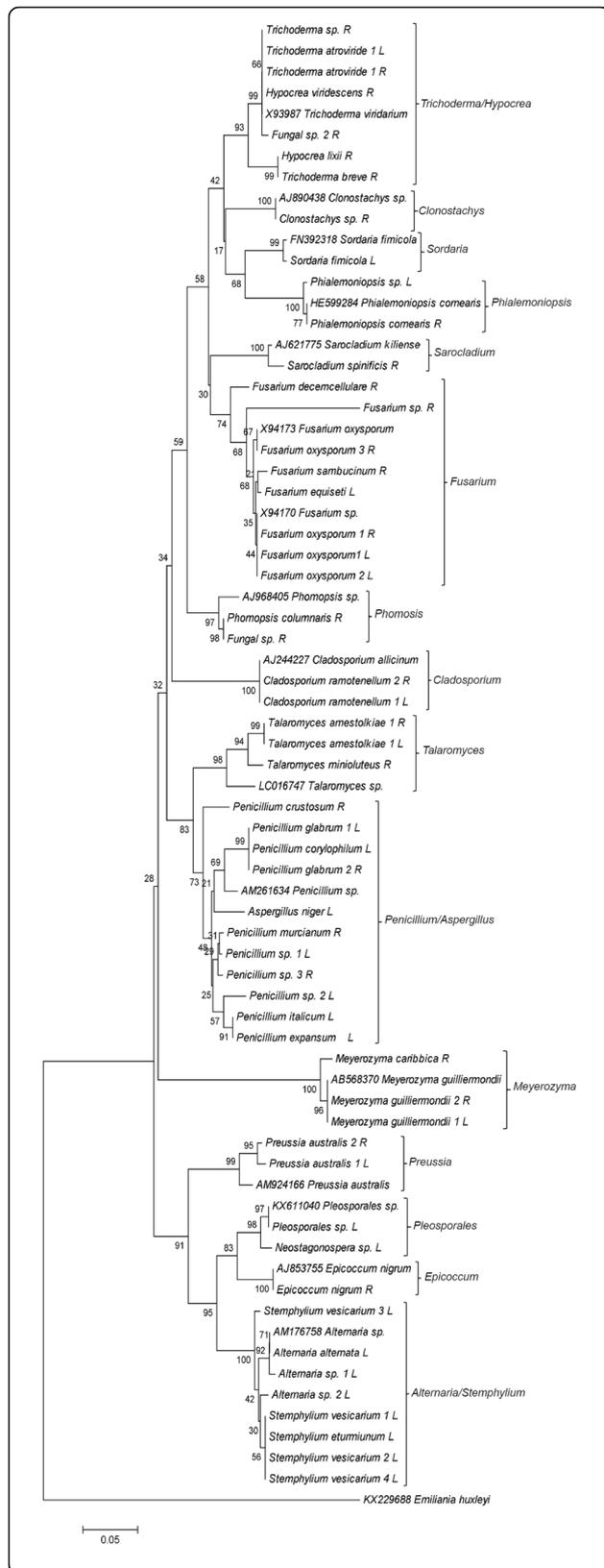


Fig. 1 Neighbor Joining (NJ) tree showed phylogenetic relationship between 64 sequences of endophytic fungi from root (R) and leaves (L), based on the ITS rDNA sequences. NCBI sequences were added for showing clades. Bootstrap 1000, values are shown at the branch nodes

diversity ($F_{1.18} = 2.01$, $P = 0.174$, nested ANOVA) were significantly different between leaf and root tissues (Table 2). The ANOSIM indicated that fungal endophyte community composition significantly differed between plant tissues ($R = 0.673$; $P = 0.001$). This was visualized with a NMDS (with Bray-Curtis distance) that showed a clear grouping in fungal endophyte communities between above- and below-ground tissues (Fig. 3). As a complementary method, β diversity analyses returned high dissimilarity values between above- and below-ground tissues (Jaccard = 0.145, Sorensen = 0.253) (with a range of 0–1, with 1 representing greatest species similarity).

