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# Present status and future of boletoid fungi (Boletaceae) on the island of Cyprus: Cryptic and threatened diversity unravelled by ten-year study

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Dedicated to the memory of our friend Yiagos Yiagou (1978–2017), for his valuable contribution to mycology in Cyprus.

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*Quercus coccifera* subsp. *calliprinos*

## ABSTRACT

Fungi historically placed in the iconic genera of *Boletus*, *Leccinum* and *Xerocomus* have been the subject of major taxonomic revisions in recent years. Yet, despite all advancements in systematics, boletoid fungi in insular ecosystems remain little explored and our knowledge of their diversity, distribution and abundance in Mediterranean ecoregions is far from complete. To shed light on this blind spot, the findings of a ten-year study from the island of Cyprus were analysed, integrating phylogenetic, ecological, morphological, phenological and chorological data. An unexpected diversity of Boletaceae fungi is unveiled, with twenty-five species phylogenetically confirmed to be present on the island, thirteen of them previously unreported. Sequencing of the ITS rDNA region, reveals cryptism within the *Butyriboletus fechtneri*, *Caloboletus radicans*, *Rubroboletus lupinus* and *Rheubarbaribolete armeniacus* species-complexes and infrageneric relationships are discussed. A strong link between boletoid fungi and Mediterranean oaks of the ilicoid group (*Quercus alnifolia*, *Quercus coccifera* subsp. *calliprinos*) is illustrated, with nineteen species (76%) overall found to be strictly or broadly associated with evergreen oaks. In stark contrast, the semi-deciduous *Quercus infectoria* subsp. *veneris* appears to be an unfavorable host for boletoid fungi, with just a single associated species so far. Phenological and chorological records indicate that most species on the island are rare, highly localized and fruit during very brief spells several years apart, mainly in response to increased annual, late summer or early autumn precipitation. The conservation status of these high-profile fungi is hence discussed, particularly in view of alarming climate changes, forecasted to have a dramatic impact on Mediterranean ecosystems in the years to come.

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## 1. Introduction

The high-profile family of Boletaceae harbours some of the most colourful and visually stunning basidiomycetes, including rare, as well as choice edible fungi of economic significance (Yun and Hall, 2004; Dentinger et al., 2010). Circumscribed with *Boletus* as its type genus (Chevallier, 1826), the family was originally assembled from a mélange of phylogenetically unrelated poroid genera, including *Cladoporus*, *Physisporus* and *Polyporus*, some later recombined into different families. In its current circumscription, the family

comprises mostly ectomycorrhizal (ECM), stipitate terrestrial fungi with tubular hymenophores and dark, usually fusiform or sub-fusiform spores, with most species oxidizing bluish, reddish or blackish due to the presence of variegatic and xerocomic acid pigments (Beaumont et al., 1968; Singer, 1986).

Boletoid fungi have been the subject of several systematic and monographic treatments (Singer, 1965, 1967; Engel et al., 1983, 1996; Alessio, 1985, 1991; Lannoy and Estadès, 2001; Ladurner and Simonini, 2003; Muñoz, 2005; Watling and Hills, 2005; Galli, 2007; Kirby, 2011), yet remarkably, the first robust phylogenetic framework for Boletales was made available only fairly recently (Binder and Hibbett, 2006). This study recognized six major clades at subordinal level and indicated that some genera within Boletaceae

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are polyphyletic. Subsequent inter- and infrageneric phylogenetic studies confirmed the long-established genera of *Boletus* and *Xerocomus* to be entirely artificial (Nuhn et al., 2013; Wu et al., 2014), leading to major taxonomic rearrangements within the family. As a result, several new genera, species and combinations were introduced from Asia (Li et al., 2011, 2014; Zhang et al., 2012, 2014, 2015a,b; Gelardi et al., 2013; Hosen et al., 2013; Zeng et al., 2014; Zhao et al., 2014a,b; Zhu et al., 2014, 2015; Biketova and Wasser, 2015; Wu et al., 2015; Cui et al., 2016; Liang et al., 2016), Europe (Gelardi et al. 2014, 2015; Vizzini et al., 2014a,b; Ariyawansa et al., 2015; Assyov et al., 2015; Crous et al., 2018); and North America (Halling et al., 2012; Arora and Frank, 2014), leaving in the genus *Boletus*, in its new restricted sense, only the residual *Boletus edulis* and closely allied white-pored species (Dentinger et al., 2010; Feng et al., 2012).

Despite these phylogenetic and taxonomical advancements, the diversity, distribution patterns and estimated abundance of boletoid fungi in Mediterranean ecoregions, particularly Mediterranean islands, remain poorly understood. More than 10,000 islands and islets are scattered across the Mediterranean basin, harbouring an astonishing concentration of biodiversity and endemism (Médail and Myers, 2004; Mittermeier et al., 2005). Mediterranean islands are characterized by high levels of speciation, but also by high rates of extinction (Paulay, 1994; Myers et al., 2000; Whittaker and Fernández-Palacios, 2007), and are refuge to many climatic relicts of plants (Médail, 2017), animals (Salvi et al., 2010) and fungi (Norstedt et al., 2001). At the same time, these vulnerable hotspots have suffered dramatic habitat loss due to anthropogenic activities and an influx of alien species; extended drought and warming induced by climate change, however, constitute the major threat for Mediterranean ecosystems nowadays (Médail and Quézel, 1997; Brooks et al., 2002; Giorgi, 2006; Giorgi and Lionello, 2008; Magnan et al., 2009; Médail, 2013, 2017). Considering one third of earth's biodiversity hotspots are found on insular ecosystems (Gerlach, 2008), this current lack of information is particularly problematic from an ecological perspective, because of the critical role fungi have in ecosystem functioning, through their strong influence on nutrient acquisition by plants, carbon recycling and community dynamics (Bardgett and Wardle, 2010; Smith and Read, 2010; van der Heijden et al., 2015).

In the volcanic island of Cyprus, current landscapes and biodiversity patterns have been deeply impacted by human pressure, probably dating as far back as 10,500 BC (Harris, 2012; Zazzo et al., 2015). With present flora comprised mostly of alien plants rather than indigenous species, the island's ecosystems, particularly narrow-endemics, are facing profound changes (Kadis and Georgiou, 2010; Médail, 2017). Extended upland forests, such as the narrow-endemic *Cedrus brevifolia* forest at Tripilos, or *Pinus nigra* subsp. *pallasiana* forests at the peaks of the Troodos massif, are expected to perish during the first half of the century, as a result of reduced rainfall and climate warming (Linares et al., 2011; Shoukri and Zachariadis, 2012). Since the vast majority of plants form mutualistic relationships with a wide array of fungi, documenting fungal diversity and understanding plant-fungi dynamics within these vulnerable ecosystems has become an urgent priority for their conservation (Richard et al., 2004, 2005; Ortega and Lorite, 2007; Büntgen et al., 2012a,b, 2015; Zotti and Pautasso, 2013).

With the exception of some archaic lineages such as *Buchwaldoboletus*, *Pseudoboletus* and perhaps *Chalciporus*, Boletaceae fungi form ectomycorrhizal associations with various members of the Fagaceae, particularly *Quercus* species (Muñoz, 2005; Binder and Hibbett, 2006; Tedersoo et al., 2010, 2013). More than twenty species of oak occur across the Mediterranean (Scarascia-Mugnozza et al., 2000), three of which are present in Cyprus (Fig. 2, Loizides et al., 2019). Of these, the narrow-endemic golden

oak of Cyprus (*Quercus alnifolia*), an evergreen member of the "Ilex" group (Denk and Grimm, 2010), is of particular ecological importance. Confined to the Troodos ophiolitic massif, *Q. alnifolia* forms pure or mixed stands with pine and other sclerophyllous vegetation, colonizing igneous and diabasic slopes at altitudes between 400 and 1800 m a.s.l. (Merlo and Croitoru, 2005; Neophytou et al., 2007). The kermes oak (*Quercus coccifera* subsp. *calliprinos*) is the second evergreen oak present on the island, mostly occurring on calcareous soils at lower elevations, from 100 to 1300 m, though both evergreen oaks can sometimes co-occur within the golden oak's habitat zone (Meikle, 1977; Tsintides et al., 2002). The semi-deciduous gall oak (*Quercus infectoria* subsp. *veneris*) is the third species of oak present in Cyprus, found from sea-level up to 1400 m; its populations, however, have been severely depleted due to logging, agriculture and poorly conceived reforestation policies (Barbero and Quézel, 1979; Meikle, 1985; Christou, 2000).

Over 80 ectomycorrhizal fungi have been linked to *Q. alnifolia* in a preliminary report, including eleven species of Boletaceae (Loizides, 2011). Prior to these records, a mere four species of Boletaceae could be traced in published literature (Viney, 2005; Loizides and Kyriakou, 2011) and, despite scattered reports (Loizides et al., 2011; Loizides and Yiannou, 2011; Loizides, 2016), boletoid fungi in Cyprus have remained tantalizingly elusive and for the most part undocumented, due to their apparent rarity and highly erratic fruiting patterns. To better understand the diversity, estimated abundance and ecological needs of this significant group of fungi, the findings of a 10 y-survey from Cyprus were analysed, using a cross-disciplinary approach. The principal objectives of our study were to: (1) provide the first comprehensive account of boletoid fungi in Cyprus based on a systematic phylogenetic assessment of field collections; (2) clarify the phylogenetic status of a number of morphologically or ecologically deviant collections; (3) decipher the temporal and phenological patterns for each species in relation to biotic (host) and abiotic (geology/climate) constraints; (4) assess the role of the various oak species in supporting Boletaceae diversity in Mediterranean ecosystems; and (5) identify urgent conservation concerns. Following the results of our analyses, the generic and infrageneric placements of several species are critically evaluated, and nomenclatural precisions are proposed. Last but not least, the future of boletoid fungi in Cyprus and Mediterranean ecoregions is discussed, particularly in view of accelerated climate changes, forecasted to have a dramatic impact on the island's ecosystems in the decades to come.

