

## OCCURRENCE AND PROPERTIES OF ENDOPHYTIC FUNGI OF THYME (*Thymus* spp.)

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### ABSTRACT

Endophytic fungi constitute an important yet still poorly explored component of the microbiome of thyme (*Thymus* spp.). This review summarizes the current knowledge on their diversity, ecological functions, and biotechnological potential based on literature published up to April 2026. Reported endophytes represent a diverse taxonomic community, comprising 49 genera and 53 species most of which belong to common ascomycete genera, such as *Alternaria*, *Fusarium*, *Colletotrichum*, *Aspergillus*, *Penicillium*, *Phoma*, and *Trichoderma*. Current evidence from experiments carried out *in planta* indicates that these microorganisms may contribute to plant growth promotion, enhanced tolerance to abiotic stress, modulation of essential oil production, and protection against plant pathogens through the synthesis of bioactive metabolites and volatile organic compounds. Moreover, in *in vitro* assays several isolates have demonstrated antimicrobial, antioxidant, cytotoxic, and enzyme-producing activities, highlighting their promising applications in sustainable agriculture and biotechnology. Although significant progress has been achieved, many aspects of the ecology, host specificity, and functional interactions of thyme-associated fungal endophytes remain insufficiently understood.

**Keywords:** thyme, Lamiaceae, endophytes, essential oils, defensive mutualism, growth promotion

### INTRODUCTION

Endophytic fungi are polyphyletic microorganisms that inhabit plants without inducing overt negative effects on their health, eventually establishing mutualistic relationships with the host. For a long time, the widespread assumption that pathogens basically were the only microorganisms capable of colonizing living plant tissues has delayed recognition that endophytic fungi are constantly associated with plants and can significantly influence their ecological fitness. Currently, they are regarded as a reservoir of unexplored biodiversity, awaiting to be exploited as plant protection agents or growth promoters, as well as for a variety of biotechnological applications [Nicoletti and Fiorentino 2015, Yadav et al. 2022]. Indeed, many studies have shown that these microbial associates may improve plant fitness through various interactions with agents of biotic adversities, such as antibiosis, parasitism, competition for space and nutrients, and the promotion of tolerance and resistance mechanisms [Rabiey et al. 2019, Morelli et al. 2020]. Moreover, their recognized role in growth promotion supports their consideration as genuine and effective plant probiotics [Pandey et al. 2022]. Beyond the intrinsic effects/properties of single strains or species, a more comprehensive ecological approach should consider that endophytes may perform these functions in the form of interacting consortia with other components of the plant microbiome [Adeleke et al. 2022].

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As with other medicinal plants, the cultivation of thyme (*Thymus vulgaris* and other *Thymus* spp.) has recently expanded, owing to its increasing use in gastronomy and the cosmetic industry [Nieto 2020, Halat et al. 2022, Waheed et al. 2024]. This ongoing boost especially concerns the organic farms, where adherence to the principles of integrated pest management is particularly important. Thus, insights into the organization of the plant associated microbes are crucial to improve our understanding of their ecological role, as well as to promote practical applications. Unlike endophytic bacteria, whose interactions with thyme have recently been the subject of several studies [Checcucci et al. 2017, Mohamad et al. 2020, 2022, Musa et al. 2020, Abdel-Hamid et al. 2021, Delbari et al. 2023, Zhao et al. 2023], the impact of endophytic fungi is less studied and recognized. In addition to endophytism in the strict sense, some fungal species have been reported to participate in a tritrophic association including gall midges of the genus *Asphondylia* (Diptera, Cecidomyidae) [Malagaris 2011, Zimowska et al. 2017, 2020, 2021]. This paper provides an overview of the occurrence and properties of the endophytic symbionts associated with thyme, based on the examination of the literature published until April 2026. To this end, we searched the Google Scholar and PubMed databases using the terms ‘thyme endophytic fungi’ and ‘*Thymus* endophytic fungi’, without any time restriction and excluding only unpublished dissertations and degree theses.

### Botanical notes on *Thymus* L.

The genus *Thymus* L. is one of the most diverse and taxonomically challenging groups within the family Lamiaceae. Belonging to the tribe Mentheae and subtribe Menthinae, the genus comprises approximately 220–250 species of perennial aromatic herbs and dwarf shrubs distributed primarily throughout the Mediterranean basin and adjacent regions of Europe, North Africa, Macaronesia, and temperate Asia extending eastwards to the Himalayas [Morales 2002, Drew and Sytsma 2012]. The Mediterranean basin represents the principal center of diversification of *Thymus*, where repeated geological, climatic, and ecological processes have promoted extensive speciation and local endemism. Major diversity hotspots occur in the Iberian peninsula, southern France, Italy, the Balkan peninsula, Greece, Anatolia, and the Caucasus, while secondary centers of diversification extend into the Irano-Turanian region and western Asia [Morales 2002, Celep and Dirmenci 2017, Bartolucci and Nachychko 2025, Bahadori et al. 2026].

