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ENVIRONMENTAL MICROBIOLOGY - RESEARCH PAPER

Diversity of saprotrophic filamentous fungi on *Araucaria angustifolia* (Bertol.) Kuntze (Brazilian pine)

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Abstract
The biodiversity of filamentous fungi and their ecological relationships in the context of decaying *Araucaria angustifolia* (an endangered conifer) substrates are still mostly unknown. The present study aimed to investigate the diversity of saprotrophic filamentous fungi, based on morphological identification, associated with *A. angustifolia*, in addition to assessing possible saprobic/plant affinity relationship, and verifying whether the study areas and substrates affect the composition of the mycobiota. A total of 5000 substrates (decaying needles and twigs) were collected during five expeditions (2014/2015) to two areas: São Francisco de Paula National Forest (FLONA-SFP) and São Joaquim National Park (PARNA-SJ), Brazil. A total of 135 species distributed among 85 genera, 40 families, nine classes, 24 orders, three subphyla, and two phyla were identified. One new genus and five new species that were previously described, and six rare species and five species with affinity for *A. angustifolia* were also recorded. The twigs showed a community of fungi with greater richness and dominance. Conversely, the values of abundance, Simpson's diversity index, and evenness were lower than those determined for needles. In terms of the study areas, FLONA-SFP showed higher values of richness, abundance, Simpson's diversity index, and evenness than PARNA-SJ. Principal coordinate analysis and similarity percentage analysis showed the influence of both substrate factors and areas in the composition of the fungal communities. The presence of new, rare, and affinity-related species reinforces the study of fungi in the context of the conservation of this conifer, as these species are threatened by co-extinction.

Keywords Araucaria forest · Biodiversity · Conservation · Hyphomycetes · Saprobic/plant affinity

Introduction

The decomposition of plant debris is fundamental for the maintenance of forest ecosystems. The disintegration of complex organic compounds and the reabsorption of the resultant nutrients by plant roots maintain the nutrient cycle [1–3]. This process is influenced by several factors: (i) the physical and chemical characteristics of the organic matter—levels of lignin, cellulose, phenolic compounds, and the presence or absence of allelopathic substances; (ii) environmental conditions, such as humidity, precipitation, and temperature; and (iii) the community of decomposing organisms, including microorganisms and microfauna [3–6].

Saprotrophic fungi are highlighted among the decomposing microorganisms because they have an enzymatic arsenal capable of decomposing diverse plant cell wall polymers, including those of a recalcitrant nature such as lignocellulosic matrices [7]. In fact, they play an extremely important role in ecosystems, decomposing complex plant substrates and, consequently, promoting soil fertility [3, 8]. For instance, in some forest ecosystems, such as the rainforest, the fertility of the soil is maintained by the action of microorganisms in the decomposition of litter (including many fungi), allowing the existence of great botanical diversity [9]. The diversity of fungi associated with the litter is essential for an optimal decomposition

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process; a single or a consortium of species can be characteristic and important at certain stages of decomposition [10]. In this context, the decrease in the diversity of saprotrophic fungi can directly affect the decomposition process; the reduction or extinction of functional species in the community may consequently impact the entire ecosystem [11, 12]. Of note, a low decomposition rate induces, in turn, a deficit between the amount of substrate in the litter and the mineralization of nutrients, with negative effects on plant growth, vegetation composition, and ecosystem balance [13].

Several factors can influence the diversity and composition of the saprotrophic filamentous fungi community, including the plant species composing the ecosystem and the type of substrates and their spatial and temporal heterogeneity [14–17]. Only via the investigation of mycodiversity in the context of plant species can the effect of the above factors on the distribution of fungal species be understood [15, 17, 18]. Another important point to be considered is the different levels of affinity relationships between saprotrophic fungi and plants. Over time, several terms have been proposed to characterize fungus/host associations: preference for a host [19], saprobic/plant exclusivity, host specificity, host recurrence, restricted occurrence to host [20], and host affinity [14]. The knowledge of such relationships contributes to better global estimates of fungal species biodiversity [21].

Considering the saprotrophic mycodiversity associated with large groups of phanerogamic plants, studies have revealed a high diversity of species associated with angiosperms [10, 15, 18, 22] and gymnosperms [23–28]. Among gymnosperms, *Araucaria angustifolia* (Bertol.) Kuntze, (Coniferae, Araucariaceae), also known as Brazilian pine, is considered a critically endangered botanical species, according to the International Union for Conservation of Nature [29]. It is the only species of the genus native to Brazil and is mainly distributed in the southern region and some states in the southeast region (Minas Gerais, Rio de Janeiro, and São Paulo) [30, 31]. In addition to Brazil, *A. angustifolia* is also distributed in Argentina and Paraguay [32, 33]. The community of filamentous fungi associated with decomposition in the context of *A. angustifolia* is mostly unknown, although some studies have been conducted [34–41]. Most fungal studies in *A. angustifolia* focused on phytopathogenic fungi [42–47] and mycorrhizae fungi [48–53].

