Halimium as an ectomycorrhizal symbiont: new records and an appreciation of known fungal diversity

Marco Leonardi 1 · Ariadne Nóbrega Marinho Furtado 2 · Ornella Comandini 3 · József Geml 4 · Andrea C. Rinaldi 5

Received: 2 July 2020 / Revised: 15 October 2020 / Accepted: 19 October 2020 © The Author(s) 2020

Abstract
Halimium is a genus of Cistaceae, containing a small group of shrub species found in open vegetation types and in degraded forest patches throughout the western and central Mediterranean region. We recently described the morpho-anatomical features of the ectomycorrhizae formed by Scleroderma meridionale on Halimium halimifolium, but the mycorrhizal biology of this host plant genus is still largely unexplored. Here, we report new data on the ectomycorrhizal fungal symbionts of Halimium, based on the collection of sporocarps and ectomycorrhizal root tips in pure stands occurring in Sardinia, Italy. To obtain a broader view of Halimium mycorrhizal and ecological potential, we compiled a comprehensive and up-to-date checklist of fungal species reported to establish ectomycorrhizae on Halimium spp. on the basis of field observations, molecular approaches, and mycorrhiza synthesis. Our list comprises 154 records, corresponding to 102 fungal species and 35 genera, revealing a significant diversity of the Halimium ectomycorrhizal mycobiota. Key ectomycorrhizal genera like Russula, Lactarius/Lactifluus, Amanita, Inocybe, and Cortinarius account for more than half of all mycobionts. A large proportion of Halimium fungal species are shared with other host plants in various ecological settings, suggesting a critical role of common mycorrhizal networks in the function played by this shrub in various Mediterranean ecosystems.

Keywords Cistaceae · Ecological networks · Ectomycorrhiza · Fungal communities · Maquis shrubland

Introduction
Shrublands occupy a specific niche in the Mediterranean biome, with an increasingly appreciated ecological function. In particular, plants occurring in this peculiar environment improve water and light regime, protect soil from erosion, and desertification, and act as “nurse” species for tree seedlings, thus favoring the establishment of late-successional species (https://php.radford.edu/~swoodwar/biomes/?page_id=98). To perform such tasks, the shrubs and small trees that integrate this vegetation system developed adaptations to withstand adverse and stressful conditions such as drought and fire (Rundel and Cowling 2013). The presence of a large number of ectomycorrhizal fungi, mainly associated with Cistaceae Juss., is another common trait of Mediterranean shrublands. The role played by ectomycorrhizal fungi in optimizing plant fitness and increasing nutrients’ availability in a wide range of terrestrial ecosystems, especially where cold and dry conditions limit decomposition, is largely appreciated (Smith and Read 1997). Cistus is the dominant ectomycorrhizal host plant in Mediterranean shrublands. Over 250 fungal species belonging to 40 genera have been reported to be associated with Cistus, with 35 host-specific species; members of the Cortinariaceae and Russulaceae make up the most of both generalist and Cistus-specific mycobionts (Comandini et al. 2006; Loizides 2016).

The genus Halimium (Dunal) Spach belongs to the Cistaceae (Page 2017), with 13 accepted species of evergreen...
or semi-deciduous small-to-large shrubs (http://www.theplantlist.org/1.1/browse/A/Cistaceae/Halimium/). However, these include *H. brasiliense* (Lam.) Grosser that is considered by other sources a synonym of *Crocanthemum brasiliensis* Spach and that has a disjunct distribution (in the New World) with respect to all other known species of *Halimium* (https://www.gbif.org/species/3596090), and *Halimium × pauanum* Font Quer, a naturally occurring hybrid between *H. lasiocalycinum* (Boiss. & Reuter) Engler & Pax and *H. lasianthum* (Lam.) Spach (Soriano 2008). A new species, *H. voldii* Kit Tan, Perdetz. & Raus has been recently described from Greece (Greuter and Raus 2000); however, both the status of this taxon and that of *H. syriacum* K. Koch, reported from subalpine levels in Lebanon and Syria, are still unresolved. *Halimium* is closely related to *Cistus*; some botanists in the past have considered *Halimium* species as belonging to *Cistus* (e.g., Demoly 2006), but the most recent molecular phylogenetic analyses have clearly shown the two genera as distinct (Guzmán and Vargas 2005, 2009; Civeyrel et al. 2011). The two genera overlap largely in distribution within the Mediterranean basin although *Halimium* is restricted to the western part of the floristic region (Civeyrel et al. 2011) (Fig. 1). *Halimium* species occur usually in open vegetation types, like matorral shrublands and garrigues, but they can also been found in degraded forest patches, at the verges of woods, abandoned fields, pasturelands, and on coastal sandy areas and dry dunes (Zunzunegui et al. 2002, 2009).

The mycorrhizal biology of *Halimium* is poorly known. The genus may form ectomycorrhizae and possibly vesicular arbuscular mycorrhizae (Camprubi et al. 2011; Buscardo et al. 2012; Beddiar et al. 2015). To expand the current knowledge of mycorrhizal interactions of *Halimium*, we started a research program focusing on the isolation and full characterization of the ectomycorrhizae formed by the fungal symbionts associated with *Halimium* spp. We recently described, for the first time, the morpho-anatomical features of an ectomycorrhiza on *Halimium*, formed by *Scleroderma meridionale* Demoulin & Malençon on *Halimium halimifolium* (L.) Willk. (Leonardi et al. 2018). In the current paper, we report new data on *Halimium* mycobionts, as observed in pure stands occurring in Sardinia, Italy, through both sporocarps and ectomycorrhizal root tip collections. Also, we provide a comprehensive and up-to-date checklist of fungal species reported to establish ectomycorrhizae on *Halimium* spp. on the basis of field observations, molecular approaches, and mycorrhiza synthesis, a type of information that is widely dispersed in the mycological literature, with no specific account existing on the topic. The data presented here reveal a high diversity of the *Halimium* ectomycorrhizal mycobiota.