## 2. Materials and methods

### 2.1. Study area

The study focused on the island of Cyprus, situated 35.1264° north and 33.4299° east in the Mediterranean basin and occupying an area of 9,251 km<sup>2</sup>. The island accommodates a diverse range of ecosystems, largely defined by the altitudinal belts formed by the Troodos ophiolitic massif, which rises to a height of 1,951 m and consists of plutonic, intrusive and volcanic rocks with serpentinized harzburgites. Surrounding Troodos are autochthonous sedimentary rock formations, mostly consisting of bentonite clays, chalks, limestones, marlstones, calcarenites and melanges (see Zomeni and Bruggeman, 2013 for a detailed analysis). The climate is typically Mediterranean, with considerable fluctuations. Average daily temperatures at coastal regions range from ~33 °C in the summer to ~7 °C in the winter, while at the higher elevations temperatures are substantially lower, ranging from ~23 °C in the summer and ~3.5 °C in the winter. Mean annual precipitation is 450 mm in the lowlands, significantly increasing to 1,100 mm at the peaks of the Troodos massif. The most dominant and widespread

ectomycorrhizal tree on the island is *Pinus brutia*, forming extensive forests from near sea-level to 1,600 m a.s.l. At higher elevations it is replaced by *P. nigra* subsp. *pallasiana*, though both pines can co-exist within a narrow phytogeographical belt between 1,400 and 1,600 m a.s.l. *Q. alnifolia* (Hab. type 9390, European Commission DG Environment, 2007) and *Q. coccifera* subsp. *calliprinos* are also widespread, but hardly ever occur in pure stands and are mostly found at the understorey of *P. brutia* and *P. nigra* subsp. *pallasiana* forests, often in mixed communities also including *Arbutus andrachne* and *Cistus* shrubs. *Quercus infectoria* subsp. *veneris* (Hab. type 93A0, European Commission DG Environment, 2007) is confined to the western parts of the island and its populations are currently comprised of relict fragmented stands and scattered trees mostly within mixed tree communities, or along the borders of cultivated land, up to 1,400 m a.s.l. Among riparian vegetation, *Alnus orientalis* is far more widespread than *Salix alba*, and often co-occurs with the endomycorrhizal *Platanus orientalis* in narrow corridors along rivers and streams up to 1,550 m a.s.l. The narrow-endemic *C. brevifolia* is rare, and currently restricted to less than a dozen heavily fragmented populations in the Paphos forest, at elevations between 900 and 1,400 a.s.l. (Hab. type 9590, European Commission DG Environment, 2007). *Cistus* shrubs typically occur at the understorey of *P. brutia* and *P. nigra* subsp. *pallasiana* forests, but in the thermomediterranean belt they also form pure stands. *Cistus creticus* and *Cistus salvifolius* are the most widespread, reaching altitudes of 1,800 m and 1,400 m a.s.l., respectively, while *Cistus monspeliensis* is less common and largely restricted to western regions of the island, particularly the Akamas peninsula. In the dune zone, *Eucalyptus camaldulensis*, *Eucalyptus gomphocephala* and *Pinus halepensis* are sparingly encountered, though none of them are indigenous to the island and are mostly confined within isolated stands and plantations.

## 2.2. Data collection

A wide range of habitats across an extended altitudinal gradient were surveyed as part of a general inventory carried out between 2007 and 2016, following a modified protocol broadly based on Richard et al. (2004). Thirty loosely delimited sites, representative of all major habitats on the island dominated by ECM trees and shrubs and ranging in size from ~500 m<sup>2</sup> to ~2 km<sup>2</sup>, were selected and regularly surveyed (see Table 1, Loizides et al., 2019), in addition to other less frequently visited localities. Selection of the permanent sites was based on preliminary observations, altitudinal range, accessibility, tree composition and mean annual precipitation. Because of the highly unpredictable and uneven distribution of seasonal rainfall on the island, surveys systematically followed rainfall episodes. Precipitation data for each locality was retrieved at least three times a week from the Cyprus Department of Meteorology's official website ([http://www.moa.gov.cy/moa/ms/ms.nsf/DMLindex\\_en/DMLindex\\_en?OpenDocument](http://www.moa.gov.cy/moa/ms/ms.nsf/DMLindex_en/DMLindex_en?OpenDocument)), and forays were planned accordingly. Surveying typically spanned between September and April, 18–20 d following the first substantial rainfall of the season (>20 mm) and regularly thereafter, usually 1–2 d following subsequent rainfall episodes, or 2–4 times a week. Exceptionally, surveys were also carried out in late spring or during the summer months, following substantial precipitation (>30 mm) at the higher elevations of Troodos (>1,400 m a.s.l.). Collection of specimens within the permanent sites was mostly opportunistic and followed fructification patterns, though identified hotspots within each site and certain tree-hosts of interest were regularly checked. Surveys usually lasted 2–4 h on each site, with 1–4 sites visited in each foray. Overall, a total of 767 forays were carried out during the decade, with a minimum of 42 and a maximum of 129 forays taking place annually, averaging 76.7 forays per season (see

Table 2, Loizides et al., 2019). At the end of the 10 y, all Boletaceae data were extracted from the general inventory data and analysed separately in the context of the present study.

## 2.3. Ecological, morphological, phenological and chorological analyses

Over 200 Boletaceae collections were studied during this inventory (Table 1), 178 of them originating from Cyprus. All specimens were photographed *in situ*, the altitude and soil characteristics were annotated, and the host plant was assigned based on analysis of plant community composition. For collections found in mixed stands, the putative host-plant was assigned based on fruiting pattern, analysis of the spatial distribution of ECM plants, and known host preferences for each species following original descriptions and monographic works (Singer, 1965, 1967; Lannoy and Estadès, 2001; Ladurner and Simonini, 2003; Muñoz, 2005; Galli, 2007; Kirby, 2011). When the precise ectomycorrhizal symbiont was uncertain, no host-plant was assigned (see Table 1 and "Discussion"). For the purpose of evaluating estimated abundance, collections found >25 m apart from one-another were considered as fruiting from different mycelia (following Dahlberg and Stenlid, 1994, and Hirose et al., 2004). Detailed macro-morphological observations were made on fresh fruit bodies, when possible from various developmental stages and oxidation of the flesh was carefully evaluated. Microscopic studies were performed under a Leica BM E binocular, an AmScope T360B trinocular, and a Zeiss axioskop microscopes at ×100, ×400 and ×1000 magnifications, following methods described by Singer (1965), Peintner et al. (2003), Ladurner and Simonini (2003), Assyov (2012), and Vizzini et al. (2014a,b). All diagnostically important microscopic structures were observed (see Loizides et al., 2019 for a detailed description). Climatological data (including normal, actual and cumulative actual/normal monthly precipitation), was obtained from Cyprus Department of Meteorology. Correlation between climatological variables (monthly, seasonal and annual precipitation levels), and fruiting abundance of boletoid fungi, was performed using Pearson's product-moment tests in R 3.2.4 (R Core Team, 2016).

## 2.4. DNA extraction, amplification and sequencing

Following morphological studies, representative specimens identified to belong to distinct species were selected for molecular analysis. A number of collections from atypical habitats or displaying unusual features were also molecularly analysed, along with comparative collections from Bulgaria, Croatia, France, Greece and Switzerland (see Table 1 and Fig. 1). DNA extraction and PCR amplification were conducted with the REDExtract-N-Amp™ Plant PCR Kit (Sigma-Aldrich, St. Louis, MO, USA), following the manufacturer's instructions. The internal transcribed spacers and 5.8S rDNA (ITS) were amplified from each collection, with the ITS-1F/ITS-4b primer pair (Gardes and Bruns, 1993), as described in Richard et al. (2015). When no band was detected by agarose-gel electrophoresis analysis, one microliter of the PCR product was used as template in a second PCR using the ITS1F/ITS4 primer pair (White et al., 1990). Amplicons were purified and sequenced by Eurofins Genomics, Ebersberg, Germany. Raw sequence data were edited and assembled with Codon Code Aligner 4.1.1 (CodonCode Corp., Centerville, MA, USA), and deposited in GenBank under the accession numbers indicated in Table 1.

**Table 1**

Boletaceae collections studied in the present work.

