



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

Marco Leonardi¹ · Ariadne Nóbrega Marinho Furtado² · Ornella Comandini³ · József Geml⁴ · Andrea C. Rinaldi⁵

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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

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✉ Andrea C. Rinaldi
rinaldi@unica.it

¹ Department of Life, Health and Environmental Sciences, University of L’Aquila, I-67100 Coppito, AQ, Italy

² Departamento de Botânica, Campus Universitário Reitor João David Ferreira Lima Centro de Ciências Biológicas, Universidade Federal de Santa Catarina, Trindade, Florianópolis, SC 88040-960, Brazil

³ Department of Life Sciences and the Environment, University of Cagliari, I-09042 Monserrato, CA, Italy

⁴ MTA-EKE Lendület Environmental Microbiome Research Group, Eszterházy Károly University, Leányka u. 6., Eger H-3300, Hungary

⁵ Department of Biomedical Sciences, University of Cagliari, I-09042 Monserrato, CA, Italy

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 *Crocantemum 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 be 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.

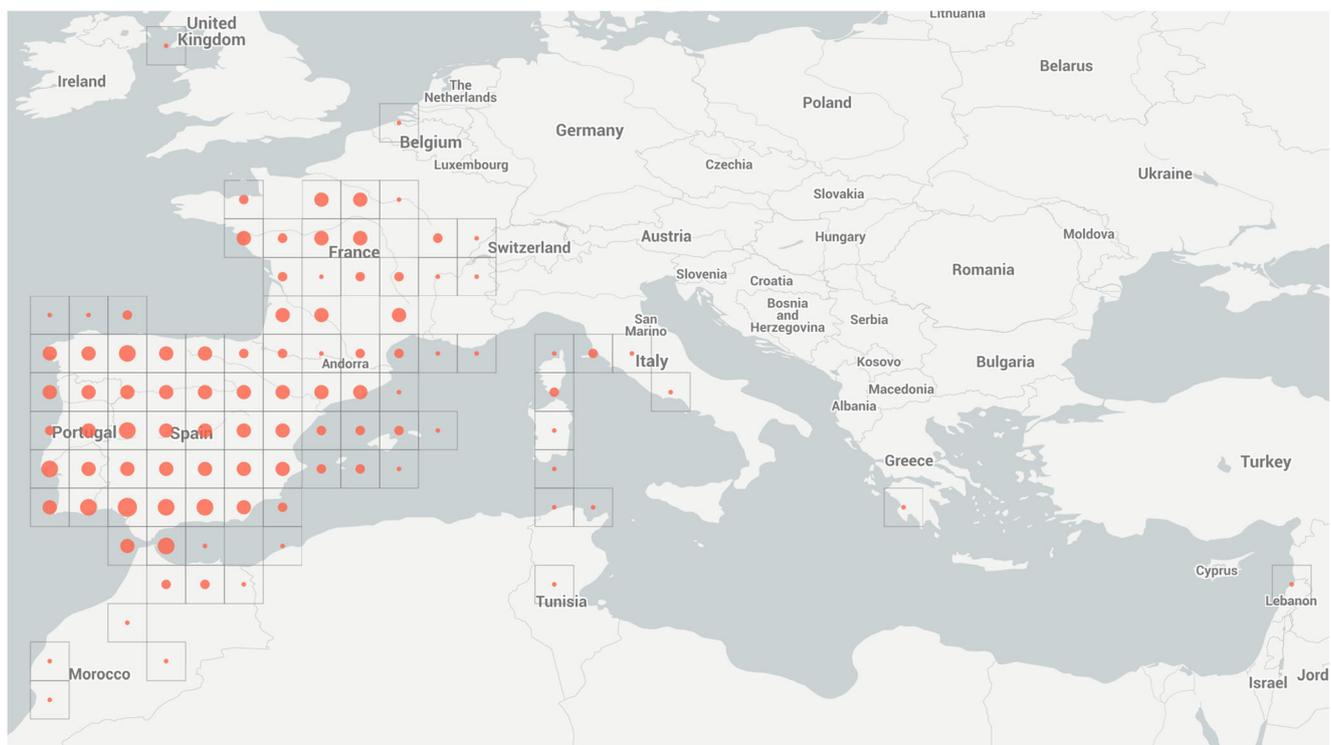


Fig. 1 Distribution map of *Halimium* spp. Occurrence data from the Global Biodiversity Information Facility (<https://www.gbif.org/>)