Modern molecular studies generally support the monophyly of *Thymus*, although relationships among infrageneric groups remain incompletely resolved and continue to be refined through phylogenomic analyses [Soorni et al. 2019, Nieto-Lugilde et al. 2026].

The complexity of *Thymus* taxonomy arises from a combination of extensive morphological variability, ecological specialization, local endemism, hybridization, polyploidization, and the proliferation of names introduced during the eighteenth and nineteenth centuries. As botanical exploration intensified across Europe and the Mediterranean region, numerous taxa were described based on subtle differences in vegetative or floral morphology, generating extensive synonymy and uncertain species circumscriptions. Consequently, modern taxonomic studies have focused on stabilizing nomenclature through typification and critical revision of historical names. Important advances in this regard were achieved by Bartolucci et al. [2013], who clarified the application of several names through lectotypification and taxonomic annotations, and by Bartolucci and Nachychko [2025], whose comprehensive revision for the Euro+Med Plant-Base provided updated nomenclature, typifications, synonymies, and distributional data for the genus.

Morphological plasticity is particularly pronounced and frequently obscures taxonomic boundaries. Plant size, growth form, leaf morphology, pubescence, and inflorescence architecture may vary substantially in response to environmental conditions including altitude, substrate, grazing pressure, drought intensity, and exposure. Consequently, populations belonging to a single species may exhibit remarkable phenotypic divergence across ecological gradients, whereas unrelated taxa occupying similar habitats may converge morphologically [Morales 2002, Federici et al. 2013].

Hybridization represents another major source of taxonomic complexity. Natural hybrids have been documented throughout the genus, particularly in regions where closely related species occur sympatrically. Hybrid populations often display intermediate morphological characteristics and mixed phytochemical profiles, complicating species identification and obscuring evolutionary relationships. Furthermore, several species complexes exhibit extensive polyploid variation, including diploid, tetraploid, and higher polyploid cytotypes. Polyploidization has long been recognized as an important evolutionary mechanism

within *Thymus*, but recent genomic investigations have demonstrated that interploidy gene flow may be far more widespread than previously assumed

The advent of molecular systematics has greatly improved understanding of evolutionary relationships within the genus, revealing the limitations of the traditional morphology-based classifications. Federici et al. [2013], using DNA barcoding approaches, demonstrated that standard plant barcode markers often fail to discriminate closely related species of *Thymus*, reflecting recent evolutionary divergence, incomplete lineage sorting, and shared ancestral polymorphism. Their results emphasized the need for integrative approaches combining molecular and morphological evidence. More recently, advances in phylogenomics have provided unprecedented insights into species relationships and diversification processes. A comprehensive genomic study of *Thymus* sect. *Mastichina* demonstrated that patterns of morphological variation, ecological niche differentiation, and genomic structure do not always coincide, revealing extensive historical introgression and complex evolutionary histories among the currently recognized taxa [Nieto-Lugilde et al. 2026]. These findings suggest that species boundaries within some groups of *Thymus* are considerably more dynamic and permeable than previously assumed.

The genus is also renowned for its extraordinary chemical diversity. *Thymus* species produce a wide range of essential oils (EOs), including thymol, carvacrol, linalool, geraniol, borneol,  $\gamma$ -terpinene, and *p*-cymene. These compounds play important ecological roles in defense against herbivores and pathogens and determine the economic significance of thyme species in medicine, food preservation, cosmetics, and perfumery [Etri and Pluhár 2024]. Chemotaxonomic studies have traditionally been used to support species delimitation; however, growing evidence indicates that phytochemical variation does not necessarily correspond to taxonomic boundaries. Najar et al. [2021] demonstrated the persistence of distinct thymol and linalool chemotypes within cultivated populations of *T. vulgaris* in central Italy, while Del Valle et al. [2026] showed that EO composition is shaped by a complex interaction between genetic background and environmental conditions. Consequently, although phytochemical profiles remain valuable taxonomic characters, they should not be used independently for species recognition.

### Occurrence of endophytic fungi in *Thymus* spp.

A list of the fungal species so far identified as endophytic associates of *Thymus* spp. is provided in Table 1, along with details on the geographical locations and the part of the plant from which isolations were carried out. Most of the findings refer to direct isolation in axenic cultures, after external sterilization of the tissues excised from the plants. However, in one case the report was based on direct microscopic observation; particularly, the arbuscular mycorrhizal fungi *Acaulospora gedanensis* and three *Glomus*-like species (namely, *Entrophospora claroidea*, *Planticonsortium tenue* and *Rhizophagus fasciculatus*) were identified in the roots of *T. vulgaris* plants growing at the Garden of Medicinal Plants of the Jagiellonian University in Kraków (Poland), along with resting spores of *Olpidium* sp. and dark septate endophytes [Zubek and Błaszowski 2009]. Taxonomic identification of the accessions in Table 1 was based exclusively on morphological characters, with two exceptions: an isolate ascribed to *Trichoderma samuelsii* (Sordariomycetes, Hypocreales), as resulting from the sequence homology of three selected molecular markers (ITS, *tef1* and *rpb2*) [Ma et al. 2023], and an isolate classified as *Neopestalotiopsis aotearoa* (Sordariomycetes, Amphisphaeriales) based on 18S rDNA sequence homology [Abdelhamid et al. 2024]. However, in the latter case it must be considered that 18S is insufficient as a marker for a reliable species identification [López et al. 2026].