![Distribution map of Halimium spp. Occurrence data from the Global Biodiversity Information Facility (https://www.gbif.org/)](https://www.gbif.org/)

Fig. 1 Distribution map of *Halimium* spp. Occurrence data from the Global Biodiversity Information Facility (https://www.gbif.org/)
Materials and methods

Collecting site and fungal sampling

Sporocarps of ectomycorrhizal fungi were harvested in a coastal sandy area (from 39° 15’ 17.42″ N, 8° 24’ 32.75″ E to 39° 15’ 46.07″ N, 8° 24’ 46.89″ E and from 58 to 123 m asl) close to Gonnese, about 70 km west of Cagliari, Sardinia, Italy. Collection surveys were conducted weekly during growing season (October–January) and monthly during the rest of the year, from 2015 through 2019. Sporocarps were photographed in situ and identified on the basis of published descriptions of macroscopic and microscopic characters. Fungal species names retrieved from literature were verified for nomenclatural and taxonomic synonyms in Index Fungorum (http://www.indexfungorum.org) and MycoBank (http://www.mycobank.org) and current names adopted. The collection site is characterized by extended stands H. halimifolium (Fig. 2) that here occurs practically in pure form. No other potential ECM host plants are present on the site, with the exception of a few scattered Cistus salviifolius L. shrubs. For ectomycorrhizae, 40 soil cores (about 20 × 20 × 20 cm) were excavated randomly in proximity of Halimium shrubs (not underneath sporocarps), at least 5 m apart from each other. Soil cores were immersed overnight in water, and ectomycorrhizal roots were carefully separated under a dissecting microscope. Ectomycorrhizae were classified into morphotypes following the methods and indications of Agerer (1991), and several tips for each type were immediately transferred into 90% EtOH and stored at −20 °C for subsequent DNA analysis or fixed in 2.5% (v/v) glutaraldehyde in 10 mM Na-phosphate buffer (pH 7.2) for morpho-anatomical description of characterizing features. Reference materials for sporocarps and ectomycorrhizae are deposited in CAG, at the collection of the Department of Biomedical Sciences, University of Cagliari, Cagliari, Italy.

Molecular characterization of the fungi

Identification of sporocarps and ectomycorrhizae using a molecular approach was based on PCR amplification and sequencing of the complete internal transcribed spacer (ITS) regions in nuclear ribosomal DNA (Gardes and Bruns 1993). Genomic DNAs of the sporocarps were isolated from 20 mg of each dried sample using DNeasy Plant Mini Kit (Qiagen, Hilden, Germany), and the ITS amplifications were performed following the protocol reported by Leonardi et al. (2005). A direct PCR approach was applied to identify ectomycorrhizal tips isolated from soil samples as described by Iotti and Zambonelli (2006). Three ectomycorrhizal tips were selected as PCR targets and directly amplified using ITS1F/ITS4 primer pairs (White et al. 1990; Gardes and Bruns 1993). Two microliters of 20 mg/ml BSA (bovine serum albumin) solution (Fermentas, Vilnius) was added to each reaction tube to prevent PCR inhibition (Leonardi et al. 2013). The amplified products were purified using the QIAquick PCR Purification Kit (Qiagen, Milan, Italy) and sequenced by Eurofins Genomics service (Ebersberg, Germany). Sequence-based fungal identification was performed following the indications and recommendations reported in Hofstetter et al. (2019). Sequences of sporocarps and ectomycorrhizae are deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/) under accession numbers specified in Table 1. In selected cases, to confirm the identity of the host shrub roots, the plastid trnL region of ECM root tip DNA was amplified using primer pairs trnC/trnD following Tedersoo et al. (2008). In these cases, the chloroplast trnL region obtained by PCR amplification of DNA extract from H. halimifolium leaves was used as positive control.

Compiling the list of records

Data on the association between Halimium spp. and ectomycorrhiza-forming fungi presented here are largely...
Table 1  Ectomycorrhizal fungi reported to be associated with *Halimium* spp.