Discussion

The main goal of this study was to compare diversity and community composition of fungal endophytes between above- and below-ground tissues of the arid plant *Aristolochia chilensis*. Although there were no differences in diversity between above- and below-ground tissues, we found, in agree with previous findings [13, 30, 31], that number of fungal isolates from below-ground tissues was greater than that from above-ground parts. It has been suggested that tissue longevity might be a relevant factor influencing this pattern [31]. Longer life of roots in comparison to leaves, particularly in arid environments, might explain the higher number of fungal endophytes associated to below-ground tissues. Different endophyte genera were found to dominate respective tissues; *Fusarium* was dominant in below-ground tissues, whereas *Penicillium* dominated above-ground parts. Both *Fusarium* and *Penicillium* have previously been reported as common inhabitants in leaves and roots of diverse plant species [24, 32–35] and in plants inhabiting arid environments [19, 24, 35]. The genus *Penicillium*, interestingly, has been found to be also a dominant endophyte in other plant species native of arid environments in Chile, including *Chenopodium quinoa* and *Prosopis chilensis* [24, 35]. Associations of *Penicillium* endophytes with these species was shown to help plants to respond better to drought stress and improve plant growth [35, 36]. Additionally, the genus *Fusarium* has been demonstrated to be a source of bioactive metabolites, which might assist host plants under attack by insects and/or pathogens [37]. Considering the increase evidence demonstrating that endophytic fungi enhance plant resistance to abiotic stress [36, 38, 39], association of *A. chilensis* with an array of fungal endophytes in its

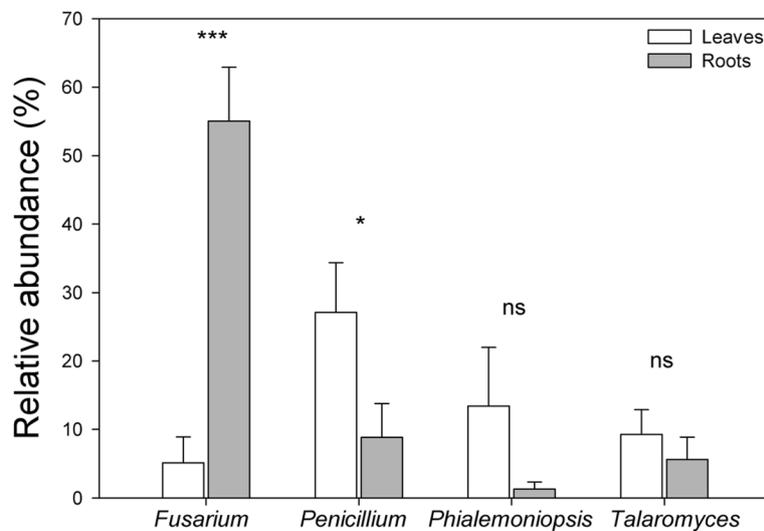


Fig. 2 Relative abundance (average + SE, $N = 10$ individuals) of the four most abundant fungal endophyte genera found in *A. chilensis* leaves (gray bars) and roots (black bars). Asterisks indicate significance level (Nested ANOVA): * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns indicates non-significant differences

tissues might be of crucial importance for its performance under arid conditions.

Community structure was found to be highly dissimilar between above- and below-ground tissues; calculation of Jaccard and Sorensen indices provided further evidence for community compositional differences between tissue types, suggesting low species turnover between above- and below-ground tissues. These results agree with previous studies that suggest that community composition is strongly determined by plant tissue type [12, 13, 40]. Taken together, endophyte colonization appears to exhibit tissue specificity, and its occurrence within the host is apparently not systemic. In *A. chilensis*, it was observed that roots and leaves shared seven fungal endophyte genera, suggesting that common taxa in both tissues may come from a similar source. Whereas previous studies have found a similar pattern as that observed here [31], other studies showed that in rare occasions a same fungal species was found in both tissues [12, 41, 42].