The available data do not allow us to make conjectures on any specific or systematic association with *Thymus* spp. of a defined fungal species. Within a sample of 11 endophytic fungi recovered from *T. vulgaris* at the Garden of Medicinal and Aromatic Plants of the Agriculture Research Centre in Giza (Egypt), *Aspergillus terreus* was the most frequently recovered species, represented by five isolates [Ali et al. 2018]. In an investigation carried out in Austria *Colletotrichum gloeosporioides* and *Ascochyta* sp. were found to be the dominant endophytic fungi, respectively in leaves and stems of *Thymus serpyllum* and *Thymus polytrichus* (currently *Thymus praecox* subsp. *polytrichus*), while *Alternaria alternata* was the most frequent species recovered from *Thymus capitatus* (syn. *Thymbra capitata*), *Thymus herba-barona* and *Thymus richardii* at the island of Mallorca, Spain [Fisher et al. 1992]. As a whole, more than 400 isolates from about 30 species were obtained in this study carried out over 30 years ago, which still represents the largest survey of endophytic fungi conducted on thyme.

**Table 1.** Fungi reported for endophytic occurrence in *Thymus* spp.

| Fungal species                                             | <i>Thymus</i> species *                                                                          | Location                    | Reference                       |
|------------------------------------------------------------|--------------------------------------------------------------------------------------------------|-----------------------------|---------------------------------|
| <i>Acaulospora gedanensis</i>                              | <i>T. vulgaris</i> R                                                                             | Kraków, Poland              | Zubek and Błaszowski 2009       |
| <i>Allophoma tropica</i> **                                | <i>T. eriocalyx</i> L                                                                            | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Alternaria alternata</i>                                | <i>T. capitatus</i> L-S, <i>T. herba-barona</i> S,<br><i>T. richardii</i> S                      | Mallorca, Spain             | Fisher et al. 1992              |
|                                                            | <i>T. eriocalyx</i> L-S, <i>T. fallax</i> L,<br><i>T. kotschyanus</i> S, <i>T. lancifolius</i> L | Hamedan, Iran               | Masumi et al. 2015              |
|                                                            | <i>T. vulgaris</i> S                                                                             | Alsharqia, Egypt            | Olama et al. 2023               |
|                                                            | <i>T. vulgaris</i> S                                                                             | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Alternaria atra</i> **                                  | <i>T. vulgaris</i> S                                                                             | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Alternaria franseriae</i>                               | <i>T. eriocalyx</i> L, <i>T. kotschyanus</i> L,<br><i>T. lancifolius</i> L                       | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Alternaria gossypina</i> **<br>( <i>A. tangelonis</i> ) | <i>T. eriocalyx</i> L-S, <i>T. kotschyanus</i> L-S,<br><i>T. lancifolius</i> L                   | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Alternaria</i> sp.                                      | <i>T. capitatus</i> S, <i>T. herba-barona</i> S,<br><i>T. richardii</i> S                        | Mallorca, Spain             | Fisher et al. 1992              |
|                                                            | <i>T. polytrichus</i> L                                                                          | Altaussee, Austria          |                                 |
|                                                            | <i>T. eriocalyx</i> L, <i>T. lancifolius</i> L                                                   | Hamedan, Iran               | Masumi et al. 2015              |
|                                                            | <i>T. algeriensis</i> R                                                                          | Bordj Bou Arreridj, Algeria | Zerroug and Sadrati 2022        |
|                                                            | <i>T. vulgaris</i> S                                                                             | Alsharqia, Egypt            | Olama et al. 2023               |
| <i>Anthostomella</i> sp.                                   | <i>T. capitatus</i> S, <i>T. richardii</i> S                                                     | Mallorca, Spain             | Fisher et al. 1992              |
| <i>Ascochyta</i> sp.                                       | <i>T. polytrichus</i> L-S, <i>T. serpyllum</i> L-S                                               | Altaussee, Austria          | Fisher et al. 1992              |
|                                                            | <i>T. richardii</i> S                                                                            | Mallorca, Spain             |                                 |
| <i>Aspergillus japonicus</i>                               | <i>T. vulgaris</i> L                                                                             | Giza, Egypt                 | Ali et al. 2018                 |
| <i>Aspergillus</i> sp.                                     | <i>T. fallax</i> L                                                                               | Hamedan, Iran               | Masumi et al. 2015              |
|                                                            | <i>T. algeriensis</i> R                                                                          | Bordj Bou Arreridj, Algeria | Zerroug and Sadrati 2022        |
| <i>Aspergillus terreus</i>                                 | <i>T. vulgaris</i> L                                                                             | Giza, Egypt                 | Ali et al. 2018                 |
| <i>Asteromella</i> sp.                                     | <i>T. polytrichus</i> L                                                                          | Altaussee, Austria          | Fisher et al. 1992              |
| <i>Aureobasidium pullulans</i>                             | <i>T. serpyllum</i> L                                                                            | Altaussee, Austria          | Fisher et al. 1992              |