Species	Voucher id	Leg.	Collection site	Coll. date	Elevation	Habitat (Putative host in bold)	Soil	GB access.
<i>Alessioporus ichnusanus</i> *	ML61972AI	M. Loizides	Cyprus, Prodromos	27-IX-2016	ca 1350 m	<i>Quercus alnifolia</i> , <i>Pinus nigra</i> subsp. <i>pallasiana</i>	Serpentine	<b>MH011928</b>
<i>Boletus aereus</i>	ML909051BA	M. Loizides	Cyprus, Troodos	15-IX-2009	ca 1650 m	<i>Cistus creticus</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML909051BA2	M. Loizides	Cyprus, Troodos	15-IX-2009	ca 1600 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML909051BA3	M. Loizides	Cyprus, Troodos	15-IX-2009	ca 1600 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i> , <i>Sorbus aria</i>	Serpentine	
	ML909022BA	M. Loizides	Cyprus, Troodos	22-IX-2009	ca 1680 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML909072BA	M. Loizides	Cyprus, Troodos	27-IX-2009	ca 1650 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML119080BA	M. Loizides	Cyprus, Troodos	8-IX-2011	ca 1700 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML11118BA	M. Loizides	Cyprus, Troodos	8-XI-2011	ca 1620 m	<i>C. creticus</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML410162BA	M. Loizides	Cyprus, Trooditissa	26-X-2014	ca 1350 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML41862BA	M. Loizides	Cyprus, Troodos	26-VIII-2014	ca 1650 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	<b>MH011853</b>
	ML41862BA2	M. Loizides	Cyprus, Troodos	26-VIII-2014	ca 1650 m	<i>C. creticus</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML41882BA	M. Loizides	Cyprus, Troodos	28-VIII-2014	ca 1600 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML418623BA3	M. Loizides	Cyprus, Troodos	26-VIII-2014	ca 1680 m	<i>Arbutus andrachne</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML41114BA	D. Markides	Cyprus, Madari	4-XI-2014	ca 1250 m	<i>C. creticus</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML511171BA	D. Markides	Cyprus, Madari	17-XI-2015	ca 1300 m	<i>Q. alnifolia</i> , <i>Pinus brutia</i>	Serpentine	
	ML511112BA	D. Markides	Cyprus, Madari	21-XI-2015	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML61952BA	M. Loizides	Cyprus, Trooditissa	25-IX-2016	ca 1350 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML61972BA	M. Loizides	Cyprus, Troodos	27-IX-2016	ca 1600 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
<i>Butyriboletus fechtneri</i> sensu lato *	ML9096BF	M. Loizides	Cyprus, Prodromos	4-IX-2009	ca 1350 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	<b>MH011855</b>
	ML90971BF	M. Loizides	Cyprus, Troodos	17-IX-2009	ca 1700 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90113BA	M. Loizides	Cyprus, Kakomallis	2-XI-2009	ca 700 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Calcareous	<b>MH011857</b>
	ML210192BF	M. Loizides	Cyprus, Kelefos	29-X-2012	ca 480 m	<i>Quercus coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	<b>MH011856</b>
	ML619523F5	M. Loizides	Cyprus, Trooditissa	25-IX-2016	ca 1300 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	<b>MH011859</b>
	ML61952BF1	M. Loizides	Cyprus, Trooditissa	25-IX-2016	ca 1300 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML61972BF	M. Loizides	Cyprus, Trooditissa	27-IX-2016	ca 1300 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	<b>MH011860</b>
	ML61972BF1	M. Loizides	Cyprus, Trooditissa	27-IX-2016	ca 1350 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML61992BF	M. Loizides	Cyprus, Trooditissa	29-IX-2016	ca 1350 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	SOMF29853	B. Assyov	Bulgaria, Logodazh	23-IX-2014	ca 680 m	<i>Quercus</i> spp.	Calcareous	<b>MH011861</b>
	SOMF29854	P. Nedelev	Bulgaria, Zgorigrad	2014	ca 760 m	<i>Fagus sylvatica</i>	Calcareous	<b>MH011862</b>
<i>Butyriboletus fuscorseus</i>	SOMF25384	B. Assyov	Bulgaria, Koman chalet	07-VI-2002	ca 650 m	<i>Quercus</i> spp.	Calcareous	<b>MH011864</b>
	SOMF29855	B. Assyov	Bulgaria, Golemo Buchino	28-VI-2013	ca 870 m	<i>Quercus</i> spp., <i>F. sylvatica</i>	Calcareous	<b>MH011865</b>
	FR2011148	F. Richard	France, N.-D. de Londres	09-IX-2011	ca 200 m	<i>Q. pubescens</i>	Calcareous	<b>MH011854</b>
<i>Caloboletus radicans</i> sensu lato	ML80011CR	A. Kontopoulos	Cyprus, Troodos	1-X-2008	ca 1800 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90921CR	M. Loizides	Cyprus, Troodos	12-IX-2009	ca 1700 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML900101CR	M. Loizides	Cyprus, Platania	10-X-2009	ca 1100 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Calcareous	
	ML210111CR	M. Loizides	Cyprus, Kelefos	11-X-2012	ca 480 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML61951CR	M. Porke	Cyprus, Prodromos	20-IX-2016	ca 1450 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i> , <i>C. creticus</i>	Serpentine	<b>MH011875</b>
	EF61012B	E. Fotiadou	Greece, Thessaloniki	02-X-2016	Unknown	<i>Quercus</i> sp., <i>Fagus sylvatica</i>	Acidic	<b>MH011874</b>
<i>Chalciporus amarellus</i>	ML701171CA	M. Loizides	Cyprus, Saittas	17-XI-2007	ca 700 m	<i>Cistus</i> sp., <i>P. brutia</i>	Calcareous	
	ML901162CA	M. Loizides	Cyprus, Platania	26-XI-2009	ca 1050 m	<i>Cistus salvifolius</i> , <i>P. brutia</i>	Basic	<b>MH011876</b>
	ML901182CA	M. Loizides	Cyprus, Kelefos	28-XI-2009	ca 500 m	<i>C. salvifolius</i> , <i>P. brutia</i>	Calcareous	
	SOMF29856	B. Assyov	Bulgaria, Bunderitsa	04-X-2015	ca 1850	<i>Picea abies</i> , <i>P. heldreichii</i>	Marble	<b>MH011877</b>
<i>Exsudoporus permagnificus</i> *	ML61992EP	M. Loizides	Cyprus, Prodromos	29-IX-2016	ca 1400 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	<b>MH011858</b>
<i>Hemileccinum impolitum</i>	ML800131HI	M. Loizides	Cyprus, Pera Pedi	13-X-2008	ca 600 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML9095HI	M. Loizides	Cyprus, Pera Pedi	5-IX-2009	ca 600 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML90015HI	M. Loizides	Cyprus, Pera Pedi	5-X-2009	ca 600 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML11121LE	D. Markides	Cyprus, Paphos	12-I-2011	ca 500 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Basic	<b>MH011852</b>
	ML110161HI	M. Loizides	Cyprus, Amiantos	16-X-2011	ca 1400 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Calcareous	
	ML111132HI	M. Loizides	Cyprus, Trooditissa	23-XI-2011	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Calcareous	
	ML210192HI	M. Loizides	Cyprus, Kelefos	29-X-2012	ca 500 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	<b>MH011846</b>
	ML410142HI	M. Loizides	Cyprus, Troodos	24-X-2014	ca 1750 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML511182HI	S. Anastasiou	Cyprus, Platres	28-XI-2015	ca 1200 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML61972HI	M. Loizides	Cyprus, Platres	27-IX-2016	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	<b>MH011851</b>
	ML61972HI2	M. Loizides	Cyprus, Trooditissa	27-IX-2016	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML61018HO	D. Markides	Cyprus, Platres	8-X-2016	ca 1200 m	<i>Q. alnifolia</i> , <i>P. brutia</i> , <i>A. andrachne</i>	Serpentine	<b>MH011850</b>
	ML61214HI	C. Savvides	Cyprus, Kelefos	4-XII-2016	ca 550 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	