Given the above, the present study aimed to investigate the diversity and distribution of the saprotrophic filamentous fungi community on decaying needles and twigs from *A. angustifolia*. We further explored the influence of study areas and substrates in the composition of these communities, as well as possible saprobic/plant ecological relationships.

Material and methods

Study areas

Two areas within the Araucaria Forest Conservation Units in Southern Brazil—the São Francisco de Paula National Forest (FLONA-SFP) (29° 23′ S and 50° 23′ W) and the São Joaquim National Park (PARNA-SJ) (28° 04′ S and 49° 39′ W)—were selected (Fig. 1). The areas have a temperate-type mesothermal climate: extremely humid, without a dry season, with well-distributed rainfall, and at least 1 month with average temperatures below 10 °C (occasional snowfall in winter common in Montanas) [54].

The FLONA-SFP, located at São Francisco de Paula Municipality, in the state of Rio Grande do Sul (RS), is a sustainable use Conservation Unit. It has an area of 1615.6 ha and altitudes that can exceed 900 masl [55]. Its vegetation cover is composed of 56% native vegetation, consisting of fragments of dense ombrophilous forest, mixed ombrophilous forest, and 39% of *A. angustifolia*, *Pinus*

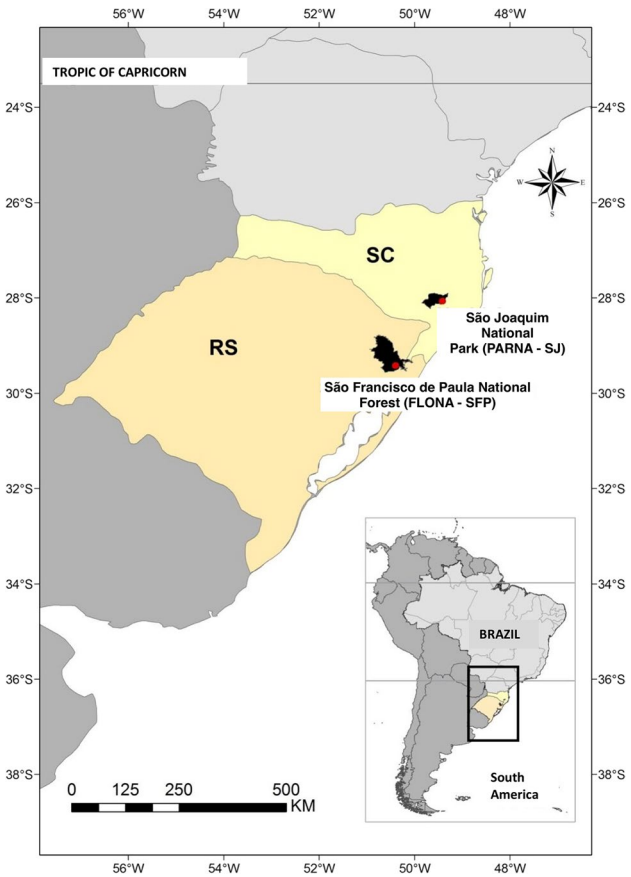

Fig. 1 Study areas. South America, Brazil, State of Santa Catarina (SC) and Rio Grande do Sul (RS) in South region of Brazil and the two areas São Francisco de Paula National Forest (FLONA -SFP) and São Joaquim National Park (PARNA -SJ)

elliottii Engelm, *P. taeda* Blanco, and *Eucalyptus* spp. [56]. The altitudes recorded at the collection points were 838, 840, and 883 masl.

The PARNA-SJ, covering the municipalities of Urubici, Grão Pará, Bom Jardim da Serra, and Orleans in the state of Santa Catarina (SC), is an Integral Protection Conservation Unit. It has an area of 49,300 ha and 350–1800 masl, with the presence of four vegetation formations: dense ombrophilous forest, mixed ombrophilous forest, altitude fields, and nebular woods [57, 58]. The altitudes recorded at the collection points were 990 and 1031 masl.

Sampling, processing, and fungal identification

Five collection expeditions were carried out in each study area (Feb, May, Aug, and Nov 2014 and Feb 2015). In each area, 10 equidistant points approximately 200 m apart were selected. At each point, 25 decaying needles (3–7 cm long) and 25 decaying twigs (5 cm long) of *A. angustifoli*a were collected and placed into properly identified paper bags. A total of 5000 samples were analyzed (1250 needles and 1250 twigs per study area). The paper bags were placed in a cardboard box and transported to the Laboratory of Mycology (LAMIC) at the Universidade Estadual de Feira de Santana. The samples were processed up to 5 days after collection as per the washing technique [59] and stored in moist chambers at room temperature (+/−25 °C). The substrates were observed daily from the second day of incubation for a period of 60 days [59]. Once reproductive structures of fungi were detected, they were transferred onto slides containing lactic acid and/or PVL resin (polyvinyl alcohol + lactophenol) [60] to make semi-permanent and permanent preparations, respectively. Identification of fungi was based on morphological characteristics of the reproductive structures, which were compared with those described in the specific literature [61]. After morphological identification, the slides were deposited at the Herbarium of Universidade Estadual de Feira de Santana (HUEFS). The species were grouped in higher ranks, such as phylum, class, order, and family, for a broader view of the fungi community present in *A. angustifolia*.