| <i>Aureobasidium</i> sp.                                   | <i>T. capitatus</i> S                                                                            | Mallorca, Spain             | Fisher et al. 1992              |
| <i>Boeremia exigua</i> var. <i>exigua</i> **               | <i>T. vulgaris</i> L-R-S                                                                         | Fajslawice, Poland          | Machowicz-Stefaniak et al. 2002 |
| <i>Botrytis cinerea</i>                                    | <i>T. serpyllum</i> S                                                                            | Altaussee, Austria          | Fisher et al. 1992              |
| <i>Chaetosphaeronema</i> sp.                               | <i>Thymus</i> sp. S                                                                              | Hamedan, Iran               | Mirzaei et al. 2023             |
| <i>Cladosporium cladosporioides</i>                        | <i>T. eriocalyx</i> L, <i>T. lancifolius</i> L                                                   | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Cladosporium oxysporum</i>                              | <i>T. serpyllum</i> L                                                                            | Altaussee, Austria          | Fisher et al. 1992              |
| <i>Cladosporium tenuissimum</i>                            | <i>T. polytrichus</i> L-S                                                                        | Altaussee, Austria          |                                 |
|                                                            | <i>T. capitatus</i> S, <i>T. herba-barona</i> L                                                  | Mallorca, Spain             | Fisher et al. 1992              |
| <i>Cladosporium variabile</i>                              | <i>T. eriocalyx</i> L, <i>T. kotschyanus</i> L                                                   | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Colletotrichum dematium</i>                             | <i>T. polytrichus</i> S                                                                          | Altaussee, Austria          | Fisher et al. 1992              |
|                                                            | <i>T. herba-barona</i> S                                                                         | Mallorca, Spain             |                                 |
| <i>Colletotrichum gloeosporioides</i>                      | <i>T. serpyllum</i> L-S                                                                          | Altaussee, Austria          | Fisher et al. 1992              |
| <i>Colletotrichum</i> sp.                                  | <i>T. kotschyanus</i> L-R                                                                        | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Coniochaeta tetraspora</i>                              | <i>T. capitatus</i> L-S, <i>T. richardii</i> S                                                   | Mallorca, Spain             | Fisher et al. 1992              |
| <i>Curvularia akaii</i>                                    | <i>T. eriocalyx</i> S, <i>T. kotschyanus</i> S                                                   | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Cylindrocarpon</i> sp.                                  | <i>T. eriocalyx</i> R                                                                            | Hamedan, Iran               | Masumi et al. 2015              |
| dark septate endophytes                                    | <i>T. vulgaris</i> R                                                                             | Kraków, Poland              | Zubek and Błaszowski 2009       |
| <i>Diaporthe</i> sp.**                                     | <i>T. polytrichus</i> L, <i>T. serpyllum</i> L                                                   | Altaussee, Austria          | Fisher et al. 1992              |
| <i>Didymella glomerata</i> **                              | <i>T. vulgaris</i> L-R-S                                                                         | Fajslawice, Poland          | Machowicz-Stefaniak et al. 2002 |
|                                                            | <i>T. eriocalyx</i> L                                                                            | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Didymella pomorum</i> **                                | <i>T. capitatus</i> L-S                                                                          | Mallorca, Spain             | Fisher et al. 1992              |
| <i>Diplodia</i> sp.                                        | <i>T. capitatus</i> S                                                                            | Mallorca, Spain             | Fisher et al. 1992              |
| <i>Ectophoma multirostrata</i> **                          | <i>T. vulgaris</i> L-R-S                                                                         | Fajslawice, Poland          | Machowicz-Stefaniak et al. 2002 |
| <i>Ectophoma pomi</i> **                                   | <i>T. kotschyanus</i> L-S                                                                        | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Entrophospora clarioidea</i> **                         | <i>T. vulgaris</i> R                                                                             | Kraków, Poland              | Zubek and Błaszowski 2009       |
| <i>Fusarium acuminatum</i>                                 | <i>T. eriocalyx</i> S                                                                            | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Fusarium equiseti</i>                                   | <i>T. eriocalyx</i> S                                                                            | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Fusarium javanicum</i>                                  | <i>T. fallax</i> R                                                                               | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Fusarium lateritium</i>                                 | <i>T. eriocalyx</i> S                                                                            | Hamedan, Iran               | Masumi et al. 2015              |
| <i>Fusarium oxysporum</i>                                  | <i>T. daenensis</i> L, <i>T. kotschyanus</i> S                                                   | Hamedan, Iran               | Masumi et al. 2015              |