<i>Imperator luteocupreus</i> *	JMB2014100203	J.-M. Bellanger	France, Montpellier	2-X-2014	ca 60 m	<i>Quercus pubescens</i> , <i>Q. ilex</i>	Calcareous	MH011849
	JMB2016111001	J.-M. Bellanger	France, Montpellier	10-XI-2016	ca 60 m	<i>Q. pubescens</i> , <i>Q. ilex</i>	Calcareous	MH011847
	JMB2016111301	J.-M. Bellanger	France, Montpellier	13-XI-2016	ca 60 m	<i>Q. pubescens</i> , <i>Q. ilex</i>	Calcareous	MH011848
	ML01811RS	M. Loizides	Cyprus, Troodissa	11-VIII-2010	ca 1300 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	MH011873
	ML110112BL	M. Loizides	Cyprus, Amiantos	21-X-2011	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Calcareous	MH011871
	ML211101BL	M. Loizides	Cyprus, Troodos	10-XI-2012	ca 1400 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	MH011872
<i>Imperator rhodopurpureus</i>	FR2011127	F. Richard	France, N.-D. de Londres	19-IX-2011	ca 200 m	<i>Q. pubescens</i> , <i>Q. ilex</i>	Calcareous	MH011867
	FR2015613	L. Deparis	Switzerland, Chancy	20-VIII-2006	ca 430 m	<i>Quercus</i> sp., <i>Picea abies</i>	Calcareous	MH011870
	FR2015605	L. Deparis	France, St Germain-sur-Rhone	24-VIII-2010	ca 460 m	<i>Quercus</i> sp.	Calcareous	MH011868
	FR2011123	F. Richard	France, N.-D. de Londres	14-IX-2011	ca 200 m	<i>Q. pubescens</i> , <i>Q. ilex</i>	Calcareous	MH011866
	FR2015611	L. Deparis	France, St Germain-sur-Rhone	17-VIII-2013	ca 460 m	<i>Quercus</i> sp.	Calcareous	MH011869
<i>Leccinellum corsicum</i>	ML902102LC	M. Loizides	Cyprus, Saittas	20-XII-2009	ca 600 m	<i>C. salvifolius</i> , <i>P. brutia</i>	Basic	
	ML0139LC	M. Loizides	Cyprus, Trimiklini	9-III-2010	ca 650 m	<i>C. salvifolius</i> , <i>C. creticus</i>	Basic	MH011881
	ML211192LC	M. Loizides	Cyprus, Kalavasos	29-XI-2012	ca 200 m	<i>Cistus</i> spp., <i>Q. coccifera</i> subsp. <i>calliprinus</i>	Basic	
	ML211192LC2	M. Loizides	Cyprus, Kalavasos	29-XI-2012	ca 180 m	<i>C. salvifolius</i> , <i>C. creticus</i>	Basic	
	ML802142LC	M. Loizides	Cyprus, Saittas	24-XII-2012	ca 600 m	<i>C. salvifolius</i> , <i>P. brutia</i>	Basic	
	ML311132LC	M. Loizides	Cyprus, Asgata	23-XI-2013	ca 150 m	<i>C. salvifolius</i> , <i>C. creticus</i>	Basic	
	ML412142LC	M. Loizides	Cyprus, Drouisia	24-XII-2014	ca 600 m	<i>C. salvifolius</i> , <i>C. monspeliensis</i>	Basic	MH011880
	ML51352L	M. Loizides	Cyprus, Pera Pedi	25-III-2015	ca 650 m	<i>C. salvifolius</i> , <i>Q. coccifera</i> subsp. <i>calliprinus</i>	Calcareous	MH011882
	ML61232LC	M. Loizides	Cyprus, Akamas	23-II-2016	ca 200 m	<i>C. salvifolius</i> , <i>C. monspeliensis</i>	Calcareous	MH011885
	PAM07020203	P.-A. Moreau	France, Corsica, Bonifacio	02-II-2007	ca 10 m	<i>C. salvifolius</i>	Calcareous	MH011834
	SOMF29857	B. Assyov	Greece, Chalkidiki	14-XII-2014	ca 15 m	<i>C. monspeliensis</i>	Acidic	MH011889
<i>Leccinellum lepidum</i>	ML700142LL	M. Loizides	Cyprus, Kelefos	24-XI-2007	ca 480 m	<i>Q. coccifera</i> subsp. <i>calliprinus</i> , <i>P. brutia</i>	Calcareous	
	ML702142LL	M. Loizides	Cyprus, Mesa Potamos	24-XII-2007	ca 700 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Calcareous	
	ML80942LL	M. Loizides	Cyprus, Troodos	24-IX-2008	ca 1650 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML80112ML	M. Loizides	Cyprus, Platania	2-XI-2008	ca 1100 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90902LL	M. Loizides	Cyprus, Troodos	20-IX-2009	ca 1700 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	MH011884
	ML90972LL	M. Loizides	Cyprus, Troodos	27-IX-2009	ca 1600 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90013LL	M. Loizides	Cyprus, Troodos	3-X-2009	ca 1650 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML902131LL	M. Loizides	Cyprus, Kannaviou	13-XII-2009	ca 1650 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Calcareous	
	ML902122LL	M. Loizides	Cyprus, Platres	22-XII-2009	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	MH011886
	ML902122LL2	M. Loizides	Cyprus, Platres	22-XII-2009	ca 1300 m	<i>Q. coccifera</i> subsp. <i>calliprinus</i> , <i>P. brutia</i>	Serpentine	
	ML902122LL3	M. Loizides	Cyprus, Platres	22-XII-2009	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i> , <i>A. andrachne</i>	Serpentine	
	ML902103LL	M. Loizides	Cyprus, Platres	30-XII-2009	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML900321LL	M. Loizides	Cyprus, Platania	30-XII-2009	ca 1100 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Calcareous	
	ML01222LL	M. Loizides	Cyprus, Trimiklini	22-II-2010	ca 600 m	<i>Q. coccifera</i> subsp. <i>calliprinus</i> , <i>P. brutia</i>	Calcareous	
	ML111191LL	Y. Yiangou	Cyprus, Platania	19-XI-2011	ca 1100 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML212111LL	M. Loizides	Cyprus, Platres	11-XII-2012	ca 1200 m	<i>Q. alnifolia</i> , <i>P. brutia</i> , <i>A. andrachne</i>	Serpentine	
	ML212171LL	M. Loizides	Cyprus, Platres	17-XII-2012	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i> , <i>A. andrachne</i>	Serpentine	
	ML212112LL	M. Loizides	Cyprus, Kelefos	21-XII-2012	ca 450 m	<i>Q. coccifera</i> subsp. <i>calliprinus</i> , <i>P. brutia</i>	Calcareous	
	ML41631LL	M. Loizides	Cyprus, Prodromos	13-VI-2014	ca 1350 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML412172LL	A. Georgiou	Cyprus, Paphos	27-XII-2014	ca 1000 m	<i>Q. coccifera</i> subsp. <i>calliprinus</i> , <i>P. brutia</i>	Serpentine	
	ML51112LL	M. Loizides	Cyprus, Kelefos	21-I-2015	ca 500 m	<i>Q. coccifera</i> subsp. <i>calliprinus</i> , <i>P. brutia</i>	Calcareous	
	ML511102LL	M. Loizides	Cyprus, Madari	20-XI-2015	ca 1300 m	<i>Q. coccifera</i> subsp. <i>calliprinus</i> , <i>P. brutia</i>	Serpentine	
	ML5128LL	M. Loizides	Cyprus, Pera Vasa	8-II-2015	ca 600 m	<i>Q. coccifera</i> subsp. <i>calliprinus</i> , <i>P. brutia</i>	Calcareous	
	ML5128LL2	C. Savvides	Cyprus, Pera Vasa	8-II-2015	ca 550 m	<i>Q. coccifera</i> subsp. <i>calliprinus</i> , <i>P. brutia</i>	Serpentine	
	ML51412LL	M. Loizides	Cyprus, Platres	21-IV-2015	ca 1100 m	<i>Q. coccifera</i> subsp. <i>calliprinus</i> , <i>P. brutia</i>	Serpentine	MH011883
	FR2011144	F. Richard	France, Puéchabon	15-XII-2011	ca 200 m	<i>Quercus ilex</i>	Calcareous	MH011878
	Pezilla70	E. Taschen	France, Pézilla-de-Conflent	24-XI-2011	ca 300 m	<i>Q. ilex</i>	Calcareous	MH011879
	SOMF29858	A. Soklić	Croatia, Tar	13-XII-2014	ca 20 m	<i>Q. ilex</i>	Calcareous	MH011887
	SOMF29859	M. Slavova	Greece, Stratoni	14-XII-2014	ca 115 m	<i>Q. ilex</i>	Acidic	MH011888
<i>Rheubarbaroletus persicolor</i> aff. *	ML41842RP	M. Loizides	Cyprus, Troodos	24-VIII-2014	ca 1550 m	<i>P. nigra</i> subsp. <i>pallasiana</i> , <i>S. aria</i> , <i>Robinia pseudoacacia</i>	Serpentine	MH011927
<i>Rheubarbaroletus persicolor</i>	SOMF28154	D. Vassilev	Bulgaria, Vaksevo	17-X-2012	ca 660 m	<i>Quercus</i> sp.	Calcareous	MH011932
	SOMF29860	B. Assyov	Greece, Sidirokastro	8-X-2015	ca 160 m	<i>Q. coccifera</i> , <i>P. brutia</i>	Calcareous	MH011931
<i>Rubroboletus dupainii</i>	FR2011125	F. Richard	France, N.-D. de Londres	10-IX-2011	ca 200 m	<i>Q. pubescens</i> , <i>Q. ilex</i>	Calcareous	MH011891
	FR2011126	F. Richard	France, N.-D. de Londres	19-IX-2011	ca 200 m	<i>Q. pubescens</i> , <i>Q. ilex</i>	Calcareous	MH011892
<i>Rubroboletus lupinus</i> sensu lato	ML900192BL	M. Loizides	Cyprus, Kakomallis	29-X-2009	ca 600 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Basic	
	ML110112BL	G. Votsis	Cyprus, Amiantos	21-X-2011	ca 1200 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML110132BL	A. Georgiou	Cyprus, Karvounas	23-X-2011	ca 1200 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	

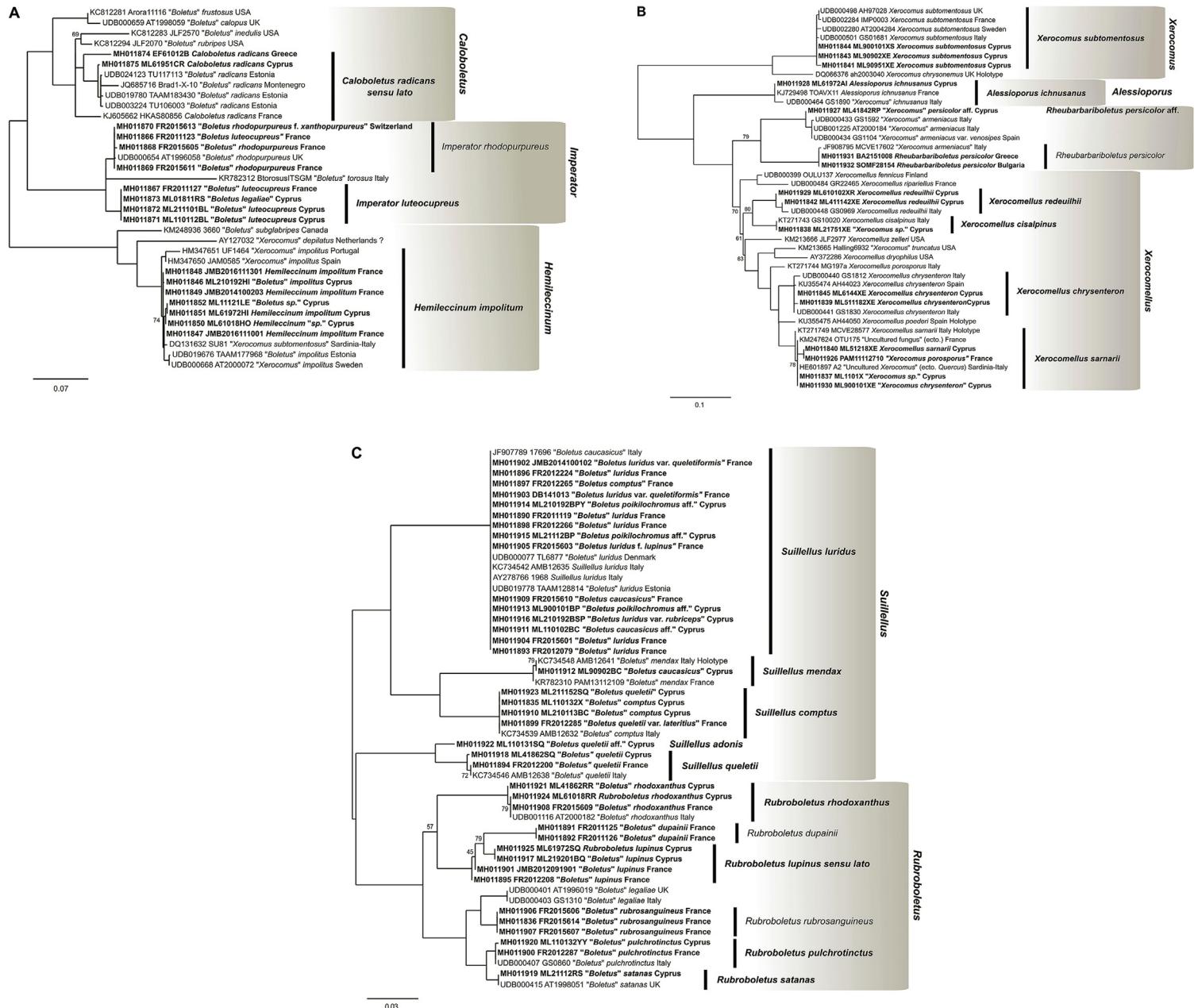
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**Table 1** (continued)