| Species | Host (*Halimium*) | Reference | Sequence |
|---------|-------------------|-----------|----------|
| **Ascomycota** | | | |
| *Cenococcum geophilum* Fr. | *H. lasianthum,*  *H. ocymoides* | Buscardo et al. 2012 (ECM) | HQ625444 |
| | *H. lasianthum* | Santolamazza-Carbone et al. 2019 (ECM) | KY595999 |
| | *H. halimifolium* | This study (ECM) | |
| **Terfezia boudieri** Chatin | *H. halimifolium* | Chevalier 2014 | |
| **Terfezia** spp. | *H. halimifolium* | This study (ECM) | |
| **Terfezia** sp. 1 | *H. ocymoides* | Buscardo et al. 2012 (ECM) | |
| **Terfezia** sp. 2 | *H. lasianthum* | Buscardo et al. 2012 (ECM) | |
| **Tuber oligospermum** Tul. & C. Tul. (Trappe) | *H. halimifolium* | This study (ECM) | |
| **Basidiomycota** | | | |
| *Alessioporus ichnusanus* (Alessio, Galli & Littini) Gelardi, Vizzi & Simonini | *H. halimifolium* | This study | |
| **Amanita cistetorum** Contu & Pacioni | *H. halimifolium* | Moreau et al. 2007a, Moreau et al. 2007b | |
| **Amanita citrina** (Schaeff.:Fr.) Pers. | *H. halimifolium* | Moreau et al. 2007a | |
| **Amanita curtipes** E.-J. Gilbert f. *curtipes* | *H. halimifolium* | Moreau et al. 2007a | |
| **Amanita gilbertii** Beausé | *H. halimifolium* | This study | |
| **Amanita gracilior** Bas & Honrubia | *H. halimifolium* | Moreno-Arroyo 2004 | |
| **Amanita malleata** (Piane ex Bon) Contu | *H. halimifolium* | Taudiere et al. 2015 | |
| **Amanita muscaria** var. *inzengae* Neville & Poumarat | *H. halimifolium* | Moreau et al. 2007a | |
| **Amanita pantherina** (D.C.:Fr.) Krombh | *H. halimifolium* | Moreau et al. 2007a | |
| **Amanita ponderosa** Maleçon & R. Heim | *H. halimifolium* | Moreau et al. 2007a | |
| **Amanita rubescens** (Pers.:Fr.) Gray | *H. halimifolium* | Moreno-Arroyo 2004 | |
| **Amphinema** sp. | *H. halimifolium* | Moreau et al. 2007a | |
| **Boletus aereus** Bull.:Fr. | *H. alyssoides* | Martinez de Azagra Paredes et al. 1998 | |
| **Boletus edulis** Bull.:Fr. | *H. halimifolium* | Oria-De-Rueda et al. 2008, 2009 | |
| **Coltricia** sp. | *H. halimifolium* | Moreno-Arroyo et al. 1998 | |
| **Cortinarius** candelaris Fr. | *H. halimifolium* | This study | |
| **Cortinarius cedreto* var. halimiorum** Brotzu & Peintner | *H. halimifolium* | Brotz & Peintner 2009 | |
| **Cortinarius coeruleopallens** Contu | *H. halimifolium* | This study | |
| **Cortinarius maculatocaespitosus** Bidaud | *H. halimifolium* | This study | |
| **Cortinarius maculatus** (L.:Fr.) Murrill | *H. halimifolium* | This study | |
| **Cortinarius palazonianus** Vila, A. Ortega & Fern.-Brime | *H. halimifolium* | Fernandez-Brime et al. 2014 | |
| **Cortinarius rigens** (Pers.) Fr. | *H. halimifolium* | This study | |
| **Cortinarius scobinaceus** Maleçon & Bertault | *H. halimifolium* | Moreau et al. 2007a, Moreau et al. 2007b | |
| Species                                      | Host (Halimium) | Reference                                                                 | Sequence     |
|----------------------------------------------|-----------------|---------------------------------------------------------------------------|--------------|
| *Cortinarius variiformis* Malikov*            | *H. halimifolium* | This study                                                                | MT594505     |
| *Cortinarius variiformis* Malençon*          | *H. halimifolium* | This study                                                                | MT594506     |
| *Descolea maculata* Bougeir*                  | *H. lasianthum*  | Santolamazzia-Carbone et al. 2019 (ECM)                                  | KY654754     |
| *Gyroporus pseudolacteus* G. Moreno, Carlavilla, Heykoop, Manjón & Vizzini* | *H. halimifolium* | This study                                                                | MT594507     |
| *Hebeloma cistophilum* Maire*                 | *H. halimifolium* | Moreau et al. 2007a, Moreau et al. 2007b, Eberhardt et al. 2009          |              |
| *Hebeloma cistophilum* Romag.*                | *Halimium sp.*   | Moreno-Arroyo 2004                                                        |              |
| *Hebeloma danense* L. Corb. & R. Hein         | *Halimium sp.*   | Moreno-Arroyo 2004                                                        |              |
| *Hortiboletus rubellus* (Krombh.) Simonini, Vizzini & Gelardi* | *H. halimifolium* | This study                                                                | MT594509     |
| *Hygrophanus chrysodon* (Batsch:Fr.) Fr.*    | *H. halimifolium* | This study                                                                | MT594510     |
| *Hygrophanus cfr. eburneus* (Bull.) Fr.*     | *H. halimifolium* | This study                                                                | MT594511     |
| *Inocybe asterospora* Quél.*                  | *Halimium sp.*   | Moreno-Arroyo 2004                                                        |              |
| *Inocybe calida* Velen.*                     | *H. halimifolium* | Moreno-Arroyo 2004                                                        |              |
| *Inocybe corydalina* Quél.*                   | *Halimium sp.*   | Moreno-Arroyo 2004                                                        |              |
| *Inocybe halophila* R. Heim.*                 | *H. halimifolium* | Moreau et al. 2007a, Moreau et al. 2007b                                |              |
| *Inocybe lacera* (Fr.) P. Kumm.*             | *H. halimifolium* | Moreno-Arroyo 2004                                                        |              |
| *Inocybe pruinosa* R. Heim*                  | *Halimium sp.*   | Moreno-Arroyo 2004                                                        |              |
| *H. halimifolium*                            | This study                                                                | MT594512     |
| *Lactarius cistophilus* Bon & Trimbach*       | *H. halimifolium* | Leonardi et al. 2018                                                      | U885433      |
| *Lactarius deliciosus* (L.) Gray              | *H. halimifolium* | de Carvalho 2016 (sECM), Albuquerque-Martins et al. 2019 (sECM)          |              |
| *Lactarius ginnensis* (Mor.-Arr. et al.) Pierotti* | *H. alyssoides, H. ocymoides* | Vidal et al. 2019                                                          |              |
| *Lactarius hepaticus* Plowr.*                 | *H. lasianthum*, H. ocymoides | Buscardo et al. 2012 (ECM)                                              | H625465      |
| *Lactarius pseudocorticulus* Basso, Neville & Pounarat | *H. halimifolium* | Moreau et al. 2007a                                                      |              |
| *Lactarius subdulcis* (Pers.) Gray*           | *H. lasianthum*  | Santolamazzia-Carbone et al. 2019 (ECM)                                  | KY681468     |
| *Lactarius tesselorum* Malençon*              | *H. halimifolium* | This study                                                                | MT594523     |
| *Lactifluus brunneoviolascens* (Bon) Verbeke* | *H. halimifolium* | Leonardi et al. 2018                                                      | KU885434     |
| *Lactifluus rugatus* Kühn. & Romagn.*         | *H. halimifolium* | This study                                                                | MT594524     |
| *Lactifluus rugatus* Kühn. & Romagn.*         | *H. halimifolium* | This study                                                                | MT594525     |
| *Leccinellum corsicum* (Rolland) Bresinsky & Manfr. Binder* | *H. halimifolium* | This study                                                                | MT594526     |
| *Lepidotus nigromarginatus* Contu & Dessi*    | *H. halimifolium* | This study                                                                | MT594527     |
| *Paxillus ammoniavirescens* Contu & Dessi*    | *H. halimifolium* | This study                                                                | MT594528     |
| *Pisolithus arrhizus* (Scop.) Rauchert*       | *Halimium sp.*   | Moreno-Arroyo 2004                                                        |              |
| *Pisolithus sp.* 1°                          | *H. halimifolium* | This study                                                                | MT594529     |

* indicates sECM when obtained.
Table 1 (continued)