Ecological analysis

Fungi present in the communities associated with the substrates (needles and twigs) and study areas (FLONA-SFP and PARNA-SJ) were identified. Species abundance was evaluated by counting the number of individuals of each species per substrate [62]. To calculate the expected number of taxa in the communities, the Chao1 richness estimator was used [63]. The diversity between the two substrates and areas studied was compared using the Simpson's diversity index (1-D), where D means the dominance of taxa that reaches values from 0 (all taxa are equally present) to 1 (one taxon dominates the community completely) and was determined as per the formula:

$$D = \sum_{i} \left(\frac{ni}{n}\right)^2$$

where ni = number of individuals of taxon i and n = total number of individuals [64].

The species distribution was assessed using the Pielou equitability index [65]. A comparison of the calculated indices between the different substrates and areas was performed with a 95% confidence interval via the bootstrap method [66]. To determine whether the communities were made up of abundant or rare species, a dominance–diversity curve was plotted based on the relative abundance of species in each substrate [67].

The constancy of the species in the different substrates was determined as per the formula:

$$C = \frac{P \times 100}{N},$$

where P = number of collections containing the species and N = total number of collections.

The species were grouped into the following constancy categories: constant, present in 50% or more collections; accessory, observed in >25% and <50% of the collections; and accidental, detected in <25% of the collections [68].

Dissimilarity in the species composition between communities was compared via the multivariate statistical method principal coordinate analysis (PCoA) [69], based on the Bray–Curtis dissimilarity matrix [70]. The one-way permutational multivariate analysis of variance (PERMANOVA) was used to assess whether the difference/dissimilarity between communities was significant [71]. The similarity percentage analysis (SIMPER) was used to determine the individual contribution of each species to the dissimilarities found between communities [72].

Analyses were performed using the PAST (version 4.03) [73] and Biodiversity Pro 2 [74] software.

Results

A total of 135 species of saprotrophic filamentous fungi distributed in 85 genera were identified in decaying needles and twigs of *A. angustifolia* in the two areas investigated (Table 1). Among the collected fungi, only two species (1.5%) belonged to the phylum Basidiomycota, *Jaculispora submersa* and *Peyronelina glomerulata*, and were classified into distinct families, orders, classes, and subphyla. The other 133 species (98.5%) belonged to the phylum Ascomycota; they were classified into 83 genera (97.6%) distributed

Table 1 Dominance values, Simpson diversity, Pielou equitability, and Chao1 richness estimator for filamentous fungi communities isolated from needles and twigs of *A. angustifolia* and the areas FLONA-SFP and PARNA-SJ

Substrate/areas	Richness (S)	Abundance (N)	Dominance (D)*	Simpson's diversity (C)*	Equitability (J)*	Chao 1*
Needles	92	1980	0.04465 (0.0417–0.0472)	0.9553 (0.9528–0.9583)	0.787 (0.7787–0.7999)	99 (93.89–117.3)
Twigs	104	1635	0.06671 (0.0606–0.07113)	0.9333 (0.9289–0.9393)	0.7225 (0.7143–0.7416)	162.5 (110.8–145.5)
FLONA-SFP	113	1885	0.04261 (0.0395–0.0451)	0.9574 (0.9548–0.9604)	0.7706 (0.7645–0.7858)	140.6 (120.3–153.1)
PARNA-SJ	78	1730	0.06541 (0.0598–0.0697)	0.9346 (0.9302–0.9402)	0.748 (0.739–0.7644)	93.3 (80.57–105.1)

*Numbers in parentheses refer to the confidence interval 95% confidence obtained by the bootstrap method

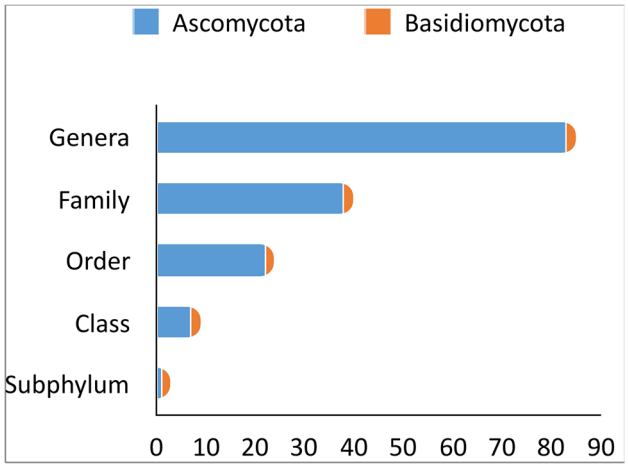

Fig. 2 Number of taxonomic categories per phylum of filamentous fungi isolated from *A. angustifolia*

in 38 families, 22 orders, seven classes, and one subphylum (Fig. 2). Among these, 22 genera (25.8%) and 38 species (28.1%) were classified as *incertae sedis* since they do not have a higher classification (Table S2).