Species	Voucher id	Leg.	Collection site	Coll. date	Elevation	Habitat (Putative host in bold)	Soil	GB access.
<i>Rubroboletus pulchrotinctus</i>	ML210192BL1	M. Loizides	Cyprus, Kelefos	29-X-2012	ca 500 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML219201BQ	M. Loizides	Cyprus, Kelefos	29-X-2012	ca 520 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML210192BL2	M. Loizides	Cyprus, Kelefos	29-X-2012	ca 500 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML210113BL1	M. Loizides	Cyprus, Kelefos	31-X-2012	ca 480 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML210113BL2	M. Loizides	Cyprus, Kelefos	31-X-2012	ca 500 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML210113BL3	M. Loizides	Cyprus, Kelefos	31-X-2012	ca 450 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML21101BQL	M. Loizides	Cyprus, Trooditissa	10-XI-2012	ca 1280 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML61972SQ	M. Loizides	Cyprus, Trooditissa	27-IX-2016	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	JMB2012091901	J.-M. Bellanger	France, Montpellier	19-IX-2012	ca 65 m	<i>Q. pubescens</i> , <i>Q. ilex</i>	Calcareous	<b>MH011917</b>
	FR2012208	F. Richard	France, Puéchabon	14-X-2012	ca 200 m	<i>Q. ilex</i>	Calcareous	
	FR2012287	E. Taschen	France, Pézilla-de-Conflent	23-X-2013	ca 1100 m	<i>Q. alnifolia</i>	Serpentine	
	ML110132YY	Y. Yiangou	Cyprus, Platania	26-X-2012	ca 300 m	<i>Q. ilex</i>	Calcareous	
	ML800191BR	A. Georgiou	Cyprus, Amiantos	19-X-2008	ca 1350 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML90971BR	Y. Yiangou	Cyprus, Troodos	17-IX-2009	ca 1700 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
<i>Rubroboletus rhodoxanthus</i>	ML90902BR	M. Loizides	Cyprus, Troodos	20-IX-2009	ca 1700 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90902BR2	M. Loizides	Cyprus, Troodos	20-IX-2009	ca 1690 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90922BR	M. Loizides	Cyprus, Troodos	22-IX-2009	ca 1670 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90922BR2	M. Loizides	Cyprus, Troodos	22-IX-2009	ca 1670 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90922BR3	M. Loizides	Cyprus, Troodos	22-IX-2009	ca 1650 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90942BR	M. Loizides	Cyprus, Troodos	24-IX-2009	ca 1700 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90942BR2	M. Loizides	Cyprus, Troodos	24-IX-2009	ca 1680 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90942BR3	M. Loizides	Cyprus, Troodos	24-IX-2009	ca 1670 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90942BR4	M. Loizides	Cyprus, Troodos	24-IX-2009	ca 1670 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90972BR	M. Loizides	Cyprus, Troodos	27-IX-2009	ca 1650 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML110113BR	M. Loizides	Cyprus, Trooditissa	31.X-2011	ca 1250 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML21117BR	M. Loizides	Cyprus, Mesa Potamos	7-XI-2012	ca 900 m	<i>Q. alnifolia</i> , <i>A. andrachne</i> , <i>P. brutia</i>	Serpentine	
	ML41862RR	M. Loizides	Cyprus, Troodos	26-VIII-2014	ca 1650 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	<b>MH011921</b>
	ML41892BR	M. Loizides	Cyprus, Troodos	29-VIII-2014	ca 1640 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
<i>Rubroboletus rubrosanguineus</i>	ML611172RR	M. Loizides	Cyprus, Trooditissa	27-IX-2016	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML61018RR	D. Markides	Cyprus, Platres	8-X-2016	ca 1200 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	<b>MH011924</b>
	FR2015609	L. Deparis	France, Petit Salève	10-VIII-2011	ca 700 m	<i>Quercus</i> sp.	Calcareous	
	FR2015606	L. Deparis	France, Les Molunes	25-IX-2005	ca 1200 m	<i>Picea abies</i>	Calcareous	<b>MH011908</b>
	FR2015614	L. Deparis	France, Le Molière	23-VII-2011	ca 900 m	<i>Picea abies</i> , <i>Fagus sylvatica</i>	Calcareous	<b>MH011906</b>
	FR2015607	L. Deparis	France, Grand Bornand	8-VII-2012	ca 1250 m	<i>Picea abies</i>	Calcareous	<b>MH011836</b>
	ML110161BS	A. Kontopoulos	Cyprus, Karvounas	16-X-2011	ca 1200 m	<i>Q. alnifolia</i> , <i>P. brutia</i> , <i>A. andrachne</i>	Serpentine	
	ML110171BS	D. Markides	Cyprus, Karvounas	17-X-2011	ca 1150 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML110132BS	M. Loizides	Cyprus, Karvounas	23-X-2011	ca 1200 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML110132BS2	G. Votsis	Cyprus, Karvounas	23-X-2011	ca 1200 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
<i>Suillellus adonis</i> *	ML110132BS3	M. Loizides	Cyprus, Amiantos	23-X-2011	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML21112RS	M. Loizides	Cyprus, Kelefos	2-XI-2012	ca 480 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	<b>MH011919</b>
	ML61942BS	M. Loizides	Cyprus, Platres	24-IX-2016	ca 1300 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML61952RS	M. Loizides	Cyprus, Trooditissa	25-IX-2016	ca 1350 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	
	ML110131SQ	M. Loizides	Cyprus, Saittas	16-X-2011	ca 700 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i> , <i>Cistus</i> sp.	Calcareous	<b>MH011922</b>
	ML110132X	G. Votsis	Cyprus, Karvounas	23-X-2011	ca 1200 m	<i>Q. alnifolia</i> , <i>P. brutia</i>	Serpentine	<b>MH011835</b>
	ML210192BC	M. Loizides	Cyprus, Kelefos	29-X-2012	ca 480 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML210113BC	M. Loizides	Cyprus, Kelefos	31-X-2012	ca 500 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	<b>MH011910</b>
	ML210113BC2	M. Loizides	Cyprus, Kelefos	31-X-2012	ca 520 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML21112BC	M. Loizides	Cyprus, Kelefos	2-XI-2012	ca 520 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
<i>Suillellus luridus</i> *	ML211152SQ	M. Loizides	Cyprus, Germasogeia	25-XI-2012	ca 150 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>Cistus</i> spp.	Calcareous	<b>MH011923</b>
	FR2012285	E. Taschen	France, Pézilla-de-Conflent	26-X-2012	ca 300 m	<i>Q. ilex</i>	Calcareous	<b>MH011899</b>
	ML800151BP	M. Loizides	Cyprus, Amiantos	15-X-2008	ca 1300 m	<i>P. brutia</i> , <i>Q. alnifolia</i> , <i>Crataegus azarolus</i> , <i>Cistus</i> sp.	Serpentine	
	ML900101BP	M. Loizides	Cyprus, Amiantos	10-X-2009	ca 1300 m	<i>Q. alnifolia</i> , <i>A. andrachne</i> , <i>P. brutia</i> , <i>Cistus</i> sp.	Serpentine	<b>MH011913</b>
	ML110102BC	M. Loizides	Cyprus, Kelefos	20-X-2012	ca 500 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	<b>MH011911</b>
	ML210192BPY	M. Loizides	Cyprus, Kelefos	29-X-2012	ca 500 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	<b>MH011914</b>
	ML210192BSP	M. Loizides	Cyprus, Kelefos	29-X-2012	ca 480 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	<b>MH011916</b>
	ML210192BLUR	M. Loizides	Cyprus, Kelefos	29-X-2012	ca 500 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	
	ML210192BLURL	M. Loizides	Cyprus, Kelefos	29-X-2012	ca 480 m	<i>Q. coccifera</i> subsp. <i>calliprinos</i> , <i>P. brutia</i>	Calcareous	