| Species | Host (Halimium) | Reference | Sequence |
|---------|----------------|-----------|----------|
| *Pisolithus* sp. 2 | *H. halimifolium* | This study (ECM) | MT594530 |
| *Rhizopogon luteolus* Fr.* | *H. halimifolium* | Moreno-Arroyo 2004 | |
| *Rhizopogon roseolus* (Corda) Th. Fr.* | *H. ocyoides* | Buscardo et al. 2012 (ECM) | |
| *Russula ammophila* (J.M. Vidal & Calonge) Trappe & T.F. Elliott | *H. halimifolium* | Moreno-Arroyo 2004 | |
| *Russula amoecicolor* Romagn. | *H. halimifolium* | Moreno-Arroyo et al. 2019 | |
| *Russula aenicolour* Romagn. | *H. halimifolium* | Moreno-Arroyo 2004 | |
| *Russula densifolia* Secr. ex Gillet | *H. lasianthum* | Buscardo et al. 2012 (ECM) | |
| *Russula littoralis* Romagn. | *H. halimifolium* | Moreau et al. 2007a | |
| *Russula montepiensis* Sarnari* | *H. halimifolium* | This study | MT594531 |
| *Russula odorata* Romagn. | *H. halimifolium* | Moreau et al. 2007a | |
| *Russula praetervisa* Samari* | *H. halimifolium* | This study | MT594536 |
| *Russula sardonia* Fr. | *H. ocyoides* | Buscardo et al. 2012 (ECM) | |
| *Russula vinaceodora* (Calonge & J.M. Vidal) | *H. halimifolium* | Carvalho et al. 2018 (ECM) | |
| *Scelodera meridionale* Demoulin & Malençon* | *H. halimifolium* | Moreno-Arroyo 2004 | |
| *Scleroderma citrinum* Pers. | *H. lasianthum* | Santolamazza-Carbone et al. 2019 (ECM) | |
| *Scleroderma polyrhizum* (J.F. Gmel) Pers. | *H. halimifolium* | Leonardi et al. 2018 | |
| *Thelephora cfr. caryophyllae* (Schaeff.) Pers. | *H. halimifolium* | Carvalho et al. 2018 (ECM) | |
| *Thelephora terrestris* Ehrh.* | *H. halimifolium* | This study (ECM) | MT594537 |
| *Tomentella badia* (Link) Stalpers | *H. lasianthum* | Santolamazza-Carbone et al. 2019 (ECM) | |
| *Tomentella terrestris* (Berk. & Broome) M.J. Larsen | *H. ocyoides* | This study | MT594538 |
| *Tricholoma equestre* (L.:Fr.) P. Kumm. | *H. halimifolium* | Moreno-Arroyo 2004 | |
| *Tricholoma portentosum* (Fr.) Quél | *H. halimifolium* | Santolamazza-Carbone et al. 2019 (ECM) | |
| *Tubariomyces hygrophoroides* Esteve-Rav., P.-A. Moreau & C.E. Hermos | *H. halimifolium* | Moreno-Arroyo 2004 | |
| *Tubariomyces inexpectata* (M. Villarreal, Esteve-Raventós, Heykoop & E. Horak) Esteve-Raventós & Matheny | *H. halimifolium* | de Carvalho 2016 (sECM) | |
| *Tylospora* sp. | *H. halimifolium* | de Carvalho 2016 | MT594542 |

1. Springer
Table 1 (continued)

| Species | Host (Halimium) | Reference | Sequence |
|---------|----------------|-----------|----------|
| Xerocomellus redeuilhii A.F.S. | H. halimifolium | | |
| Taylor, U. Eberh., Simonini, Gelardi & Vizzini | | | |
| Zygomycota | | | |
| Youngiomyces multiplex (Thaxt.) Y.J. Yao | H. alyssoides | Vidal et al. 1997 | |

ECM description or report of naturally occurring ectomycorrhizae, and/or sequence isolated from ECM or roots. All other records are about sporocarp collections, if not specified otherwise; sECM description or report of synthesized ectomycorrhizae

1 For names of taxa and synonymy, we followed Index Fungorum (http://www.indexfungorum.org/) and MycoBank (http://www.mycobank.org). The higher classification system used in this paper is that outlined by Kirk et al. (2008) in the Dictionary of the Fungi

2 Usually reported as specific or typical Cistus mycobiont (see Comandini et al. 2006)

3 Previously reported as associated with Cistus (see Comandini et al. 2006; Gelardi et al. 2014; Loizides 2016)

4 Dubious or suspect record

5 Often reported as associated with Helianthemum spp. (see Loizides 2016)

6 The status of the close T. asa is still unclear (see Index Fungorum and Boutahir et al. 2013)

7 As Torrendia pulchella Bres.

8 Now considered a synonym of C. pallens (see Olariaga et al. 2017)

9 Deposited as Cortinarius halimiorum

10 Reported by Moreau et al. (2007a) as C. belleri M.M. Moser. See also Ortega et al. 2006

11 Usually associated with Eucalyptus and introduced in Europe through reforestations (see Santolamazza-Carbone et al. 2019)

12 As Inocybe brunnecorafa Stangl & J. Veselsky

13 Sometimes reported as a synonym of I. pruinosa R. Heim (see [MB#252517])

14 Usually reported as associated with Pinus (e.g., Basso 1999

15 Deposited as Lactifluus luteolus

16 As Leccinum corsicum (Rolland) Sing

17 In the Mediterranean region, Pisolithus most likely occurs as a species complex, not completely resolved yet (see Díez et al. 2001; Martin et al. 2002; Lebel et al. 2018)

18 As Macowanites amorphophilus (J.M. Vidal & Calonge) J.M. Vidal & Calonge, usually in dunal systems with Pinus pinea, P. pinaster, and Cistus (see also http://www.micobotanicajaen.com/Revista/Articulos/DMerinoA/SetasDunas002/MacowanitesAmorphophilus.pdf)

19 As Russula drimeia Cooke

20 As Macowanites vinaceodorus Calonge & J.M. Vidal, usually in dunal systems with Pinus pinea and Cistus (Moreno-Arroyo et al. 2005)

21 As Sebacina vermifera (Oberw.)

22 Sequence not deposited

23 As Inocybe inexpectata Villarreal, Esteve-Rav., Heykoop & E. Horak in Moreau et al. 2007a

Based on reports of field observations of sporocarps associations with potential hosts. The dataset contains both personal collections and observations and information collated from a variety of published and web-based sources. Literature databases available to authors (e.g., Agricola, Scopus, PubMed, ISI Web of Science, ResearchGate) were searched for articles on Halimium and associated mycobionts. Sequences of Halimium ECM fungi were retrieved from either GenBank or UNITE. Fungal taxa belonging to genera for which the mycorrhizal status is currently uncertain were not listed (for a comprehensive list of ectomycorrhizal fungal genera and the criteria used to ascertain mycorrhizal status, see Rinaldi et al. 2008 and Comandini et al. 2012). Only records clearly mentioning (potential) Halimium hosts were included in the data matrix (this includes records from mixed Cistus/Halimium stands). Evidence from studies on the morpho-anatomical and/or molecular characterization of ectomycorrhizae formed by fungal species on Halimium spp. were also inserted in the data set, excluding uncultured fungus sequences and fungal species not identified at least at genus level. In addition to studies concerning naturally occurring, field-collected mycorrhizae, data coming from synthesized mycorrhizae were also considered, although it must be stressed that associations induced in laboratory experiments may not occur under field conditions. Despite all efforts to cover as many bibliographic sources as possible, our literature survey might clearly be partial and incomplete. Reports of putative mycorrhizal relationships based solely on sporocarps associations rather than confirmed by direct inspection of ectomycorrhizae are obviously subject to an unquantifiable degree of error, especially when
more than one potential plant hosts are present (e.g., mixed *Halimium* stands with *Cistus, Pinus,* and/or *Quercus*). Finally, the identification of some fungi in the references that we have considered may not be correct.