The order with the largest number of families was Pleosporales (10), followed by Helotiales (3) and Hypocreales (3) (Fig. 3). Among families, Chaetosphaeriaceae showed the greatest richness (10), followed by Dictyosporiaceae (6) (Table S1). The genera with the largest number of species isolated were *Chalara* (7), *Dactylaria* (5), and *Helicosporium* (5) (Table S2).

Considering the investigated substrates, the twigs showed the highest species richness (S = 104) and the lowest abundance (N = 1635); conversely, the needles showed the lowest richness (S = 92) and the highest abundance (N = 1980). The FLONA-SFP study area presented higher species richness (S = 116) and abundance (N = 1885) than PARNA-SJ (S = 78; N = 1730). Furthermore, the following results were observed with respect to the richness estimator Chao1: needles (99), twigs (162.5), FLONA-SFP, (140.6), and PARNA-SJ (93.3).

The fungi community associated with needles showed a lower species dominance (D = 0.04), greater evenness (J = 0.78), and, consequently, a higher Simpson diversity index value (C = 0.95) than that associated with twigs (D = 0.06; J = 0.72; C = 0.93). Moreover, FLONA-SFP contained lower species dominance (D = 0.04) and higher values of evenness (J = 0.77) and diversity index (C = 0.95), while PARNA-SJ showed higher dominance (D = 0.06) and lower evenness (J = 0.74) and diversity index (C = 0.93). These differences found in the values of the different indices calculated between the substrates and areas were significant based on the 95% confidence interval (Table 1).

The distribution of species per constancy category revealed the predominance of accidental species, followed by accessory and constant species for the needles and twigs (Fig. 4). *Parasympodiella laxa* and *Helicosporium ramosum* were the most constant species from needles and twigs, respectively, with both occurring in 100% of the collections. The dominance–diversity curve further supported these findings (Fig. 5). The fungal communities from both substrates presented few species with high abundance (dominant) and a predominance of species with one or two occurrences (rare) (Fig. 5). The most abundant species on needles were *Anungitea fragilis* (152), *Chalara microspora* (112), *Helicosporium ramosum* (118), *Parasympodiella laxa* (210), and *Zygosporium gibbum* (145). The most abundant species on twigs were *Clonostachys rosea* (130), *Helicosporium guianense* (266), *H. ramosum* (143), and *P. laxa* (194) (Table S1). Interestingly, 31 (22.9%) and 43 species (31.8%) were detected exclusively on needles and twigs, respectively.

Sixty-one species were shared between the two substrates, resulting in an overlap of 45.2%. Among species shared by needles and twigs, *A. fragilis* (192), *Ch. cylindrosperma* (142), *Ch. microspora* (175), *Cl. rosea* (228), *Dactylellina*

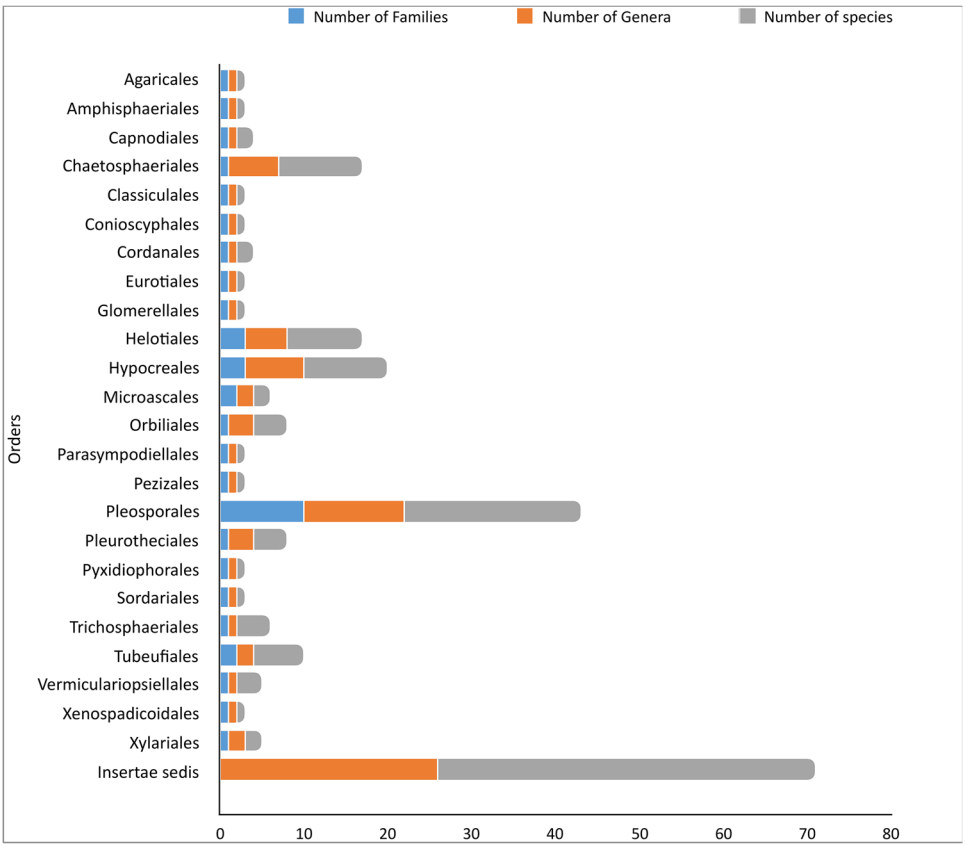

Fig. 3 Numbers of families (blue), genera (orange), and species (gray) classified by order of filamentous fungi associated with *A. angustifolia*