| Fungal species                       | <i>Thymus</i> species *                                                                                                      | Location                                  | Reference                                 |
|--------------------------------------|------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------|-------------------------------------------|
| <i>Fusarium reticulatum</i>          | <i>T. eriocalyx</i> F-S                                                                                                      | Hamedan, Iran                             | Masumi et al. 2015                        |
|                                      | <i>T. eriocalyx</i> L, <i>T. kotschyanus</i> R                                                                               | Hamedan, Iran                             | Masumi et al. 2015                        |
| <i>Fusarium</i> sp.                  | <i>T. algeriensis</i> R                                                                                                      | Bordj Bou Arreridj, Algeria               | Zerroug and Sadrati 2022                  |
|                                      | <i>T. vulgaris</i> S                                                                                                         | Alsharqia, Egypt                          | Olama et al. 2023                         |
| <i>Fusarium subglutinans</i>         | <i>T. eriocalyx</i> S                                                                                                        | Hamedan, Iran                             | Masumi et al. 2015                        |
| <i>Fusarium tricinctum</i>           | <i>T. polytrichus</i> S                                                                                                      | Altaussee, Austria                        | Fisher et al. 1992                        |
| <i>Gilmaniella humicola</i>          | <i>T. richardii</i> S                                                                                                        | Mallorca, Spain                           | Fisher et al. 1992                        |
| <i>Godronia</i> sp.**                | <i>T. herba-barona</i> S, <i>T. richardii</i> S                                                                              | Mallorca, Spain                           | Fisher et al. 1992                        |
| <i>Heterophoma nobilis</i> **        | <i>T. vulgaris</i> L-R-S                                                                                                     | Fajstawice, Poland                        | Machowicz-Stefaniak et al. 2002           |
| <i>Hormonema</i> sp.                 | <i>T. richardii</i> S                                                                                                        | Mallorca, Spain                           | Fisher et al. 1992                        |
| <i>Hypoxylon</i> sp.**               | <i>T. capitatus</i> S, <i>T. richardii</i> S                                                                                 | Mallorca, Spain                           | Fisher et al. 1992                        |
|                                      | <i>T. polytrichus</i> L, <i>T. serpyllum</i> L-S                                                                             | Altaussee, Austria                        | Fisher et al. 1992                        |
|                                      | <i>T. capitatus</i> S, <i>T. herba-barona</i> L-S, <i>T. richardii</i> L-S                                                   | Mallorca, Spain                           |                                           |
| <i>Mycelia sterilia</i>              | <i>T. vulgaris</i> L                                                                                                         | Giza, Egypt                               | Ali et al. 2018                           |
|                                      | <i>T. daenensis</i> R, <i>T. eriocalyx</i> F-L-R-S, <i>T. kotschyanus</i> R-S, <i>T. lancifolius</i> L, <i>T. vulgaris</i> S | Hamedan, Iran                             | Masumi et al. 2015                        |
| <i>Neopestalotiopsis aotearoa</i>    | <i>T. vulgaris</i> S                                                                                                         | Mansoura, Egypt                           | Abdelhamid et al. 2024                    |
| <i>Olpidium</i> sp.                  | <i>T. vulgaris</i> R                                                                                                         | Kraków, Poland                            | Zubek and Błaszowski 2009                 |
| <i>Paraboeremia selaginellae</i> **  | <i>T. eriocalyx</i> L                                                                                                        | Hamedan, Iran                             | Masumi et al. 2015                        |
| <i>Paraphoma chrysanthemicola</i> ** | <i>T. eriocalyx</i> F                                                                                                        | Hamedan, Iran                             | Masumi et al. 2015                        |
| <i>Penicillium chrysogenum</i>       | <i>T. vulgaris</i> L                                                                                                         | Giza, Egypt                               | Ali et al. 2018                           |
| <i>Penicillium</i> sp.               | <i>T. algeriensis</i> S                                                                                                      | Bordj Bou Arreridj, Algeria               | Zerroug and Sadrati 2022                  |
| <i>Phialophora</i> sp.               | <i>T. richardii</i> L-S                                                                                                      | Mallorca, Spain                           | Fisher et al. 1992                        |
| <i>Phoma haematocycla</i>            | <i>T. daenensis</i> L                                                                                                        | Hamedan, Iran                             | Masumi et al. 2015                        |
|                                      | <i>T. polytrichus</i> L-S, <i>T. serpyllum</i> L-S                                                                           | Altaussee, Austria                        | Fisher et al. 1992                        |
| <i>Phoma</i> sp.                     | <i>T. capitatus</i> S, <i>T. herba-barona</i> L-S, <i>T. richardii</i> L-S                                                   | Mallorca, Spain                           |                                           |
|                                      | <i>T. eriocalyx</i> S                                                                                                        | Hamedan, Iran                             | Masumi et al. 2015                        |
|                                      | <i>T. algeriensis</i> L                                                                                                      | Bordj Bou Arreridj, Algeria               | Zerroug and Sadrati 2022                  |
| <i>Planticonsortium tenue</i> **     | <i>T. vulgaris</i> R                                                                                                         | Kraków, Poland                            | Zubek and Błaszowski 2009                 |
| <i>Plenodomus pimpinellae</i> **     | <i>T. eriocalyx</i> S                                                                                                        | Hamedan, Iran                             | Masumi et al. 2015                        |
| <i>Pyrenophora dematioidea</i> **    | <i>T. daenensis</i> L                                                                                                        | Hamedan, Iran                             | Masumi et al. 2015                        |
| <i>Pyrenophora tetrarrhenae</i> **   | <i>T. eriocalyx</i> S                                                                                                        | Hamedan, Iran                             | Masumi et al. 2015                        |
| <i>Rhizophagus fasciculatus</i> **   | <i>T. vulgaris</i> R                                                                                                         | Kraków, Poland                            | Zubek and Błaszowski 2009                 |
| <i>Rhizopus</i> sp.                  | <i>T. algeriensis</i> R                                                                                                      | Bordj Bou Arreridj, Algeria               | Zerroug and Sadrati 2022                  |
| <i>Sclerophomella glaucii</i> **     | <i>T. vulgaris</i> L-R-S                                                                                                     | Fajstawice, Poland                        | Machowicz-Stefaniak et al. 2002           |
|                                      | <i>T. polytrichus</i> L-S, <i>T. serpyllum</i> L-S                                                                           | Altaussee, Austria                        | Fisher et al. 1992                        |
| <i>Septoria</i> sp.                  | <i>T. capitatus</i> S, <i>T. richardii</i> L                                                                                 | Mallorca, Spain                           |                                           |
| <i>Sordaria fimicola</i>             | <i>T. richardii</i> S                                                                                                        | Mallorca, Spain                           | Fisher et al. 1992                        |
| <i>Sporormiella intermedia</i>       | <i>T. richardii</i> L                                                                                                        | Mallorca, Spain                           | Fisher et al. 1992                        |
| <i>Stemphylium</i> sp.               | <i>T. lancifolius</i> L                                                                                                      | Hamedan, Iran                             | Masumi et al. 2015                        |
| <i>Stemphylium vesicarium</i> **     | <i>T. capitatus</i> S, <i>T. richardii</i> S                                                                                 | Mallorca, Spain                           | Fisher et al. 1992                        |
| <i>Subplenodomus valerianae</i> **   | <i>T. eriocalyx</i> R, <i>T. kotschyanus</i> L-S                                                                             | Hamedan, Iran                             | Masumi et al. 2015                        |
| <i>Taeniolella stilbospora</i>       | <i>T. herba-barona</i> S                                                                                                     | Mallorca, Spain                           | Fisher et al. 1992                        |
| <i>Trichoderma harzianum</i>         | <i>T. serpyllum</i> S                                                                                                        | Altaussee, Austria                        | Fisher et al. 1992                        |
| <i>Trichoderma samuelsii</i>         | <i>T. mongolicus</i>                                                                                                         | Yinchuan, China                           | Ma et al. 2023                            |
| unidentified yeasts                  | <i>T. eriocalyx</i> L-S, <i>T. fallax</i> S, <i>T. lancifolius</i> S                                                         | Hamedan, Iran<br>Central and Western Iran | Masumi et al. 2015<br>Masumi et al. 2015b |
|                                      | <i>T. vulgaris</i> L-R-S                                                                                                     | Fajstawice, Poland                        | Machowicz-Stefaniak et al. 2002           |
| <i>Westerdykella capitulum</i> **    | <i>T. eriocalyx</i> L                                                                                                        | Hamedan, Iran                             | Masumi et al. 2015                        |