**Results**

**The *Halimium* ectomycorrhizal guild**

Our effort to gauge the diversity of ectomycorrhizal fungi linked to *Halimium*, through both direct field sampling and the compendium of literature records, resulted in 154 listed entries, corresponding to 102 species belonging to 35 genera from Ascomycota, Basidiomycota, and Zygomycota (Table 1). This tally excludes a few cases of possible synonymy, e.g., *Inocybe halophila* R. Heim = *I. pruinosa* R. Heim and *Cantharellus cfr. pallens* = *C. subpruinosus* Eyssart. & Buyc, and the dubious record of *Lactarius subdulcis* (Pers.) Gray, a known *Fagus* symbiont whose sequence was probably misbranded and it is likely to be *L. hepaticus* Plowr. Fifty-seven of the listed records, which refer to 41 different species, were provided by our field work in *Halimium* plots in southwestern Sardinia, Italy; of these, 29 species are reported here for the first time as linked to *Halimium*. Most of the ecologically key ectomycorrhizal fungal genera are represented in the list, with *Russula* (13 species), *Amanita* (12 spp.), *Inocybe* (10 spp.), *Lactarius/Lactifluus* (9 spp., including the synthesized ECMs of *L. deliciosus* (L.) Gray, see below), and *Corinarius* (8 spp.), accounting for more than half of all species. As in other genera of Cistaceae (e.g., *Cistus* and *Helianthemum*), it is apparent from the entries in the list that hypogeous ascomycetes make a significant part of the *Halimium* ectomycorrhizal contingent (Table 1). Several *Terfezia* species, including the newly described *T. dunensis* Ant. Rodr., Cabero, Luque & Morte (Crous et al. 2019), were reported as associated with *Halimium*. In our plots, we isolated the ECMs formed by *Tuber oligospermum* Tul. & C. Tul. (Trappe) on *H. halimifolium* (see Fig. 3e), molecularly confirming the identity of host plant (data not shown). Belonging to the *Puberulum* group, or the so-called whitish truffles, *T. oligospermum* has been reported previously as a *Quercus* and *Cistus* mycobiont (Comandini et al. 2006; Lancellotti et al. 2016), and it is the first *Tuber* species ever to be proven to form ECMs with *Halimium*.

While the vast majority of records of *Halimium*-linked ectomycorrhizal fungi derives from aboveground observations of sporocarps, a fairly good number of collections and molecular characterizations of ECM tips have permitted to open a window on the belowground reality. In particular, the works conducted by Buscardo et al. (2012), de Carvalho (2016), and Carvalho et al. (2018) in *Pinus*-dominated forests with understorey shrubs in Portugal, and by Santolamazza-Carbone et al. (2019) in mixed shrublands in northwestern Spain, have resulted in the molecular identification of an array of ectomycorrhizal fungi in the *Halimium* spp. roots. These included *Cenococcum geophilum* Fr., *Terfezia* spp., *Amanita citrina* (Schaeff.:Fr.) Pers., *Amphimema* sp., *Descolea maculata* Bougher, *Hebeloma cistophilum* Maire, *Laccaria* spp., *Lactarius hepaticus*, *Rhizopogon* spp., *Russula* spp., *Scleroderma* spp., *Serendipita vermifera* (Oberw.) P. Roberts, *Thelephora terrestris* Ehrl., *Tomentella* spp., *Tomentellopsis* spp., and *Tyluspora* sp. (Table 1). In addition, Albuquerque-Martins et al. (2019) described the synthesized ECMs of *H. halimifolium* with *Tricholoma equestre* (L.:Fr.) P. Kumm., *T. portentosum* (Fr.) Quél, and *Lactarius deliciosus*. However, it is well-known that successful pure-culture synthesis of ectomycorrhizae not necessarily reflects naturally occurring partnerships between given host plant-mycobiont pairs (although *Halimium*-linked *T. equestre* has been collected also in the field). During our study, through random sampling of soil in the proximity of *H. halimifolium* shrubs, we isolated eleven distinct morphotypes (Table 1; Fig. 3). In six cases (*Astraeus hygrometricus* (Pers.) Morgan, *Lactarius hepaticus*, *Lactifluus rugatus* Kühn. & Romagn., *Russula odorata* Romagn., *Scleroderma meridionale*, and *Thelephora terrestris*), sporocarps of the same species were also collected. Five other species (*Tuber oligospermum*, *Inocybe* sp. 3, *Pisolithus* sp. 2, *Russula praetervisa* Sarnari, and *Russula* sp.) were collected only belowground. The full morphological characterization of selected morphotypes is under way, and will be presented in a complimentary work.

**Walking hand in hand with *Halimium***

Some of the mycorrhizal fungi we found associated with *Halimium* deserve a special mention and further notes. One of the most common ectomycorrhizal fungal species present in our *H. halimifolium* plots was *Scleroderma meridionale* (MycoBank MB#323250). Basidiomata of this species are large, globose, characterized by a smooth-to-finely furfuraceous peridium of an intense sulfur yellow color, which becomes brighter in the long pseudostipe, usually immersed deep in the soil (Fig. 4a). The habit is solitary, occasionally gregarious, found mostly in sandy soils and dunes. Originally described on the basis of collections from southern Portugal, continental France, Corsica, and Morocco, it occurs in all the Mediterranean basin, including Greece, Macedonia, and Turkey (Rusevska et al. 2014; Dimou et al. 2016). It is also reported from North America, from Florida to Arizona, and Oregon (Guzmán and Ovrebo 2000; Kuo 2004, http://www.svims.ca/council/Sclero.htm). However, the identity of these collections still awaits confirmation: indeed, preliminary molecular data seem to indicate that the North American “*S. meridionale*” belongs to a distinct, so far undescribed, taxon (D. Puddu, M. Leonardi, A.C. Rinaldi, unpublished data).
Based on field observations, *S. meridionale* has been reported as associated with both evergreen and deciduous species of *Quercus*, *Pinus*, and also *Cistus* (Comandini et al. 2006; Phosri et al. 2009; Dimou et al. 2016). We recently described the morpho-anatomical features of the ectomycorrhizae formed by *S. meridionale* on *H. halimifolium*, with the help of confocal laser scanning microscopy; the mycobiont and host plant identity from the ECM root tips were verified through molecular tools (Leonardi et al. 2018). This was the first description of an ectomycorrhiza on *Halimium*. The features of this ECM—flely mantle surface, whitish with silver patches, mantle surface characterized by a network of branched hyphae organized in hyphal bundles, small dimension of mycorrhizal system—are similar to those reported for the few described naturally occurring *Scleroderma* ECMs and to other ECMs formed by *Cistaceae* (Leonardi et al. 2018).