	ML210113BSP	M. Loizides	Cyprus, Kelefos	31-X-2012	ca 450 m	<b><i>Q. coccifera</i> subsp. <i>calliprinos</i>, <i>P. brutia</i></b>	Calcareous	
	ML21112BP	M. Loizides	Cyprus, Kelefos	2-XI-2012	ca 500 m	<b><i>Q. coccifera</i> subsp. <i>calliprinos</i>, <i>P. brutia</i></b>	Calcareous	<b>MH011915</b>
	FR2015610	L. Deparis	France, Chevalines	17-VII-1999	ca 600 m	<b><i>Picea abies</i>, <i>Carpinus betulus</i>, <i>F. sylvatica</i></b>	Calcareous	<b>MH011909</b>
	FR2015601	L. Deparis	France, Col de Cou	25-VII-1999	ca 1200 m	<i>Picea abies</i> , <i>Abies</i> sp.	Calcareous	<b>MH011904</b>
	FR2015603	L. Deparis	France, Grand Bornand	7-IX-2003	ca 1150 m	<b><i>Picea abies</i></b>	Calcareous	<b>MH011905</b>
	FR2011119	F. Richard	France, Puéchabon	14-IX-2011	ca 200 m	<b><i>Q. ilex</i></b>	Calcareous	<b>MH011890</b>
	FR2012079	E. Taschen	France, Pézilla-de-Conflent	24-XI-2011	ca 300 m	<b><i>Q. ilex</i></b>	Calcareous	<b>MH011893</b>
	FR2012224	F. Richard	France, Puéchabon	15-X-2012	ca 200 m	<b><i>Q. ilex</i></b>	Calcareous	<b>MH011896</b>
	FR2012265	E. Taschen	France, Pézilla-de-Conflent	26-X-2012	ca 300 m	<b><i>Q. ilex</i></b>	Calcareous	<b>MH011897</b>
	FR2012266	E. Taschen	France, Pézilla-de-Conflent	26-X-2012	ca 300 m	<b><i>Q. ilex</i></b>	Calcareous	<b>MH011898</b>
	JMB2014100102	J.-M. Bellanger	France, Puéchabon	30-IX-2014	ca 200 m	<b><i>Q. ilex</i></b>	Calcareous	<b>MH011902</b>
	DB141013	D. Borgarino	France, Buoux	13-X-2014	ca 500 m	<b><i>Q. pubescens</i></b>	Calcareous	<b>MH011903</b>
<b><i>Suillellus mendax</i> *</b>	ML90902BC	M. Loizides	Cyprus, Troodos	20-IX-2009	ca 1700 m	<b><i>Q. alnifolia</i></b>	Serpentine	<b>MH011912</b>
<b><i>Suillellus queletii</i> *</b>	ML41862SQ	M. Loizides	Cyprus, Troodos	26-VIII-2014	ca 1650 m	<b><i>Q. alnifolia</i>, <i>P. nigra</i> subsp. <i>pallasiana</i>, <i>C. creticus</i></b>	Serpentine	<b>MH011918</b>
<b><i>Xerocomellus chrysenteron</i></b>	FR2012200	F. Richard	France, Puéchabon	15-X-2012	ca 200 m	<b><i>Q. ilex</i></b>	Calcareous	<b>MH011894</b>
	ML80015XE	M. Loizides	Cyprus, Troodos	5-X-2008	ca 1750 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i>, <i>Prunus avium</i></b>	Serpentine	
	900151XE	M. Loizides	Cyprus, Troodos	15-X-2009	ca 1750 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i>, <i>P. avium</i></b>	Serpentine	
	ML511182XE	M. Loizides	Cyprus, Troodos	28-XI-2015	ca 1750 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i>, <i>P. avium</i></b>	Serpentine	<b>MH011839</b>
	ML6144XE	M. Loizides	Cyprus, Cedar Valley	04-IV-2016	ca 1100 m	<i>Cedrus brevifolia</i> , <i>Abies</i> sp., <i>P. brutia</i>	Serpentine	<b>MH011845</b>
<b><i>Xerocomellus cisalpinus</i> *</b>	ML21751XE	M. Loizides	Cyprus, Cedar Valley	15-VII-2012	ca 1100 m	<i>C. brevifolia</i> , <i>Abies</i> sp., <i>P. brutia</i>	Serpentine	
<b><i>Xerocomellus redeuilihi</i> *</b>	ML80932XE	M. Loizides	Cyprus, Moniatis	23-IX-2008	ca 750 m	<i>Q. alnifolia</i> , <i>Platanus orientalis</i> , <i>Alnus orientalis</i>	Alluvial	
	ML1117XE	M. Loizides	Cyprus, Fassouri	7-I-2011	ca 5 m	<i>Eucalyptus gomphocephala</i> , <i>Tamarix</i> sp.	Alluvial	
	ML411142XE	M. Loizides	Cyprus, Akrotiri	24-XI-2014	ca 10 m	<b><i>Pinus halepensis</i></b>	Basic	<b>MH011842</b>
	ML411142XE	M. Loizides	Cyprus, Akrotiri	24-XI-2014	ca 10 m	<b><i>Pinus halepensis</i></b>	Basic	
	ML411182XE	M. Loizides	Cyprus, Akrotiri	28-XI-2014	ca 10 m	<b><i>Pinus halepensis</i></b>	Basic	
	ML610102XR	S. Lewis	Cyprus, Pissouri	20-X-2016	ca 240 m	<b><i>P. brutia</i></b>	Calcareous	<b>MH011929</b>
	ML610132XR	M. Loizides	Cyprus, Pissouri	23-X-2016	ca 240 m	<b><i>P. brutia</i></b>	Calcareous	
<b><i>Xerocomellus sarnarii</i> *</b>	ML900101XE	M. Loizides	Cyprus, Platania	10-X-2009	ca 1120 m	<b><i>Q. alnifolia</i>, <i>P. brutia</i></b>	Basic	<b>MH011930</b>
	ML901132XE	M. Loizides	Cyprus, Platania	23-XI-2009	ca 1100 m	<i>Q. alnifolia</i> , <i>P. brutia</i> , <i>Abies</i> sp.	Basic	
	ML1101X	Y. Yiangou	Cyprus, Prodromos	13-X-2011	ca 1450 m	<b><i>Quercus infectoria</i> subsp. <i>veneris</i></b>	Acidic	<b>MH011837</b>
	ML51218XE	C. Hobart	Cyprus, Platres	8-XII-2015	ca 1200 m	<b><i>Q. alnifolia</i></b>	Serpentine	<b>MH011840</b>
	PAM11112710	P.-A. Moreau	France, Mérindol	27-XI-2011	ca 200 m	<b><i>Q. pubescens</i></b>	Calcareous	<b>MH011926</b>
<b><i>Xerocomus subtomentosus</i></b>	ML80842XE	M. Loizides	Cyprus, Troodos	24-VIII-2008	ca 1640 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i>, <i>A. andrachne</i>, <i>S. aria</i></b>	Serpentine	
	ML80872XE	M. Loizides	Cyprus, Troodos	27-VIII-2008	ca 1640 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i>, <i>A. andrachne</i>, <i>S. aria</i></b>	Serpentine	
	ML801103XE	M. Loizides	Cyprus, Troodos	30-IX-2008	ca 1650 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i></b>	Serpentine	
	ML800112XE	M. Loizides	Cyprus, Troodos	2-X-2008	ca 1700 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i></b>	Serpentine	
	ML800111XS	M. Loizides	Cyprus, Troodos	11-X-2008	ca 1750 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML800151XS	M. Loizides	Cyprus, Troodos	15-X-2008	ca 1650 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i></b>	Serpentine	
	ML9094XE	M. Loizides	Cyprus, Prodromos	4-IX-2009	ca 1350 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90951XE	M. Loizides	Cyprus, Troodos	15-IX-2009	ca 1650 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i></b>	Serpentine	<b>MH011841</b>
	ML90902XE	M. Loizides	Cyprus, Troodos	20-IX-2009	ca 1650 m	<b><i>Q. alnifolia</i></b>	Serpentine	<b>MH011843</b>
	ML90922XS	M. Loizides	Cyprus, Troodos	22-IX-2009	ca 1700 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML90013XS	M. Loizides	Cyprus, Troodos	3-X-2009	ca 1500 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML900101XS	M. Loizides	Cyprus, Platania	10-X-2009	ca 1100 m	<b><i>Q. alnifolia</i>, <i>P. brutia</i>, <i>P. orientalis</i></b>	Serpentine	<b>MH011844</b>
	ML21803XS	M. Loizides	Cyprus, Prodromos	30-VIII-2012	ca 1400 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	ML4161XS	M. Loizides	Cyprus, Troodos	1-VI-2014	ca 1640 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i></b>	Serpentine	
	ML41611XS	M. Loizides	Cyprus, Troodos	11-VI-2014	ca 1640 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i></b>	Serpentine	
	ML41613XS	M. Loizides	Cyprus, Prodromos	13-VI-2014	ca 1350 m	<i>Q. alnifolia</i> , <i>P. nigra</i> subsp. <i>pallasiana</i>	Serpentine	
	61952XS	M. Loizides	Cyprus, Trooditissa	25-IX-2016	ca 1250 m	<b><i>Q. alnifolia</i>, <i>P. brutia</i></b>	Serpentine	
	61972XS	M. Loizides	Cyprus, Troodos	27-IX-2016	ca 1640 m	<b><i>P. nigra</i> subsp. <i>pallasiana</i></b>	Serpentine	
	61972XS2	M. Loizides	Cyprus, Platres	27-IX-2016	ca 1200 m	<b><i>Q. alnifolia</i>, <i>P. brutia</i></b>	Serpentine	

ITS GenBank accession of sequenced collections in the last column. Species present in Cyprus and putative ECM hosts in bold characters.  
Species previously unreported in Cyprus annotated with an asterisk (\*).