\* *T. lancifolius* and *T. polytrichus* are now regarded as subspecies of *T. daenensis* and *T. praecox*, respectively.

\*\* For these records, the species names were updated according to Mycobank.

F: flower; L: leaf; R: root; S: stem

Another large set of isolates (95) was collected in a study carried out in the Hamedan province of Iran considering six *Thymus* species: once more, *A. alternata* was the most common endophyte with 16 isolates recovered from all the above-ground plant parts, followed by several species identified within the genera *Fusarium* and *Phoma sensu lato* [Masumi et al. 2015a]. Fungi belonging to the above three genera were again the most frequent in an investigation carried out on *Thymus algeriensis* in Algeria [Zerroug and Sadrati 2022], while *Alternaria* and *Fusarium* were the only genera represented in a small sample of five isolates recovered from *T. vulgaris* in Egypt [Olama et al. 2023]. Moreover, earlier investigations on field-grown *T. vulgaris* in the Lublin region of Poland documented a diverse assemblage of *Phoma sensu lato* fungi colonizing shoots, leaves and, less frequently, roots of *T. vulgaris*. Several species were identified that have been recently renamed after taxonomic revision, with the new binomial indicated in brackets: *Phoma capitulum* (= *Westerdykella capitulum*), *P. glaucii* (= *Sclerophomella glaucii*), *P. dictamnica* (= *Heterophoma nobilis*), *P. glomerata* (= *Didymella glomerata*), *P. multirostrata* var. *microspora* (= *Ectophoma multirostrata*), and *P. exigua* var. *exigua* (*Boeremia exigua* var. *exigua*) [Machowicz-Stefaniak et al. 2002]. Subsequent pathogenicity studies demonstrated that, among these taxa, only *P. exigua* var. *exigua* was confirmed as an occasional (facultative) pathogen of thyme, causing reduced seed germination, seedling damping-off, and necrosis of roots and hypocotyls following artificial inoculation [Machowicz-Stefaniak et al. 2008], whereas the remaining species were reported only as endophytic colonizers, without any evidence of pathogenicity. Besides *Phoma* [Zimowska 2022], *Alternaria* and *Fusarium* are also under revision with reference to the recent concepts in fungal taxonomy [Li et al. 2022, Crous et al. 2022]; hence, a re-interpretation according to the updated nomenclature is desirable and appropriate for the available data concerning these genera, which have also been reported among the most common endophytic associates of many other plant species [Ahmed et al. 2023, Nicoletti et al. 2020, Manathunga et al. 2024, Nicoletti and Zimowska 2023].