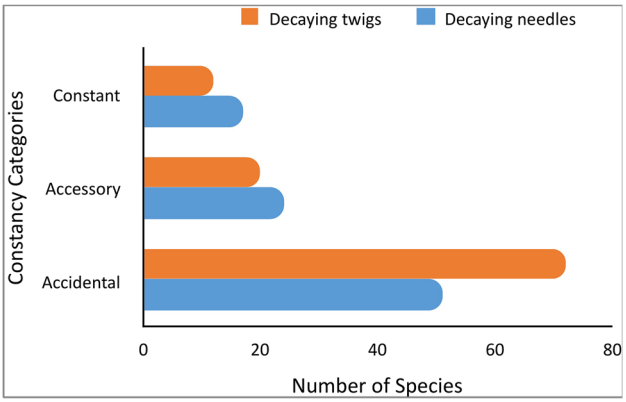

Fig. 4 Number of species isolated from needles (blue) and twigs (orange), considering the constancy categories of fungi isolated from *A. angustifolia*

lysipaga (119), *H. guianense* (285), *H. ramosum* (261), *P. laxa* (404), *Polyscytalum gracilisporum* (127), *Veronaea botryosa* (102), and *Z. gibbum* (171) were the most frequent in this study. Conversely, among the rare species, 18 (13.3%) and 16 (11.8%) were detected only once and twice, respectively, on needles. On twigs, 35 (25.9%) and 10 species (7.4%) were detected only once and twice, respectively. In the study areas, 19 species (14.0%) were detected exclusively in PARNA-SJ and 57 species (42.2%) exclusively in FLONA-SFP, and 59 species (43.7%) were shared between the two study areas (Table S1).

On the biodiversity of filamentous fungi associated with *A. angustifolia*, a new genus *Arthromoniliphora araucariae* [40] and five new species, *Chaetochalara mutabilis* [36], *Cryptocoryneum parvulum* [37], *Dictyosporium araucariae* [39], and *Trichoconis foliicola* [38], were previously published; additionally, another new species of *Endophragmiella* was discovered (unpublished data) (Table 1). Among these new taxa, three occurred only on needles: *C. parvulum* was registered on 15 needles and present in 80% of collections; *D. araucariae* was found on 30 needles and present in 40% of collections; and *T. foliicola* was observed on 52 needles and present in 50% of collections.

Interestingly, PCoA revealed a tendency of separation of filamentous fungal communities from the two substrates and from the two areas studied (Fig. 6). The first principal coordinate represents the variability of filamentous fungi communities from needles and twigs (21.27%). while the second principal coordinate represents the variability of filamentous fungi communities detected in the different study areas (FLONA-SFP and PARNA-SJ; 18.43%). This ordering obtained by PCoA was confirmed by PERMANOVA, which revealed the differences in the fungi communities between the substrates and areas studied were statistically significant ($F = 2.885$; $p = 0.0001$). Moreover, the SIMPER analysis

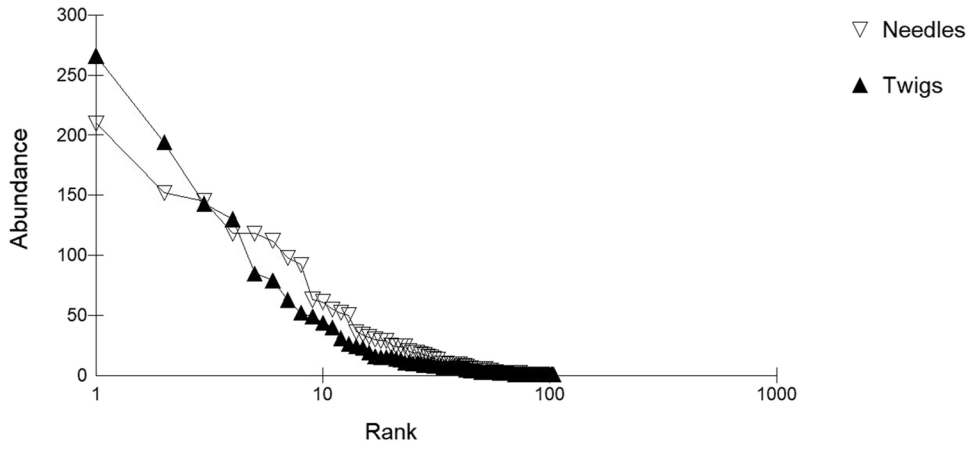

Fig. 5 Dominance–diversity curve of filamentous fungi isolated from needles and twigs of *A. angustifolia*