Materials and methods

Collecting site and fungal sampling

Sporocarps of ectomycorrhizal fungi were harvested in a costal 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 salvifolius* 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

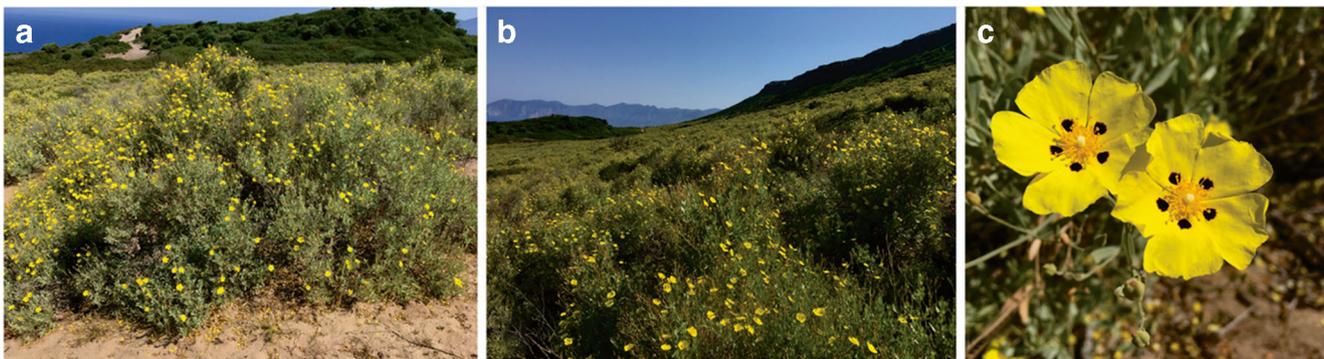


Fig. 2 *Halimium halimifolium*, Cistaceae, in southwestern Sardinia. **a** Plant in blossom. **b** View of ECM collection stand. **c** Flower close-up

Table 1 Ectomycorrhizal fungi reported to be associated with *Halimium* spp.