Table 2 Diversity indices for endophytic fungi inhabiting leaf and root tissues in *Aristolochia chilensis*

	Leaves	Roots
Abundance (*)	16.2 ± 3.9	30.8 ± 5.2
Richness (ns)	6.4 ± 0.58	5.6 ± 1.2
Shannon diversity (ns)	1.46 ± 0.11	1.11 ± 0.19
Simpson diversity (ns)	0.68 ± 0.05	0.54 ± 0.07

The average ± SE ($N = 10$ individuals) are shown. Asterisks indicate significance level: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns indicates non-significant differences

Different ecological processes might contribute to a high degree of organ specificity for fungal endophyte communities. On the one hand, an important factor is the spore source; leaves and roots may obtain fungal endophytes from different sources [43], including airborne spores for leaf endophytic fungi and inoculum present in the nearby soil for root-associated fungal endophytes. On the other hand, additional biotic and abiotic factors, including host tissue chemistry, temperature and precipitation may also be involved in shaping fungal endophyte communities [44–47]. For example, differences in host chemistry may differentially promote differences in fungal endophyte community and in dominant members of the community [44, 48]. Moreover, it was demonstrated that distinct ecological processes structure above- and below-ground endophyte communities in coastal dune ecosystems [49]. Whereas the strongest filter for leaf endophyte communities was host species, the abiotic environment primarily structured root endophyte communities [49]. Fungal endophyte communities are highly dynamic [45, 50], and processes involved in success endophyte colonization still need to be deeply elucidated.

In conclusion, based on a culture dependent approach, our study reveals that *A. chilensis* harbors a similar diversity of endophytic fungi in above- and below-ground tissues. Nevertheless, dominant endophytic fungi were found to be dependent on tissue type, which potentially resulted in marked differences in community structure between both tissues. More research is required to improve understanding of endophyte colonization dynamics in different host tissues, as well as of the consequences of these interactions for establishment and