#### Biochemical and ecological properties of endophytic fungi in *Thymus* spp.

It is a key issue in mycological research to accurately investigate the biochemical properties of endophytic fungi in view of possible biotechnological exploitation [Gupta et al. 2023, Agrawal and Bhatt 2023]. Indeed, secondary metabolites are regarded as the main factor influencing the interspecific relationships established with both the plant host and all components of its associated microbiome, with substantial effects on plant growth and protection. With reference to *Thymus* spp., it has been shown that the EOs contained in the leaf glandular tissues represent one of the primary selective factors shaping the endophytic community composition [Checcucci et al. 2017].

As also demonstrated on several crop species, the beneficial effects of two well-known endophytic basidiomycetes belonging to the Sebaciales, namely *Serendipita* (= *Sebacina*) *vermifera* and *Serendipita* (= *Piriformospora*) *indica* [Ray and Craven 2016, Saleem et al. 2022], have been documented on *T. vulgaris* plants cultured *in vitro* and *in vivo*. Besides an increase in height and root length, as well as in fresh and dry weights of shoots and roots, oil yield was found to be enhanced in all the inoculated plants, and its analysis carried out by means of gas chromatography coupled with mass spectrometry (GC-MS) showed a notably increased content of thymol along with a decrease in its isomer carvacrol [Dolatabadi et al. 2011].

At least in part, the growth-promoting effects induced by Sebaciales are attributed to the direct and indirect production of auxins and other phytohormones. In this respect, more circumstantial evidence has been obtained for an isolate of *N. aotearoa* from *T. vulgaris*, which was found to produce indole-3-acetic acid (IAA) at a concentration of 11.16 µg mL<sup>-1</sup> [Abdelhamid et al. 2024]. On the other hand, the inoculation with fungal endophytes isolated from other Lamiaceae species was found to significantly improve growth, chlorophyll, and carotenoid content in thyme plants under drought stress. Moreover, lipid peroxidation levels were significantly reduced, and the higher activity of antioxidant enzymes and improved redox state of glutathione were considered to be crucial for the increased resistance to drought [Kamyab et al. 2024].

Besides influencing EO production and composition in the host plants, endophytic fungi of thyme may also directly synthesize these compounds. This is the case of a strain of *A. alternata* isolated from *T. vulgaris* in Egypt producing an array of volatile organic compounds (VOCs), some of which were common to the host plant [Olama et al. 2023]. Moreover, ethyl acetate extracts from culture of a strain of *A. terreus*, again from *T. vulgaris* in Egypt, were found to contain carvacrol and thymol in higher concentrations than

those determined in the host plant. Other compounds characteristic of the EOs were detected in the GC-MS analysis, such as terpineol,  $\alpha$ -phellandrene, camphene,  $\alpha$ -pinene, isopregol, dihydrocarveol, borneol, citronellal, humulene, ascaridole, geraniol, caryophyllene, cedrenol, along with some mycotoxins, namely aflatoxin G2, cyclopaldic acid, nivalenol, and typical plant secondary metabolites, such as glaucine, scoparone, scoprophulein, trispherine, luteolin, trimethylquercetin and other flavonoids. This compound assortment accounts for the notable antioxidant properties determined for the culture extract of this strain, as well as for the cytotoxicity against HEPG-2 hepatoma cells, with an  $IC_{50}$  value of  $3.53 \pm 0.4 \mu\text{g mL}^{-1}$  [Ali et al. 2018]. In addition, high antibacterial and antifungal activities against *Escherichia coli*, *Staphylococcus aureus*, *Aspergillus flavus* and *Candida albicans* were documented for the culture extract of this strain by the same research group [El-Ela Sayed et al. 2020].

An endophytic isolate of *T. samuelsii* recovered from the stem of *Thymus mongolicus* displayed antagonistic activity in a co-culture experiment towards a panel of eight pathogenic fungi, including *A. alternata*, *Alternaria solani*, *Botrytis cinerea*, *Cytospora mali*, *Fusarium graminearum*, *Fusarium oxysporum*, *Fusarium sambucinum*, and *Neocosmospora solani*, with inhibition rates ranging between 31.0% and 68.5%. However, the antifungal activity of its fermentation broth and crude extract was low. GC-MS analysis showed that VOCs were the key antifungal compounds released in the co-cultures, with the main component identified as 6-pentyl-2H-pyran-2-one [Ma et al. 2023].