Species	Host (<i>Halimium</i>)	Reference	Sequence
Ascomycota			
<i>Cenococcum geophilum</i> Fr.	<i>H. lasianthum</i> ,	Buscardo et al. 2012 (ECM)	HQ625444
	<i>H. ocymoides</i>		
<i>Terfezia boudieri</i> Chatin ^a	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	KY595999
	<i>H. halimifolium</i>		
	<i>H. halimifolium</i>		
<i>Terfezia dunensis</i> Ant. Rodr., Cabero, Luque & Morte	<i>H. halimifolium</i>	Chevalier 2014	MN438324
<i>Terfezia</i> spp.	<i>H. halimifolium</i>	Crous et al. 2019	
<i>Terfezia</i> sp. 1	<i>H. halimifolium</i>	Chatin 1891	HQ625472
<i>Terfezia</i> sp. 2	<i>H. ocymoides</i>	Olaizola Suárez et al. 2012	
<i>Tuber oligospermum</i> Tul. & C. Tul. (Trappe) ^{b#}	<i>H. lasianthum</i>	Buscardo et al. 2012 (ECM)	HQ625473
	<i>H. halimifolium</i>	This study (ECM)	MT594491
Basidiomycota			
<i>Alessioporus ichnusuanus</i> (Alessio, Galli & Littini) Gelardi, Vizzini & Simonini [#]	<i>H. halimifolium</i>	This study	MT594492
<i>Amanita cistetorum</i> Contu & Pacioni*	<i>H. halimifolium</i>	Moreau et al. 2007a, Moreau et al. 2007b	HQ625456
<i>Amanita citrina</i> (Schaeff.:Fr.) Pers.	<i>H. halimifolium</i>	Moreau et al. 2007a	
	<i>H. ocymoides</i>	Buscardo et al. 2012 (ECM)	
<i>Amanita curtipes</i> E.-J. Gilbert f. <i>curtipes</i> [#]	<i>H. halimifolium</i>	Moreau et al. 2007a	MT594493
<i>Amanita gilbertii</i> Beauseign [#]	<i>H. halimifolium</i>	This study	
<i>Amanita gracilior</i> Bas & Honrubia	<i>Halimium</i> sp.	Moreno-Arroyo 2004	Taudiere et al. 2015
<i>Amanita malleata</i> (Piane ex Bon) Contu	<i>H. halimifolium</i>	Taudiere et al. 2015	
<i>Amanita muscaria</i> var. <i>inzengae</i> Neville & Poumarat [#]	<i>H. halimifolium</i>	Moreau et al. 2007a	MT594494
<i>Amanita pantherina</i> (D.C.:Fr.) Krombh [#]	<i>H. halimifolium</i>	Moreau et al. 2007a	
<i>Amanita ponderosa</i> Malençon & R. Heim [#]	<i>Halimium</i> sp.	Moreno-Arroyo 2004	KY595998
<i>Amanita rubescens</i> (Pers.:Fr.) Gray [#]	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
<i>Amanita torrendii</i> Justo [#]	<i>Halimium</i> sp.	Moreno-Arroyo 2004 ^c	EU231946
<i>Amanita vaginata</i> f. <i>alba</i> (Bull.) Vesely	<i>H. halimifolium</i>	Taudiere et al. 2015	
<i>Amphinema</i> sp.	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	MT594497
<i>Astraeus hygrometricus</i> (Pers.:Pers.) Morgan [#]	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
	<i>H. halimifolium</i>	Moreau et al. 2007a	MT594495
	<i>H. halimifolium</i>	This study	
	<i>H. halimifolium</i>	This study (ECM)	MT594496
<i>Boletus aereus</i> Bull.:Fr. [#]	<i>H. alyssoides</i>	Martínez de Azagra Paredes et al. 1998	
	<i>H. lasianthum</i>		
	<i>H. ocymoides</i> ,		
	<i>H. viscosum</i>	Oria-De-Rueda et al. 2008, 2009	
<i>Boletus edulis</i> Bull.:Fr. [#]	<i>H. halimifolium</i>	Moreau et al. 2007a	EU231946
	<i>H. lasianthum</i>	Oria-De-Rueda et al. 2005, 2008, 2009	
	<i>H. alyssoides</i>	Dentinger et al. 2010	
<i>Boletus</i> sp.	<i>H. halimifolium</i>	This study	MT594497
<i>Cantharellus</i> cfr. <i>pallens</i> Pilát	<i>H. halimifolium</i>	This study	MT594498
<i>Cantharellus subpruinus</i> Eyssart. & Buyck ^d	<i>H. halimifolium</i>	Moreau et al. 2007a	
<i>Coltricia perennis</i> (L.:Fr.) Murrill	<i>H. halimifolium</i>	Moreau et al. 2007a	MT594499
<i>Coltricia</i> cfr. <i>perennis</i> (L.:Fr.) Murrill	<i>H. halimifolium</i>	This study	
	<i>H. halimifolium</i>	This study	MT594499
<i>Cortinarius candularis</i> Fr.	<i>H. halimifolium</i>	This study	MT594500
<i>Cortinarius cedretorum</i> var. <i>halimiorum</i> Brotzu & Peintner	<i>H. halimifolium</i>	Brotzu and Peintner 2009	AY900018 ^e
<i>Cortinarius coeruleopallescens</i> Contu*	<i>H. halimifolium</i>	This study	MT594501
<i>Cortinarius maculatocaesпитosus</i> Bidaud	<i>H. halimifolium</i>	This study	MT594502
	<i>H. halimifolium</i>	This study	MT594503
<i>Cortinarius palazonianus</i> Vila, A. Ortega & Fern.-Brime	<i>H. halimifolium</i>	Fernandez-Brime et al. 2014	MT594504
<i>Cortinarius rigens</i> (Pers.) Fr.	<i>H. halimifolium</i>	This study	
<i>Cortinarius scobinaceus</i> Malençon & Bertault*	<i>H. halimifolium</i>	Moreau et al. 2007a ^f , Moreau et al. 2007b	

Table 1 (continued)