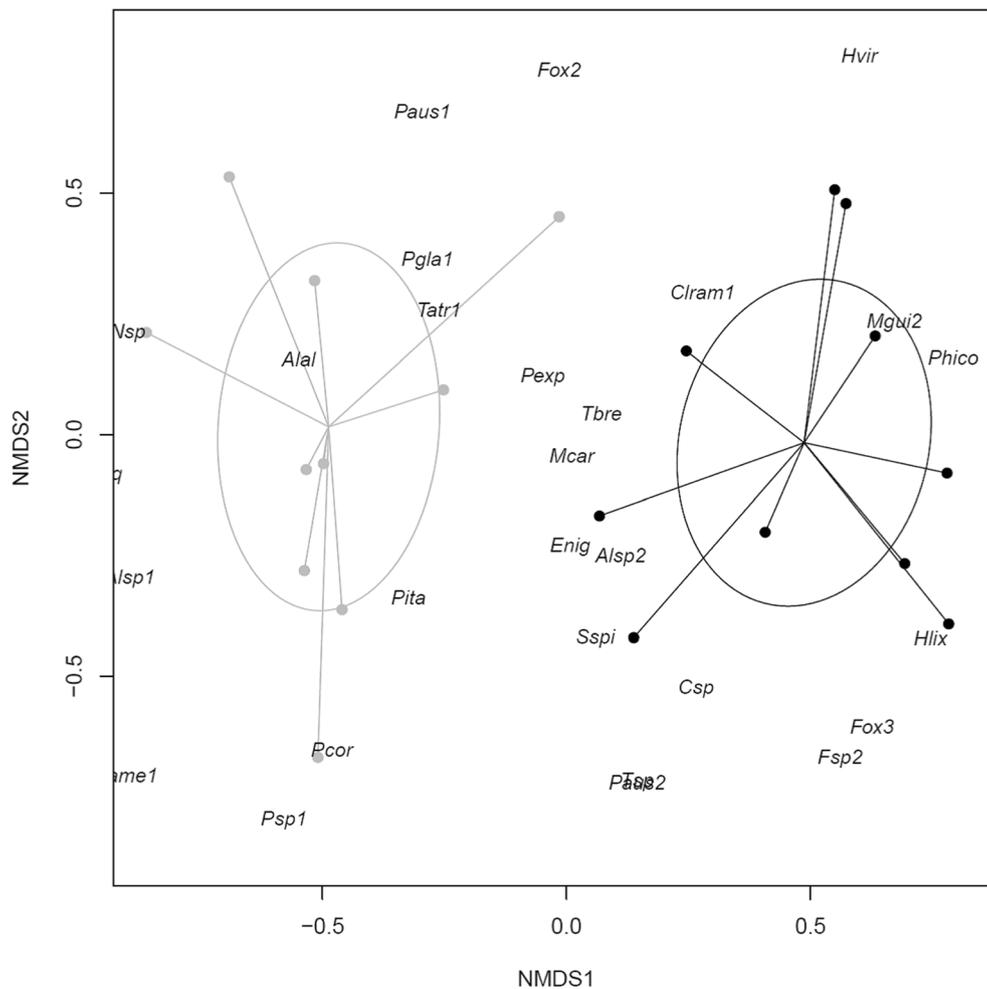


Fig. 3 Non-metric multidimensional scaling ordinations for fungal endophyte communities associated with *Aristolochia chilensis* as a function of above- (gray lines) and below ground (black lines) tissues. Arrows show significant indicator species associated with leaf and root tissues (Alal: *Alternaria alternata*; Alsp1: *Alternaria sp.1*; Alsp2: *Alternaria sp.2*; Clram1: *Cladosporium ramotenellum1*; Csp: *Clonostachys sp.*; Enig: *Epicoccum nigrum*; Fox2: *Fusarium oxysporum2*; Fox3: *Fusarium oxysporum*; Fsp2: *Fungal sp.2*; Hlix: *Hypocrea lixii*; Hvir: *Hypocrea viridiscens*; Mcar: *Meyerozyma caribbica*; Mgui2: *Meyerozyma guilliermondii2*; Nsp: *Neostagonospora sp.*; Pcor: *Penicillium corylophilum*; Pexp: *Penicillium expansum*; Pgl1: *Penicillium glabrum1*; Pita: *Penicillium italicum*; Phico: *Phialemoniopsis cornearis*; Paus1: *Preussia australis1*; Paus2: *Preussia australis2*; Psp1: *Penicillium sp.1*; Sspi: *Sarocladium spinificis*; Tatr1: *Trichoderma atroviride1*; Tbre: *Trichoderma breve*; Tsp: *Trichoderma sp.*)

performance of the host plant. Further experimental studies are required to elucidate the effects of dominant endophytic fungi on plant tolerance of *A. chilensis* to arid environmental conditions.

Conclusions

Different endophyte taxa were found to dominate respective tissues, which potentially influence differences in community structure between above- and below-ground tissues in *A. chilensis*. A full understanding of dynamics and processes involved in endophyte colonization and community composition still requires more research, and need to include the effects of environmental factors as well as of host plant traits. Simultaneous studies of above- and below- ground endophytes

seem necessary to obtain insights into the ecological significance of such communities for host performance.

Abbreviations

OTU: Operational taxonomic units; %: Percent; mg: milligrams; mM: millimolar; μ M: micromolar; μ L: microliter; min: minute; rpm: Revolutions per minute; bp: Base pair; DNA: Deoxyribonucleic acid

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Authors' contributions

Experimental design: MJG-A, MG-T. Fieldwork: MJG-A. Lab work: MJG-A and AU. Data analysis: MJG-A, CV. Manuscript preparation: MJG-A, MG-T. All authors read and approved the final version of the manuscript.

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Availability of data and materials

The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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