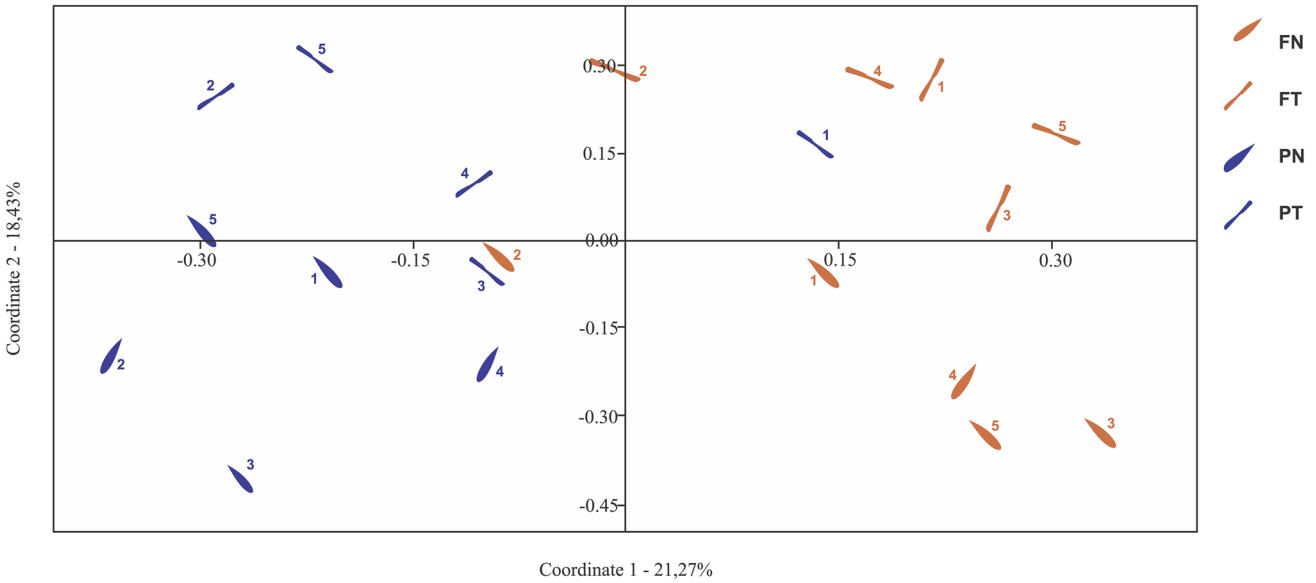

Fig. 6 Ordering in two dimensions using PCoA for communities of filamentous fungi isolated from needles (N) and twigs (T) of *A. angustifolia*, in PARNA-SJ (P) (blue) and FLONA-SFP (F) (orange). Collection expeditions were identified with numbers 1 to 5, next to the samples

indicated a considerable dissimilarity between the fungal communities from the two areas (FLONA-SFP and PARNA-SJ), with an overall average of 54.52%. Three species, *P. laxa*, *Z. gibbum*, and *A. fragilis*, were the major contributors to this result (Table 2). With respect to the substrates, the SIMPER analysis revealed an average of 49.32% dissimilarity, with the species *H. guianense*, *Z. gibbum*, and *A. fragilis* contributing the most to this result (Table 2).

Discussion

Species composition

In this study, the decaying needles and twigs of *A. angustifolia* showed a wide variety of saprotrophic filamentous fungi. All of them represent fungi asexual forms, which is not unexpected since asexual reproduction is more common than sexual reproduction in the natural environment [75]. Of note, for most asexual fungi, no sexual counterparts were identified. Previously, the connection between sexual and asexual reproduction forms was only possible via the study of fungi developed as pure cultures under aseptic conditions in the laboratory. Only in the last decade has the connection between sexual and asexual reproduction been widely observed, following the popularization of complex molecular techniques. Using these new techniques combined with phylogenetic studies, a more accurate classification was possible, allowing the inclusion of asexual species (with unknown sexual morphological characteristics) in some of the higher hierarchical categories such as classes, orders, and families [75]. However, even considering these indisputable

Table 2 Analysis of similarity percentage (SIMPER) for filamentous fungi communities isolated from needles and twigs of *A. angustifolia* and the areas FLONA-SFP and PARNA-SJ

Samples	Average dissimilarity (SIMPER in %)	Promoting species dissimilarity	Contribution (%)
FLONA-SFP x PARNA-SJ	54.52%	*Parasympodiella laxa*	9
		Zygosporium gibbum	8.4
		Anungitea fragilis	8.3
		Dactylellina lysipaga	5.4
		Chalara cylindrosperma	4.3
Needles x twigs	49.32%	*Helicosporium guianense*	13.9
		Zygosporium gibbum	6.7
		Anungitea fragilis	6.3
		Polyscytalum gracilisporum	6.1
		Veronaea botryosa	4.6

advances, hundreds to thousands of species have still not been subjected to molecular studies and, consequently, are not associated with any class, order, or family. These species are included in *incertae sedis*, representing a position not yet known within the formal higher classification.

The fungal community associated with *A. angustifolia* was mainly represented by the phylum Ascomycota (133 species), followed by Basidiomycota (two species). The low number of asexual Basidiomycota was expected, as there are fewer asexual fungi known within this phylum than those within Ascomycota [61, 76]. Among the 83 ascomycetes genera isolated in this study, 22 genera (26.5%) were considered *incertae sedis*, indicating that more effort is needed to better elucidate the higher classification of the group. The other 61 genera (73.4%) were classified into higher taxonomic categories and all belonged to the subphylum Pezizomycotina, the largest subphylum of Ascomycota [77].