Species	Host (<i>Halimium</i>)	Reference	Sequence
<i>Cortinarius variiformis</i> Malençon [#]	<i>H. halimifolium</i>	This study	MT594505
	<i>H. halimifolium</i>	This study	MT594506
<i>Descolea maculata</i> Bougher ^g	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	KY654754
<i>Gyroporus pseudolacteus</i> G. Moreno, Carlavilla, Heykoop, Manjón & Vizzini	<i>H. halimifolium</i>	This study	MT594507
<i>Hebeloma cistophilum</i> Maire*	<i>H. halimifolium</i>	Moreau et al. 2007a, Moreau et al. 2007b, Eberhardt et al. 2009	
	<i>H. halimifolium</i>	This study	MT594508
	<i>H. lasianthum</i> , <i>H. ocymoides</i>	Buscardo et al. 2012 (ECM)	HQ625447
<i>Hebeloma cylindrosporium</i> Romag. [#]	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
<i>Hebeloma dunense</i> L. Corb. & R. Heim	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
<i>Hortiboletus rubellus</i> (Krombh.) Simonini, Vizzini & Gelardi	<i>H. halimifolium</i>	This study	MT594509
<i>Hygrophorus chrysodon</i> (Batsch:Fr.) Fr. [#]	<i>H. halimifolium</i>	This study	MT594510
<i>Hygrophorus</i> cfr. <i>eburneus</i> (Bull.) Fr. [#]	<i>H. halimifolium</i>	This study	MT594511
<i>Inocybe asterospora</i> Quél.	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
	<i>H. halimifolium</i>		
<i>Inocybe calida</i> Velen.	<i>H. halimifolium</i>	Moreno-Arroyo 2004 ^h	
<i>Inocybe corydalina</i> Quél.	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
<i>Inocybe halophila</i> R. Heim. ⁱ	<i>H. halimifolium</i>	Moreau et al. 2007a, Moreau et al. 2007b	
<i>Inocybe lacera</i> (Fr.) P. Kumm.	<i>H. halimifolium</i>	Moreno-Arroyo 2004	
<i>Inocybe pruinoso</i> R. Heim [#]	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
<i>Inocybe tigrina</i> Heim	<i>H. halimifolium</i>	This study	MT594512
	<i>H. halimifolium</i>	This study	MT594513
	<i>H. halimifolium</i>	This study	MT594514
<i>Inocybe</i> sp. 1	<i>H. halimifolium</i>	This study	MT594515
<i>Inocybe</i> sp. 2	<i>H. halimifolium</i>	This study	MT594516
<i>Inocybe</i> sp. 3	<i>H. halimifolium</i>	This study (ECM)	MT594517
	<i>H. halimifolium</i>	This study (ECM)	MT594518
<i>Laccaria bicolor</i> (Maire) P.D. Orton [#]	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	KY655010
<i>Laccaria proxima</i> (Boud.) Pat.*	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
<i>Laccaria</i> sp.	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	KY655006
<i>Lactarius cistophilus</i> Bon & Trimbach*	<i>H. halimifolium</i>	Leonardi et al. 2018	KU885433
	<i>H. halimifolium</i>	This study	MT594519
<i>Lactarius deliciosus</i> (L.) Gray	<i>H. halimifolium</i>	de Carvalho 2016 (sECM), Albuquerque-Martins et al. 2019 (sECM)	
<i>Lactarius giennensis</i> (Mor.-Arr. et al.) Pierotti [#]	<i>H. alyssoides</i> , <i>H. ocymoides</i>	Vidal et al. 2019	
<i>Lactarius hepaticus</i> Plowr. ¹	<i>H. lasianthum</i> , <i>H. ocymoides</i>	Buscardo et al. 2012 (ECM)	HQ625465
	<i>H. halimifolium</i>	This study	MT594520
	<i>H. halimifolium</i>	This study (ECM)	MT594521
	<i>H. halimifolium</i>	This study (ECM)	MT594522
<i>Lactarius pseudoscrobiculatus</i> Basso, Neville & Poumarat	<i>H. halimifolium</i>	Moreau et al. 2007a	
<i>Lactarius subdulcis</i> (Pers.) Gray [?]	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	KY681468
<i>Lactarius tesquorum</i> Malençon*	<i>H. halimifolium</i>	This study	MT594523
<i>Lactifluus brunneoviolascens</i> (Bon) Verbeke	<i>H. halimifolium</i>	Leonardi et al. 2018	KU885434 ^m
	<i>H. halimifolium</i>	This study	
<i>Lactifluus rugatus</i> Kühn. & Romagn. [#]	<i>H. halimifolium</i>	This study	MT594524
	<i>H. halimifolium</i>	This study (ECM)	MT594525
<i>Leccinellum corsicum</i> (Rolland) Bresinsky & Manfr. Binder*	<i>H. halimifolium</i>	Moreau et al. 2007a ⁿ	
	<i>H. halimifolium</i>	This study	MT594526
	<i>H. halimifolium</i>	This study	MT594527
<i>Paxillus ammoniavirescens</i> Contu & Dessi [#]	<i>H. halimifolium</i>	This study	MT594528
<i>Pisolithus arrhizus</i> (Scop.) Rauschert [#]	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
	<i>H. halimifolium</i>	Moreau et al. 2007a	
<i>Pisolithus</i> sp. 1 ^o	<i>H. halimifolium</i>	This study	MT594529