Another interesting species recorded in our collection site was *Alessioporus ichnusanus* (MB#808530). The taxon corresponds to a boletoid species recently segregated from *Xerocomus* Quél. to typify the new genus *Alessioporus* Gelardi, Vizzini & Simonini which currently accommodates two species. Its type and epitype were collected in Sardinia in 1980 (Galli 1981) and in 2003 (Gelardi et al. 2014), respectively, in *Quercus* spp. and *Cistus* spp. forests, in the province of Medio Campidano, 60 km from our *Halimium* plots. In addition to the type collections, the taxon has been recorded in different localities in Sardinia, as well as in Sicily, continental Italy (Brotzu 1988; Alessio 1991; Brotzu and Colomo 2009; Gelardi 2010; Illice et al. 2011) and other Mediterranean countries, as France (Eyssartier and Roux 2011), Greece (Polimis et al. 2012), and Spain (Muñoz 2005). *Alessioporus ichnusanus* can be recognized by the ochraceous-brown, dark olive-brown to copper-brown pileus with brownish-black fibrils (Fig. 4b). But one of the most important morphological character that define this species is a narrow pseudo-anululus in the middle part of the stipe formed by the remnants of the connection between the pileus margin and the stipe cortex during the primordial stage (Galli 2013). Currently, *Alessioporus ichnusanus* is considered an uncommon or rare species that has recently been included in the Red List of Italian macrofungi as an endangered species (Rossi et al. 2013) and in the IUCN red list as vulnerable (Persiani 2019; Angelini et al. 2020).

Keeping with the Boletales, *Gyroporus pseudolacteus* G. Moreno, Carlavilla, Heykoop, Manjón & Vizzini (MycoBank MB#356882) is an interesting finding. This species has been recently described from a material collected in Spain, on sandy soil under *Pinus pinaster* (Crous et al. 2016). To the best of our knowledge, this is the first confirmed record of this species not only for Sardinia but also for Italy. *Gyroporus pseudolacteus* can be distinguished from the common and closely related *Gyroporus cyanescens* (Bull.) Quél. by its larger habit, the longer stipe in relation to the pileus diameter, and the “deep and persistently indigo blue when handled or bruised” (Crous et al. 2016) (Fig. 4c). According to Vizzini and co-workers, *G. cyanescens* should be considered a complex of cryptic species (Vizzini et al. 2015) which is being unraveled with the help of molecular tools (see Crous et al., 2017), even though some of these taxa are still being treated as synonyms by some fungal names databases. While this is the first mention of *Halimium* as the probable host, the putative association of *Gyroporus* with cistaceous plants is not unprecedented. Although the six (not universally accepted) known European species of *Gyroporus*—*G. ammophilus* (M.L. Castro & L. Freire) M.L. Castro & L. Freire; *G. castaneus* (Bull.) Quél.; *G. cyanescens*; *G. lacteus* Quél.; *G. pseudocyanescens* G. Moreno, Carlavilla, Heykoop, Manjón & Vizzini; and *G. pseudolacteus*—are usually reported from under coniferous (*Pinus*) or deciduous (*Castanea, Fagus, Quercus*) hosts (Vizzini et al. 2015; Crous et al. 2016, 2017), *G. ammophilus* was found along the Atlantic coast of the Iberian Peninsula “on fixed dunes in association with *Pinus* spp., or, less frequently with other trees and shrubs, such as *Quercus suber* L. and *Cistus salviaefolius* (sic!), on sandy soils” (Castro and Freire 1995).

*Lactarius hepaticus* (MycoBank MB#224000) was, by far, the most common milkcap in our *Halimium* stands (Fig. 4d). This was an unexpected finding, since this species belonging to the subgenus *Russularia* is commonly associated with *Pinus* and, more occasionally, other conifers such as *Picea* and *Pseudotsuga* (Heilmann-Clausen et al. 1998; Basso 1999). Uncommon to rare/absent in northern Europe is more frequent in Britain, the Netherlands, and, above all, in the Mediterranean area. This species is characterized by its convex to planar with a depressed center cap, with liver-brown color (hence the epithet); the milk is white, turning yellow on a tissue (Pierotti 2005). Intriguingly, in central Portugal, *L. hepaticus* was part of shared ECM networks between understory shrubs and pine trees in a *Pinus*-dominated forest, being detected with molecular tools on the roots of both *Pinus pinaster* and *Halimium lasianthum* and *H. ocyoides* (Lam.) Willk. (Buscardo et al. 2012). Along the coastal area in Sardinia, where our *Halimium* plots are situated, *Pinus* stands are also frequent, originated from extensive reforestation plans carried out during the last century. We collected *L. hepaticus* in these stands as well, where *H. halimifolium* is frequent both in the understory and at the edges of the pine forest. *Lactarius hepaticus* was abundant as sporocarps among *Halimium* shrubs and on their roots in proximity of *Pinus*, confirming the existence of shared ECM networks, but it occurred also in pure *Halimium* plots distant several kilometers from pine trees stands, in areas where *Pinus*, at the best of our knowledge, has never been present. This suggests colonization of new ECM plant hosts (like *Halimium*) by *L. hepaticus* by means other than root networking, such as spore dispersal. More work is underway to investigate *L. hepaticus* ecological plasticity.
Lactifluus brunneoviolascens (Bon) Verbeken (MycoBank MB#564601) is another uncommon species, reported here for the second time in Sardinia (see Lalli and Pacioni 1992). It was previously named L. luteolus Peck, which is now known to be the correct name for a North American species (Verbeken et al. 2012; De Crop et al. 2017). Both species belong to the newly erected section Phlebonemi (R. Heim ex Verbeken) Verbeken (= Lactarius subsect. Luteoli Pacioni & Lalli) (Verbeken et al. 2012). Lactifluus brunneoviolascens is easily distinguished in the field by the whitish/whitish-cream color of the pileus, with velvety cuticle, dry even in very humid weather, finely crenulated at the edge, stained ochre-brown with age; the context is firm, whitish then darker ochre-brownish, with a sweet taste and an unpleasant fishy smell; the latex is fluid, abundant, opalescent white, immutable if isolated on glass, slowly but strongly browning in contact with the lamellae or on absorbent paper (Fig. 4e). We studied two different collections of this Lactifluus from almost pure H. halimifolium stands. Another collection was recently recorded from southeastern Sardinia, under Quercus (Alberto Mua, personal communication), a more usual habitat (sometimes it also occurs in mixed Quercus-Pinus forests) for this species with a prevalently Mediterranean distribution that prefers dry and sandy soils (Basso 1999; Pierotti 2002).