**Fig. 1. Phylogeny of Boletaceae with emphasis on collections from Cyprus.** Maximum likelihood phylogenies of the 14 Boletaceae genera represented on the island, organized as: (A) *Caloboletus*–*Hemileccinum*–*Imperator*, (B) *Alessioporus*–*Rheubarbariboletus*–*Xerocomus*, (C) *Rubroboletus*–*Suillellus*, (D) *Butyriboletus*–*Exsudoporus*, (E) *Leccinellum*, and (F) *Boletus*–*Chalciporus*. The 99 sequences newly generated for the present work are highlighted in bold. Species represented on the island are labelled in bold. Unmarked branches are well supported (SH-aLRT values > 0.8), otherwise support values are indicated. The asterisk in panel F points to a doubtful published sequence.

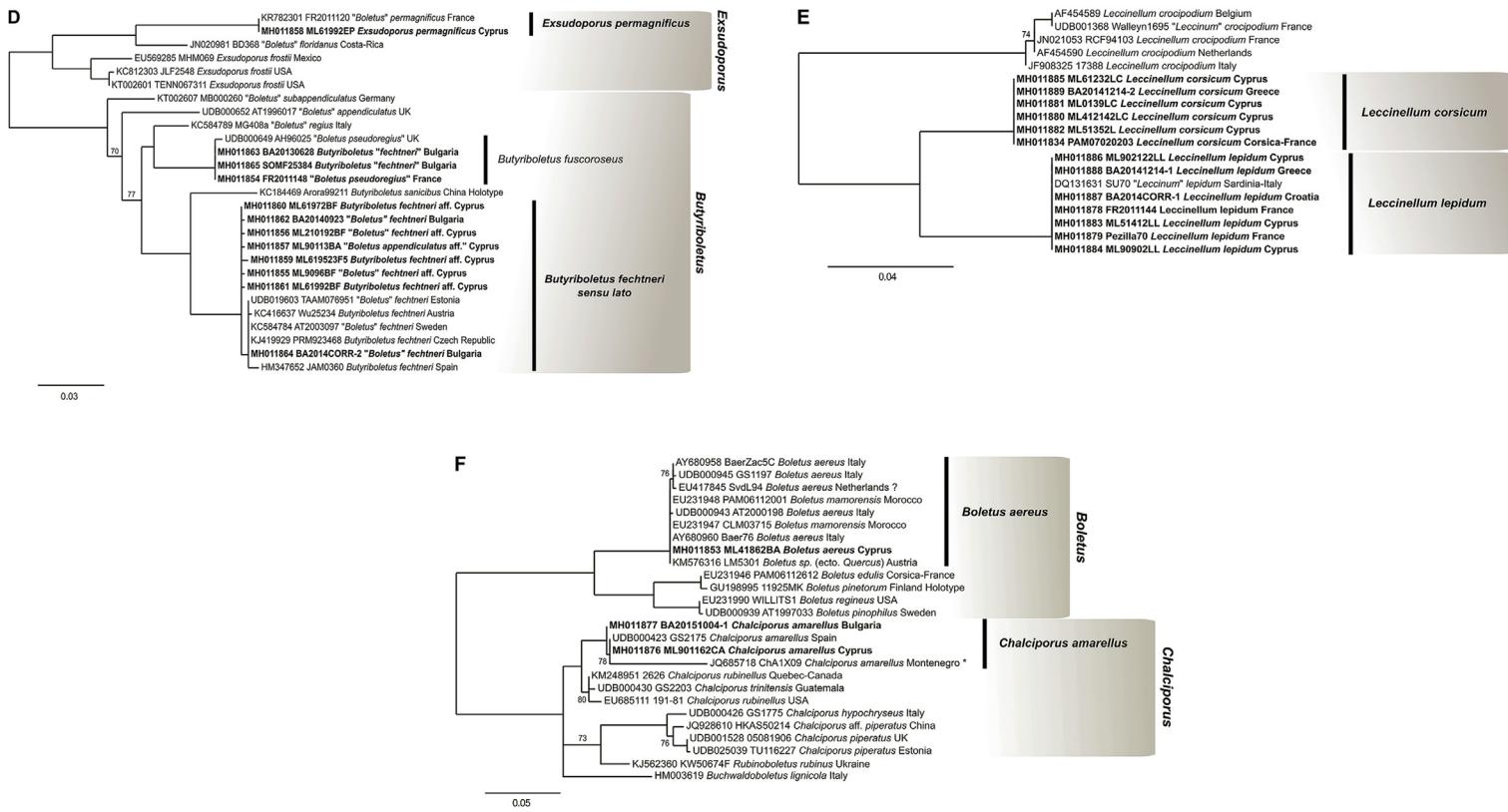
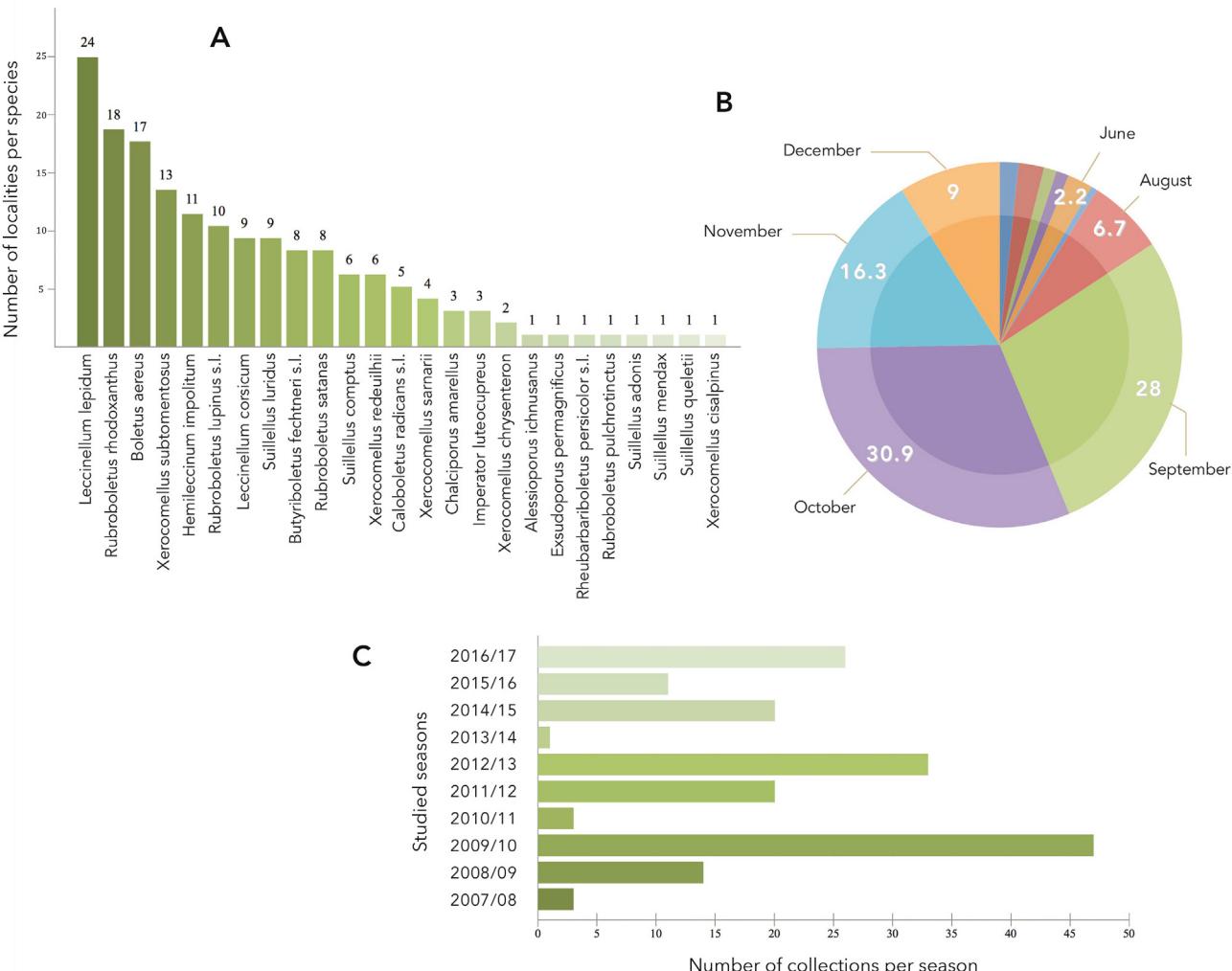


Fig. 1. (continued).



**Fig. 2. Abundance and phenology of Boletaceae fungi on Cyprus.** A: Number of documented localities per species; B: Phenological graph showing percentage (%) of Boletaceae collections per month over the studied decade, with most productive months annotated; C: Number of Boletaceae collections per season between 2007 and 2016.

## 2.5. Phylogenetic analyses

Phylogenetic analyses were performed online at [www.phylogeny.lirmm.fr](http://www.phylogeny.lirmm.fr) (Dereeper et al., 2008). Multiple sequence alignment was carried out with MUSCLE 3.7 (Edgar, 2004), using full processing mode and 16 iterations. When required, alignments were edited manually or with Gblocks 0.91b, set to lowest stringency in the selection of conserved blocks (Castresana, 2000; Talavera and Castresana, 2007). Maximum likelihood (ML) phylogenetic analyses were performed with PhyML 3.0 (Guindon et al., 2010), using the GTR + I + Γ model of evolution. Branch support was assessed using the non-parametric, Shimodaira–Hasegawa, version of the approximate likelihood-ratio test (SH-aLRT), implemented in the latest release of PhyML and which ensures high accuracy when SH-aLRT > 0.8 (Anisimova et al., 2011; Bellanger et al., 2015). Phylogenies were built using FigTree 1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree/>) and edited with Inkscape 0.91 (<https://inkscape.org/fr/>).