Table 1 (continued)

Species	Host (<i>Halimium</i>)	Reference	Sequence
<i>Pisolithus</i> sp. 2	<i>H. halimifolium</i>	This study (ECM)	MT594530
<i>Rhizopogon luteolus</i> Fr. [#]	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
	<i>H. ocymoides</i>	Buscardo et al. 2012 (ECM)	HQ625448
<i>Rhizopogon roseolus</i> (Corda) Th. Fr. [#]	<i>H. ocymoides</i>	Buscardo et al. 2012 (ECM)	HQ625451
<i>Russula ammophila</i> (J.M. Vidal & Calonge) Trappe & T.F. Elliott	<i>Halimium</i> sp.	Moreno-Arroyo 2004 ^P	
	<i>Halimium</i> sp.	Moreno-Arroyo et al. 2005 ^P	
	<i>Halimium</i> sp.	Vidal et al. 2002 ^P	AJ438037
	<i>Halimium</i> sp.	Vidal et al. 2019	MK105623
	<i>H. halimifolium</i>	Vidal et al. 2019	
<i>Russula amoenicolor</i> Romagn.	<i>H. halimifolium</i>	Moreau et al. 2007a	
<i>Russula cistoadelpha</i> M.M. Moser & Trimbach*	<i>H. halimifolium</i>	This study	
<i>Russula densifolia</i> Secr. ex Gillet	<i>H. lasianthum</i>	Buscardo et al. 2012 (ECM)	HQ625470
<i>Russula littoralis</i> Romagn.	<i>H. halimifolium</i>	Moreau et al. 2007a	
<i>Russula monspeliensis</i> Sarnari*	<i>H. halimifolium</i>	This study	MT594531
<i>Russula odorata</i> Romagn. [#]	<i>H. halimifolium</i>	This study	MT594532
	<i>H. halimifolium</i>	This study	MT594533
	<i>H. halimifolium</i>	This study	MT594534
	<i>H. halimifolium</i>	This study (ECM)	MT594535
<i>Russula praetervisa</i> Sarnari [#]	<i>H. halimifolium</i>	This study (ECM)	MT594536
<i>Russula sardonica</i> Fr.	<i>H. ocymoides</i>	Buscardo et al. 2012 (ECM) ^q	HQ625452
<i>Russula tyrrhenica</i> Sarnari*	<i>H. halimifolium</i>	Moreau et al. 2007a	
<i>Russula vinaceodora</i> (Calonge & J.M. Vidal) Trappe & T.F. Elliott	<i>Halimium</i> sp.	Moreno-Arroyo et al. 2005 ^t	
	<i>Halimium</i> sp.	Vidal et al. 2002 ^P , Vidal et al. 2019	AJ438034
<i>Russula</i> sp.	<i>H. halimifolium</i>	Carvalho et al. 2018 (ECM)	LT746014
<i>Russula</i> sp. 1	<i>H. halimifolium</i>	This study (ECM)	MT594537
<i>Scleroderma citrinum</i> Pers.	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	KY694393
<i>Scleroderma meridionale</i> Demoulin & Malençon [#]	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
	<i>H. halimifolium</i>	Leonardi et al. 2018	MG264160
	<i>H. halimifolium</i>	Leonardi et al. 2018 (ECM)	MG367369
	<i>H. halimifolium</i>	This study	MT594538
<i>Scleroderma polyrhizum</i> (J.F. Gmel) Pers.	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	KY693661
<i>Scleroderma</i> sp.	<i>H. halimifolium</i>	This study	MT594539
<i>Serendipita vermifera</i> (Oberw.) P. Roberts	<i>H. halimifolium</i>	de Carvalho 2016 (ECM) ^s	^t
	<i>H. halimifolium</i>	Carvalho et al. 2018 (ECM) ^s	LT746013
<i>Thelephora</i> cfr. <i>caryophyllea</i> (Schaeff.) Pers. [#]	<i>H. halimifolium</i>	This study	
<i>Thelephora terrestris</i> Ehrh. [#]	<i>H. halimifolium</i>	Moreau et al. 2007a	
	<i>H. halimifolium</i>	This study	MT594540
	<i>H. halimifolium</i>	This study (ECM)	MT594541
	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	KY693686
	<i>H. lasianthum</i> , <i>H. ocymoides</i>	Buscardo et al. 2012 (ECM)	HQ625443
<i>Tomentella badia</i> (Link) Stalpers	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	KY693714
<i>Tomentella terrestris</i> (Berk. & Broome) M.J. Larsen	<i>H. ocymoides</i>	Buscardo et al. 2012 (ECM)	HQ625474
<i>Tomentella</i> sp.	<i>H. halimifolium</i>	Carvalho et al. 2018 (ECM)	LT746015
<i>Tomentellopsis submollis</i> (Svrček) Hjortstam	<i>H. lasianthum</i>	Santolamazza-Carbone et al. 2019 (ECM)	KY693726
<i>Tomentellopsis</i> sp.	<i>H. ocymoides</i>	Buscardo et al. 2012 (ECM)	HQ625483
<i>Tricholoma equestre</i> (L.:Fr.) P. Kumm.	<i>Halimium</i> sp.	Moreno-Arroyo 2004	
	<i>H. halimifolium</i>	de Carvalho 2016 (sECM), Albuquerque-Martins et al. 2019 (sECM)	
<i>Tricholoma portentosum</i> (Fr.) Quél	<i>H. halimifolium</i>	de Carvalho 2016 (sECM), Albuquerque-Martins et al. 2019 (sECM)	
<i>Tubariomyces hygrophoroides</i> Esteve-Rav., P.-A. Moreau & C.E. Hermos	<i>H. halimifolium</i>	Alvarado et al. 2010	
<i>Tubariomyces inexpectata</i> (M. Villarreal, Esteve-Raventós, Heykoop & E. Horak) Esteve-Raventós & Matheny	<i>H. halimifolium</i>	Moreau et al. 2007a ^u	
<i>Tylospora</i> sp.	<i>H. halimifolium</i>	de Carvalho 2016 (ECM)	^t
		This study	MT594542