Among the various Cortinarius species encountered during this study and likely linked to Halimium, Cortinarius coeruleopallescens Contu (MycoBank MB#459976) deserves a mention (Fig. 4f). This taxon, not uncommon in our plots, was described in 1999, when Marco Contu raised to species level a fungus he encountered in Sardinia, and that had been observed by other researchers 2 years earlier in Spain and originally thought to be a variety of C. croceocoeruleus (Pers.) Fr., C. croceocoeruleus var. meridionalis Bidaud, A. Ortega & Mahiques (Ortega et al. 1997; Contu 1999). The collections from both Spain and Sardinia were associated with Cistus, while C. croceocoeruleus is typical of central European coniferous and broadleaved forests. Another species linked to Halimium and worthy of remark is Cortinarius cedretorum var. halimiorum Brotzu & Peintner (Mycobank MB#580057) (Table 1). This beautiful variety in the subgenus Phlegmacium was described (originally reported in a field guide as C. halimiorum; see Brotzu and Colomo 2009) on the basis of material collected on a dune system in the northeastern part of Sardinia (Brotzu and Peintner 2009). Despite the fact that the vegetation system in this case is more complex than the one present in our H. halimifolium stands, with psammophile coastal associations where H. halimifolium is present together with other floristic entities, such as Cistus spp., Pistacia lentiscus L., Juniperus phoenicea L., and Arbutus unedo L. (see Arrigoni 1996), the link between this specific Cortinarius and Halimium was apparent to the researchers (Brotzu and Peintner 2009).
Discussion

Using the dataset assembled in Table 1, it is not straightforward to compare the above- and belowground composition of Halimium-linked ECM fungal communities. It should be remarked, indeed, that the dataset contains records from studies conducted with different goals and methodologies. For example, with the exception of the present work, studies providing ECM records did not consider sporocarps at all (Buscardo et al. 2012; de Carvalho 2016; Carvalho et al. 2018; Santolamazza-Carbone et al. 2019). Conversely, many sporocarp observations are derived from surveys that disregarded belowground views. It is technically easier to collect and identify sporocarps than ECMs, and belowground diversity tends to be undersampled. To get a clearer picture of soil and root fungal communities in Halimium scrublands, we started an ongoing metabarcoding project in our Sardinian Halimium stands. Preliminary results show the presence on Halimium roots of additional ECM genera, such as Geopora, Helvella, and Wilcoxina, and species, like Astraeus telleriae M.P. Martin, Phosri & Watling (Geml et al., unpublished data). This study, when complete, will render a more complete view of the composition of belowground ECM community and its correlation with aboveground diversity.

So far, no Halimium-specific or preferential ECM mycobiont has emerged, with the possible exception of Cortinarius cedretorum var. halimiorum Brotzu & Peintner. However, since our knowledge of this host plant and its ECM guild is rudimental, this ecological liaison will most likely be recognized in the near future, possibly accompanied by the description of new fungal species. Our failure to identify a perfect molecular match for several of the sequences obtained during this study supports this speculation. Nearly 40% of the species listed in Table 1 (41, counting Terfezia spp.) have been previously reported as Cistus-associated (see Comandini et al. 2006; Loizides 2016). This includes well-known “Cistus-specific” mycobionts, such as Amanita cistetorum Contu & Pacioni, Hebeloma cistophilum, Lactarius cistophilus Bon & Trimbach, Lactarius tesquorum Malençon (see Nuytinck et al. 2004; Comandini and Rinaldi 2008), and Leccinellumcorsicum (Rolland) Bresinsky & Manfr. Binder. Given the Halimium-Cistus phylogenetic affinity, and the co-occurrence of the two host plants in many ecological settings, the extensive ECM sharing is not particularly surprising, at least when the concept of host-specificity is applied at the plant family level (Cistaceae). Another cluster of Halimium mycobionts are also linked to Quercus, on the basis of a number of field observations (Leonardi et al. 2016; Comandini et al. 2018). This group includes Alessioporus ichnusanus (Alessio, Galli & Littini) Gelardi, Vizzini & Simonini (also known to be associated to a lesser extent, with Cistus spp.); Hortiboletus rubellus (Krombh.) Simonini, Vizzini & Gelardi; Xerocomellus redeuilhii A.F.S. Taylor, U. Eberh., Simonini, Gelardi & Vizzini; Lactifluus rugatus; and Scleroderma meridionale. Finally, a bunch of Halimium symbionts are shared with Pinus, as demonstrated in studies carried out in Portugal (Buscardo et al. 2012; de Carvalho 2016; Carvalho et al. 2018). Again, “host-specific” Pinus mycobionts, such as Rhizopogon spp., Russula sardonia Fr. (= Russula drimeia Cooke), and Lactarius hepaticus, were detected on both Halimium and Pinus roots, together with
more generalist fungal species like *Serendipita vermifera* (Oberw.) P. Roberts, *Thelephora terrestris*, and *Tomentella terrestris* (Berk. & Broome) M.J. Larsen. In the study in central Portugal by Buscardo and colleagues, it is showed that about 30% of the identified ECM fungal species were common to pine and *Halimium* spp., with shared ECM fungal species representing up to 80% of the total fungal abundance in some stands (Buscardo et al. 2012). To expand even further the plasticity of *Halimium* as ECM host plant, *H. lasianthum* was shown to establish symbiotic interactions with the Australian *Descolea maculata* Bougher in Spain, spreading from nearby *Eucalyptus* plantations (Santolamazza-Carbone et al. 2019). In Corsica, *H. halimifolium* was reported to have a contingent of 12 ECM fungal species, shared in different proportions with *Cistus*, *Quercus*, and *Pinus*, but also with other host plants like *Castanea*, *Fagus*, *Corylus*, *Populus*, *Salix*, *Alnus*, *Betula*, and *Abies* (Taudiere et al. 2015).