Sordariomycetes and Dothideomycetes are the largest classes within the phylum Ascomycota. Because of their ability to degrade the lignocellulosic matrix of plant substrates, fungi from these classes are abundant in litter [78]. Not unexpectedly, our study, as well as other studies on saprobic microfungi [79–81], highlighted these classes as the most representative among wood, twigs, leaves, herbaceous plants, and soil decomposers.

In this study, the most representative order was Pleosporales, the largest within the Dothideomycetes class, and its representatives are found in the most diverse substrates and environments. The number of asexual fungi within this order is quite broad [82], which contributes to its large occurrence in this work. The next relevant order was Helotiales (Leotiomycetes class). Helotiales include many well-described species of readily cultured saprotrophic soil fungi, with many important species interacting with humans, animals such as bats (*Geomyces* ssp.) [83], and plants (*Sclerotium* ssp.) [84]. The Hypocreales order, also relevant within the fungi isolated here, belongs to Sordariomycetes class. This order is composed of ecologically diverse saprobic and pathogenic species found in a wide variety of substrates [85, 86].

The most representative families within Sordariales were Chaetosphaeriaceae and Dictyosporiaceae. Members of these families are found widely on decaying wood and plant debris and are important lignocellulose degraders [61, 87, 88]. Importantly, these families also stood out considering the number of saprobic asexual fungi species associated with palm trees in the Brazilian Amazon Forest [81]. The genera *Chalara*, *Dactylaria*, and *Helicosporium*, also quite relevant in our study (as the number of species identified), have a worldwide distribution [61] and are commonly found in other species of gymnosperms [27, 89, 90].

Diversity of species by substrate

The studied *A. angustifolia* substrates have a saprotrophic filamentous fungal community with a high species richness and diversity, as observed for other gymnosperms [24–27]. The presence of a few dominant species and a high proportion of rare species, as per the dominance–diversity curve (Fig. 5), is an expected pattern as shown by various ecological studies on diverse organism communities [91, 92], including microfungi [79, 93–97]. Among the fungi species, the following were the most abundant: *A. fragilis* (occurring in 233 needles and 41 twigs), *Ch. microspora* (147 needles and 63 twigs), *Cl. Rosea* (104 needles and 119 twigs), *H. guianense* (19 needles and 258 twigs), *H. ramosum* (144 needles and 126 twigs), and *P. laxa* (221 needles and 194 twigs); and they colonized up to 70% of the needles' and twigs' surface area. This observation suggests a fundamental role of these species in the decomposition of the substrates studied [79] and possibly a strategy of differentiated growing in relation to other species, especially those that develop more slowly. It is important to note, however, that rare species also play important ecological roles, as the

decomposition process is carried out by several species, each probably having a specific role [12, 98].

Are substrates a determining factor of the composition and diversity of filamentous fungal communities?

In the present study, a significant difference was found between filamentous fungal communities isolated from the different substrates analyzed (Table 2). These differences may be associated with substrate species specificity [5, 12]. In fact, other studies reported this as an important factor affecting the constitution of fungal communities [5, 79, 81, 99]. Overall, the different tissues that make up plant parts (leaves, petioles, trunks, barks, roots, twigs, and branches) contribute to the recurrence of certain species of fungi and the consequent formation of different communities. In other words, different substrates support different fungal communities [99–101].

Saprobic/plant affinity ratio

Most species isolated in the present study have been associated with other plants, within both gymnosperms (46 species) [27, 46, 47] and angiosperms (118 species) [10, 46, 102, 103]. For instance, Cai et al. investigated bamboo-associated fungi and observed that most isolated species had already been reported in other plants, suggesting a low specificity [79]. This may be owing to the high ability of fungi to colonize different plants [104].

On the contrary, of the six new species found in *A. angustifolia*, only *Chaetochalara mutabilis* was registered in another plant species (*Calophyllum brasiliense* Cambess) [36]. The other five new species may represent a new saprobic/plant affinity relationship, as Paulus et al. suggested [14]. However, one cannot rule out the possibility that these species may be found in other plants or unexplored niches in the future.

Interestingly, among these new species, *C. parvulum*, *D. araucariae*, and *T. foliicola* occurred abundantly and recurrently only on needles. These data allow us to infer that these species have an affinity relationship with this part of the plant (needles), which may be related to its chemical composition and plant tissue. Another substrate specificity observed was the exclusive occurrence of *C. parvulum* on the stomata, suggesting the affinity of this fungal species to this group of leaf epidermis cells. Many phytopathogenic fungi use this characteristic route of infection (via the stomata) [105]. However, there is no evidence of this type of interaction for *C. parvulum* because living leaves were not analyzed.