Table 1 (continued)

Species	Host (<i>Halimium</i>)	Reference	Sequence
<i>Xerocomellus redeuilhii</i> A.F.S. Taylor, U. Eberh., Simonini, Gelardi & Vizzini	<i>H. halimifolium</i>		
Zygomycota <i>Youngiomyces multiplex</i> (Thaxt.) Y.J. Yao	<i>H. alyssoides</i>	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

[§] 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*

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

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

? Dubious or suspect record

^a Often reported as associated with *Helianthemum* spp. (see Loizides 2016)

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

^c As *Torrendia pulchella* Bres.

^d Now considered a synonym of *C. pallens* (see Olariaga et al. 2017)

^e Deposited as *Cortinarius halimiorum*

^f Reported by Moreau et al. (2007a) as = *C. belleri* M.M. Moser. See also Ortega et al. 2006

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

^h As *Inocybe brunneorufa* Stangl & J. Veselsky

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

^j Usually reported as associated with *Pinus* (e.g., Basso 1999)

^m Deposited as *Lactifluus luteolus*

ⁿ As *Leccinum corsicum* (Rolland) Sing

^o 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)

^p As *Macowanites ammophilus* (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/MacowanitesAmmophilus.pdf>)

^q As *Russula drimeia* Cooke

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

^s As *Sebacina vermifera* (Oberw.)