The ability of *Cistaceae* to develop common mycelial networks by sharing ECM fungal partners with neighboring plants is a crucial ecological trait that has not been appropriately appreciated. As stressed by Randy Molina and Thomas Horton, “common mycelial networks (CMNs) of mycorrhizal fungi connecting neighboring host plants affect ecosystem processes and community dynamics including seedling establishment, plant succession, and ecosystem resiliency” (Molina and Horton 2015). Based on our current knowledge of *Halimium* and *Cistus* ECM communities, it is apparent that these are largely shaped by “ecological specificity” rather than host-specificity. Despite the fact that both genera have host preferential (or even exclusive) fungal partners, large part of their mycorrhizal associations seem rather driven by environmental (soil composition, for example) and biological factors, like the presence of other host plants in the same or neighboring areas, thus going beyond host-fungus genetic compatibility due to co-evolution. Either in pure shrublands, as in our Sardinian stands, or at the edges or in the understory of *Quercus* and *Pinus* forests, especially when growing on poor and/or degraded soils, *Halimium* might thus play a key ecological role, maintaining ECM fungal diversity, favoring vegetation succession and dynamics, and assisting ecosystem resilience following disturbance, thanks to common mycelial networks and possibly spore dispersal of ECM mycobionts. A similar function has been recognized for *Cistus*. In Spain, many of the fungal species associated with *Cistus ladanifer* L. were found to be shared with *Pinus pinaster* Alton, suggesting a role in the regeneration of *Pinus* stands after wildfire (Martín-Pinto et al. 2006). In this context, it is relevant to note that *Cistus* and possibly *Halimium* are dual-mycorrhizal plants, capable of hosting both arbuscular mycorrhizal and ectomycorrhizal associations. Several early successional ECM hosts like *Alnus*, *Populus*, and *Salix* share this feature. In the Mediterranean ecosystem, *Cistaceae* definitely play a major role in secondary succession following major disturbances like fire (or even human activity). Benefits deriving from dual-mycorrhizal colonization thus extend from interested plants—endowed with greater survival, growth, and nutrient uptake—to ecosystems, favoring establishment and improving survival on adverse sites of connected ECM plants (Teste et al. 2020).

**Conclusions**

We are just starting to unveil the complexity of *Halimium* mycorrhizal biology and ecology, especially for what concerns host-specificity of associated mycobionts and patterns of shared mycorrhizal networks with neighboring host plants. The general poor knowledge of *Halimium* as an ectomycorrhizal host has led to relatively few records of potentially associated fungal species based on observations of sporocarp occurrence. Hopefully, this and other works will increase the awareness of researchers, providing us in the near future with fresh data coming from fungal forays. Also, well-planned molecular studies examining mycorrhizal specificity at the root tip scale are bound to disclose many details of the structure and dynamics of *Halimium*-linked ectomycorrhizal communities in multiple ecological settings.

**Funding** Open access funding provided by Università degli Studi di Cagliari within the CRUI-CARE Agreement. ANMF was supported by Coordenação de Aperfeiçoamento Pessoal de Nível Superior—Brazil—Finance Code 001 (CAPES-DS and PDSE fellowship grants).

**Data availability** All associated data are deposited in public repositories.

**Compliance with ethical standards**

**Conflict of interest** The author declares that they have no conflict of interest.

**Ethics approval** not applicable.

**Consent to participate** not applicable.

**Consent to publication** not applicable.

**Code availability** not applicable

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.
islands of Naxos and Amorgos (Cyclades, Greece). Ann Bot Fenn 49:145–161

Rinaldi AC, Comandini O, Kuyper TW (2008) Ectomycorrhizal fungal diversity: separating the wheat from the chaff. Fungal Divers 33:1–45

Rossi G, Montagnani C, Gargano D, Peruzzi L, Abeli T, Ravera S, Cogoni A, Fenu G, Magrini S, Gennai M, Foggi B, Wagensommer RP, Venturella G, Blasi C, Raimondo FM, Orsenigo S. (2013) Lista Rossa della Flora Italiana. 1. Policy Species e altre specie minacciate. Comitato Italiano IUCN e Ministero dell’Ambiente e della Tutela del Territorio e del Mare. Roma, Italy: Stamperia Romana

Rundel PW, Cowling RM (2013) Mediterranean-climate ecosystems. In: Levin SA (ed.) Encyclopedia of biodiversity, 2nd ed.: 212–222

Rusevska K, Karadelevi M, Phosri C, Dueñas M, Watling R, Martin MP (2014) Rechecking of the genus Scleroderma (Gasteromycetes) from Macedonia using barcoding approach. Turk J Bot 38:375–385

Santolamazza-Carbone S, Durán-Otero M, Calviño-Cancela M (2019) Context dependency, co-introductions, novel mutualisms, and host shifts shaped the ectomycorrhizal fungal communities of the alien tree Eucalyptus globulus. Sci Rep 9:7121

Smith SE, Read DJ (1997) Mycorrhizal symbiosis. Academic Press, San Diego

Soriano I (2008) Algunos tipos de cistáceas béticas y rifeñas de los herbarios BC, MA y MAF. Collectanea Botanica (Barcelona) 27: 29–35

Taudiere A, Munoz F, Lesne A, Monnet A-C, Bellanger J-M, Selosse M-A, Moreau P-A, Richard F (2015) Beyond ectomycorrhizal bipartite networks: projected networks demonstrate contrasted patterns between early- and late-successional plants in Corsica. Front Plant Sci 6:881

Tedersoo L, Jairus T, Horton BM, Abarenkov K, Suvi T, Saar I, Kõljalg U (2008) Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. New Phytol 180:479–490

Teste FP, Jones MD, Dickie IA (2020) Dual-mycorrhizal plants: their ecology and relevance. New Phytol 225:1835–1851

Verbeek A, Van de Putte K, De Crop E (2012) New combinations in Lactifluus. 3. L. subgenera Lactifluus and Piperati. Mycotaxon 120: 443–450

Vidal JM, Vila J, Garcia F, Perez-Jarauda T (1997) Algunos hongos hipogeos de Castilla-León (España): Youngiomycetes multiplex y Genea thaxterii, primeras citas para Europa. Revista Catalana de Micologia 20:85–98

Vidal JM, Calonge FD, Martin MP (2002) Macowanites ammonophilus (Russulales), a new combination based on new evidences. Revista Catalana de Micologia 24:69–74

Vidal JM, Alvarado P, Loizides M, Konstantinidis G, Chachula P, Mlezko P, Moreno G, Vizzini A, Krakhnualniy M, Paz A, Cabero J, Kaounas V, Slavova M, Moreno-Arroyo B, Llistosella J (2019) A phylogenetic and taxonomic revision of sequestrate Russulaceae in Mediterranean and temperate Europe. Persoonia 42:127–185

Vizzini A, Angelini C, Ercole E (2015) Molecular confirmation of Gyroporus lacteus and typification of Boletus cyanescens. Phytotaxa 226:27–38

White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR protocols: a guide to methods and applications. Academic Press, San Diego, pp 315–322

Zunzunegui M, Díaz Barradas MC, Aguilar F, Ain Lhout F, Clavijo A, García Novo F (2002) Growth response of Halimium halimifolium at four sites with different soil water availability regimes in two contrasted hydrological cycles. Plant Soil 247:271–281

Zunzunegui M, Ain-Lhout F, Díaz Barradas MC, Álvarez-Cansino LA, Esquivias MP, García Novo F (2009) Physiological, morphological and allocation plasticity of a semi-deciduous shrub. Acta Oecol 35: 370–379

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.