In a study including 89 endophytic isolates from several *Thymus* spp., some strains stood out for their antimicrobial effects, as assayed either directly or through their culture extracts; that is, strains of *Fusarium subglutinans*, *Fusarium equiseti*, *Fusarium javanicum*, *Fusarium lateritium*, *F. oxysporum*, *A. alternata*, *Allophoma tropica*, *Subplenodomus valerianae* and *Chaetosphaeronema* sp. displaying inhibitory effects against *B. cinerea*. The latter strain was the only one to show clear antibacterial effects in assays carried out against a panel of four strains belonging to *E. coli*, *S. aureus*, *Xanthomonas arboricola* pv. *juglandis* and *Streptomyces scabies*; conversely, a higher effectiveness was displayed by the culture extracts of *F. equiseti* and *F. lateritium* against *S. aureus*, and of *A. alternata*, *F. equiseti*, *F. oxysporum*, *F. subglutinans* and *S. valerianae* against *S. scabies* [Mirzaei and Masumi 2023]. In a previous study by the same research group, six strains of unidentified yeasts collected from three *Thymus* spp. also showed limited antifungal effects (14.70–37.25% growth inhibition) against *B. cinerea* [Masumi et al. 2015b].

Additional data on the antimicrobial properties have been collected for several endophytic isolates which were only identified at the genus level. This list includes a panel of 16 isolates belonging to the genera *Aspergillus*, *Alternaria*, *Fusarium*, *Penicillium*, *Phoma* and *Rhizopus*, which exhibited varying degrees of antibacterial and antifungal activities *in vitro* against *Bacillus cereus*, *Enterococcus faecalis*, *E. coli*, *Pseudomonas aeruginosa*, *Salmonella typhimurium*, *S. aureus*, *Fusarium caeruleum*, *F. oxysporum* and *Phytophthora infestans* [Zerroug and Sadrati 2022].

Finally, some extent of antimicrobial properties were documented for the ethyl acetate culture extracts of isolates of *Alternaria* and *Fusarium* collected from *T. vulgaris* in Egypt; in particular, this refers to antibacterial activity in assays carried out against *Bacillus subtilis*, *P. aeruginosa* and *S. aureus*, as well as to antifungal activity against *Aspergillus niger* and *C. albicans*. Moreover, these extracts were determined to possess antioxidant properties in assays based on the diphenyl-2-picryl hydrazyl (DPPH) radical scavenging activity, with  $IC_{50}$  values up to  $36.80 \mu\text{g mL}^{-1}$  [Olama et al. 2023].

Besides the implications related to the antimicrobial, cytotoxic and antioxidant properties, potential biotechnological exploitation may also concern the production of enzymes. In this respect, in the screening of a set of 89 endophytic isolates from several *Thymus* spp. collected in Western Iran high levels of asparaginase and amylase production were recorded from strains of *F. subglutinans* and *Curvularia akaii*, respectively [Masumi et al. 2014].

## CONCLUSIONS

This paper provides an overview of the current knowledge on the diversity, ecological functions, and biotechnological potential of endophytic fungi associated with *Thymus* species. These fungi represent a taxonomically diverse community comprising 49 genera and 53 species, mostly belonging to common

ascomycete genera such as *Alternaria*, *Fusarium*, *Colletotrichum*, and *Phoma*; considering that most identifications were based on morphological characters, a more rigorous taxonomic reassessment would be desirable. The currently available data are limited, and do not allow to establish if any species has developed a mutualistic association reflecting ecological significance. Nevertheless, some of these microorganisms have proved to be able to modulate production of EOs and contribute to plant growth promotion, enhanced tolerance to abiotic stress, and protection against plant pathogens through the synthesis of bioactive metabolites and volatile organic compounds. Moreover, several isolates have been demonstrated antimicrobial, antioxidant, and cytotoxic activities, deserving further assessments with a view to their effective application in sustainable agriculture and biotechnology. On the other hand, the occurrence of potential pathogens and species known as mycotoxin producers calls for additional work aimed at verifying their safety with respect to both plant and human health.

Future research in the field should focus particularly on the culture-independent characterization of the fungal endophytic communities, the standardization of sampling and isolation methods, the use of appropriate molecular markers for the isolate identification and the deposition of the obtained DNA sequences in recognized public repositories, and a more detailed investigation of host and organ specificity. Moreover, it is desirable that the experimental protocols be designed to more diffusely include controlled inoculation assays, field validation, and biosafety screening.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DECLARATION OF THE USE OF GENERATIVE AI TOOLS IN THE PROCESS OF PREPARING THE PAPER

The authors declare that no genAI tools were used in the process of preparing the paper.

## AUTHORS CONTRIBUTION

The authors contributed in equal parts to collecting information and writing this paper.

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