^t Sequence not deposited

^u 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. subpruinosa* Eyssart. & Buyck, 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 *Cortinarius* (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., *Amphinema* sp., *Descolea maculata* Bougher, *Hebeloma cistophilum* Maire, *Laccaria* spp., *Lactarius hepaticus*, *Rhizopogon* spp., *Russula* spp., *Scleroderma* spp., *Serendipita vermifera* (Oberw.) P. Roberts, *Thelephora terrestris* Ehrh., *Tomentella* spp., *Tomentellopsis* spp., and *Tylospora* 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* Samari, 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—felty 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).

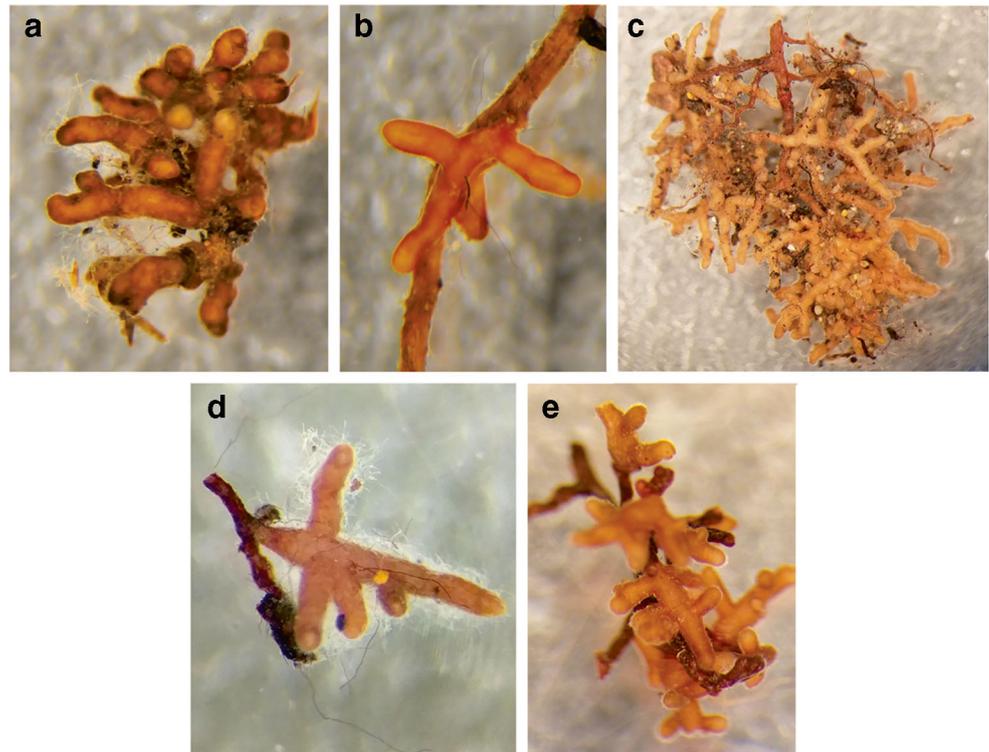
Another interesting species recorded in our collection site was *Alessioporus ichnusanus* (MB#808530). The taxon corresponds to a boletoid species recently segregated from *Xerocomus* Quél. to typify the new genus *Alessioporus* Gelardi, Vizzini & Simonini which currently accommodates two species. Its 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 (Polemis 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-annulus 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 (MycBank 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 (MycBank 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 applanate 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. ocymoides* (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.

Fig. 3 Habit of some of the ectomycorrhizal morphotypes collected under *Halimium halimifolium* during this study. **a** *Astraeus hygrometricus*. **b** *Lactarius hepaticus*. **c** *Russula monspeliensis*. **d** *Russula praetervisa*. **e** *Tuber oligospermum*



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 north-eastern 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).



Fig. 4 Sporocarps of selected species discussed in the text. **a** *Scleroderma meridionale*. **b** *Alessiopus ichnusanus*. **c** *Gyroporus pseudolacteus*. **d** *Lactarius hepaticus*. **e** *Lactifluus brunneoviolascens*. **f** *Cortinarius coeruleopallescens*

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. Martín, 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 *Leccinellum corsicum* (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 *Alessiopus 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 sardonica* 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 seems 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* Aiton, 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.

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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.

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