Pseudaegerita conifera is another example of a fungal species with affinity to needles. It was previously recorded only on *Pinus halepensis* Mill needles [106], and now on *A. angustifolia* needles. This species was originally identified to be associated with submerged needles [106]. *Pseudaegerita* is characterized as aero-aquatic because of the presence of clathrate conidia [107]. All species of this genus are commonly found in aquatic environments or near riverbanks and forest streams [106]. However, in the present study, *Ps. conifera* was isolated from a terrestrial environment. This may be related to the possible proximity of the collection sites with streams or with the high humidity of the studied areas during the collection expeditions.

The affinity relationship between saprotrophic fungi and specific parts of plants may be associated with the nutritional conditions provided. With respect to needles, they have xeromorphic characteristics, with lignified hypodermis, stomata containing guard cells with extremely lignified periclinal walls, pectin secretion in the spongy parenchyma, and secretory channels of phenolic compounds between vascular bundles [108]. An important factor essential for the establishment of such relationships is the presence of an enzymatic framework in fungal species capable of decomposing such tissue and leaf structures [8].

Among the species associated with *A. angustifolia* twigs, the fungus *Sterigmatobotrys macrocarpus* stood out in the present study. In the literature, this species has always been associated with coniferous wood (*Abies* Mill., *Agathis* Salisb., *Dacrydium* Torell, *Picea* A. Dietr., *Podocarpus* Pers., and *Taxus* L.) both in terrestrial and aquatic environments [46, 109] and can, thus, be considered a fungus with an affinity for coniferous wood. This is probably owing to the common characteristics of coniferous wood (which differs from that of angiosperms): presence of long fibers, predominance of a single cell type—longitudinal tracheids [110], higher concentration of lignin [111], and structurally different lignin [112].

Chalara stipitata has previously been recorded on the leaves of *Agathis australis* (D. Don) Loudon and *Podocarpus hallii* Kirk [113, 114]. In the present work, *Ch. stipitata* was registered on nine needles and eight twigs of *A. angustifolia*, developing well in both substrates. With this similar abundance in needles and twigs, we cannot infer that there is an affinity for a specific gymnosperm part, even if we consider the studies reporting the presence of this fungal species only in leaves of this group of vascular plants. However, we cannot exclude an affinity for gymnosperms, since, almost half a century after the discovery of this saprobic fungus, no reports in the context of angiosperms are available. This affinity may be related to the nutritional characteristics of particular plant structures already mentioned. This said, further taxonomic/ecological investigations on the mycobiota associated with different parts of gymnosperms must be carried out to better understand these complex relationships.

Diversity and composition of filamentous fungi species in the study areas

The analysis of the composition of filamentous fungi species comparing the two studied areas showed that the "area factor" is also important for the determining of fungal communities. A high dissimilarity between the areas was demonstrated via SIMPER analysis.

Although the Araucaria forest areas studied have the same climate and similar altitudes, they also present important environmental differences: FLONA-SFP is an area that is composed mostly of dense vegetation of native Araucaria forest, while PARNA-SJ is composed of Araucaria forests discontinued by grass fields. This environmental heterogeneity can influence the composition of the fungal communities [115] and contribute to the differences in diversity and composition of microfungi observed in this study.

The PCoA analysis corroborated the abovementioned results. Remarkably, this observation was also reported in the context of composition studies of palm-associated fungal communities. Distinct collection sites significantly interfered with the fungal occurrence, with more similar compositions reported in palm trees from the same *versus* distinct sites [116, 117]. Additionally, differences in fungal communities in bamboos from two different sites were also observed [118]. Considering endophytic fungi and their characteristic fungus/plant interactions, site-specific/environmental factors were also shown to exert a great influence on the fungal communities. In a study on fungi associated with *Pinus radiata* D. Don, the fungi communities varied from one site to another [119].

Conclusions

The study of the mycobiota associated with *A. angustifolia* decomposing needles and twigs revealed that this plant species is a reservoir of great filamentous fungi biodiversity, with different communities associated with its different substrates. A high species richness was observed, including rare and new species. Saprobic/plant affinity ecological relationships were also noted. These factors should be considered for the conservation of this conifer and the consequent conservation of its mycobiota, which plays a fundamental role in the process of decomposition and the consequent maintenance of ecosystems.

The fungi associated with this critically endangered conifer are also at risk of co-extinction in future. Understanding whether the fungi considered closely associated with *A. angustifolia* can colonize other conifers (or any other plant) is, therefore, extremely important. Further studies are required to ensure the preservation of these fungal species in nature. In contrast, the axenic culture of these fungi is a real possibility, although the genetic variability of the population in this context will probably be reduced.

Our data showed that both substrates and study areas are determining factors for the composition of fungal communities. Thus, future research in other niches of this plant, such as reproductive structures and bark, as well as other areas of occurrence of *A. angustifolia*, could enrich the knowledge on the associated mycobiota. Such studies may even allow the identification of new fungal species.

There is still an absence of multidisciplinary studies, in particular ecological ones, on critically endangered plants (including *Araucaria angustifolia*). Our data clearly shows that these plants can contribute to the generation of new and extremely valuable data. However, numerous sites, substrates, and niches are still untapped and these should be considered in the context of global fungal biodiversity estimates.

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Declarations

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