## 2.6. Nomenclature, terminology and herbarium material

Nomenclature follows Index Fungorum (<http://www.indexfungorum.org>), Mycobank (<http://www.mycobank.org>),

and recently proposed combinations based on phylogenetic inferences. Generic placement of *Exsudoporus permagnificus*, *Rubroboletus dupainii*, *Rubroboletus pulchrotinctus*, *Rubroboletus rhodoxanthus* and *Rubroboletus rubrosanguineus* follows Vizzini et al. (2014a,b) and Zhao et al. (2014b), respectively (see also “Discussion” and Fig. 1). The “rare” status is here applied to species recorded in two or three localities during the studied decade. The “very rare” status is applied to species recorded only in one locality during this period. Exsiccatae are kept at LIP (Herbarium of the Faculty of Pharmacy of Lille, France), the CEFE laboratory (Centre d’Ecologie Fonctionnelle et Evolutive, Montpellier, France), SOMF (Institute of Biodiversity and Ecosystem Research, Sofia, Bulgaria), and in the private collections of the authors.

## 3. Results

### 3.1. Diversity of boletoid fungi in Cyprus

The sequencing and phylogenetic analysis of 99 selected Boletaceae collections, 55 of which originated from Cyprus, revealed the presence of 25 species on the island, belonging to 14 genera (see Table 1 and Fig. 1A–F). Thirteen species, representing 7 genera, had

never been documented in Cyprus prior to this study, namely *Alessioporus ichnusanus* (Fig. 5A), *Butyriboletus fechtneri* s.l., *E. permagnificus* (Fig. 5F), *Imperator luteocupreus* (Fig. 5H), *Rheubarbariboletus persicolor* aff., *Suillellus adonis* (Fig. 5P), *Suillellus comptus* (Fig. 5Q), *Suillellus luridus* (Fig. 5R), *Suillellus mendax* (Fig. 5S), *Suillellus queletii* (Fig. 5T), *Xerocomellus cisalpinus* (Fig. 5V), *Xerocomellus redeuilhii* (Fig. 5W) and *Xerocomellus sarnarii* (Fig. 5X). Furthermore, our analysis revealed crypticism within *Bu. fechtneri*, *Caloboletus radicans*, *Rubroboletus lupinus* and *Rheubarbariboletus armeniacus*. This overlooked diversity will require specific or infraspecific taxonomic treatments from a wider geographical range, and is further discussed in the next section.

### 3.2. Fruiting patterns and estimated abundance

The most frequently occurring species, *Leccinellum lepidum*, was documented in 24 localities during the course of this study. Contrastingly, 11 out of the 25 species were documented in less than three localities each and are considered to be rare (3 species, namely *Chalciporus amarellus*, *I. luteocupreus*, *Xerocomellus chrysenteron*, which are known from two or three localities), or very rare (8 species, namely *A. ichnusanus*, *E. permagnificus*, *R. persicolor* s.l., *Ru. pulchrotinctus* (Fig. 5M), *S. adonis*, *S. mendax*, *S. queletii* and *X. cisalpinus*, which are known from one locality each). Two thirds (66.6%) of fruit body emergence episodes during the studied decade occurred in September and October (Fig. 2B). To a lesser extent, fruiting events occurred in November (15.1%), August (7.2%) and December (6.7%). Notably, more than half (61%) of all fruiting events in the colder months (December–February) belonged to a single species, *L. lepidum*. Strong inter-annual variation in Boletaceae fruiting was observed during the study period, with three highly prolific years (2009, 45 collections; 2012, 31 collections and 2016, 25 collections; Fig. 2C), alternating with poorly productive ones (2013, one collection; 2010, two collections and 2007, three collections). Pearson's correlation tests showed that the annual number of collections was significantly and positively correlated with annual ( $P = 0.048$ ), autumn ( $P = 0.005$ ), August ( $P = 0.01$ ) and December ( $P = 0.02$ ) rainfall amounts (Fig. 4). The occurrence of the late-fruiting and abundant *L. lepidum* was significantly correlated with August rainfall amount ( $P = 0.044$ ), but not with annual ( $P = 0.23$ ), autumn ( $P = 0.47$ ), or December ( $P = 0.5$ ) rainfall amounts. Overall, 15 out of the 25 species documented appeared in three or fewer seasons during the studied decade.

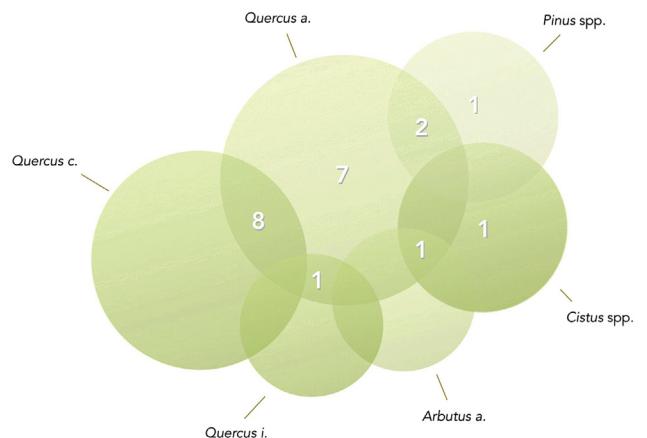
### 3.3. Host relationships

Regarding the surrounding ectomycorrhizal vegetation, 85.2% of boletoid collections were found in mixed forests and only 14.8% in monospecific stands (Table 1). The most frequent putative host present in the immediate vicinity of collected fruit bodies, was the narrow-endemic *Q. alnifolia* (110 out of 178 collections, or 61.8%). The second evergreen oak species on the island, *Q. coccifera* subsp. *calliprinos*, was present in around 30 collections (16.9%). By contrast, only one boletoid collection was found near the semi-deciduous *Q. infectoria* subsp. *veneris* (Fig. 3). More than half (6/11) of the rare or very rare species documented (*I. luteocupreus*, *A. ichnusanus*, *E. permagnificus*, *Ru. pulchrotinctus*, *S. mendax*, *S. queletii*), appear to be exclusively associated with *Q. alnifolia* on the island.

## 4. Discussion

### 4.1. An unexpected diversity unravelled

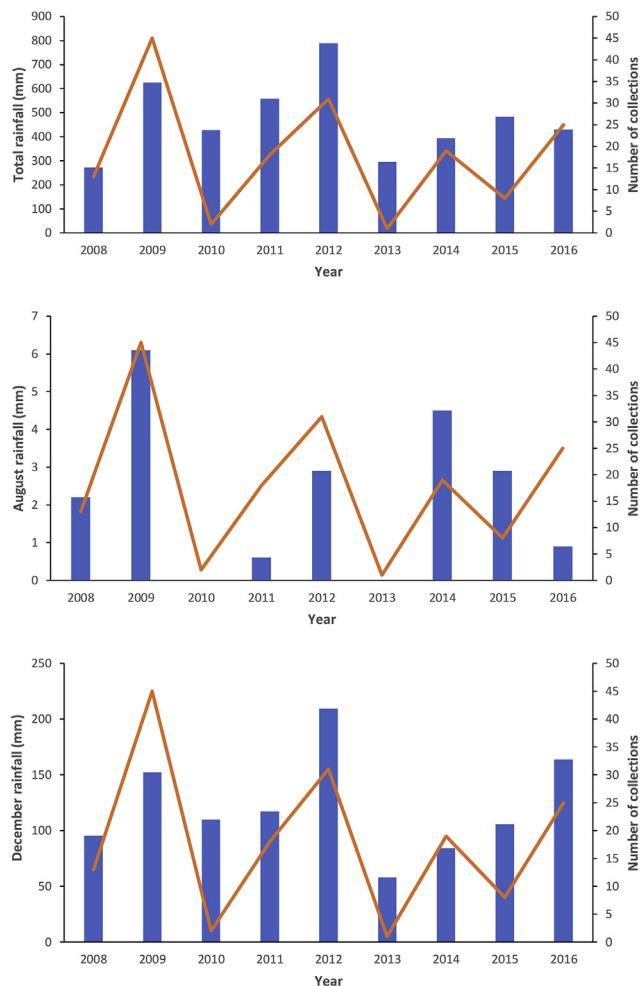
Contrary to previously available data suggesting Boletaceae



**Fig. 3. Most common Boletaceae hosts in Cyprus.** Number of associated species per host, based on above-ground observations between 2007 and 2016: *Quercus c.* = *Quercus coccifera* subsp. *calliprinos*; *Quercus a.* = *Quercus alnifolia*; *Pinus spp.* = *Pinus brutia*, *P. halepensis*, *P. nigra* subsp. *pallasianna*; *Cistus spp.* = *Cistus creticus*, *C. monspeliensis*, *C. salviifolius*; *Arbutus a.* = *Arbutus andrachne*; *Quercus i.* = *Quercus infectoria* subsp. *veneris*.

fungi are poorly represented in Cyprus, the results of this long-term study paint a very different picture. An unexpectedly rich diversity of boletoid fungi is unveiled, with at least twenty-five species phylogenetically confirmed to be present on the island, thirteen of them previously unreported. Interestingly, our phylogenetic analyses have detected crypticism within four species-complexes. Cypriot collections identified as *B. radicans* display typical features of this species and share a clade with four published sequences from Estonia and Montenegro (Figs. 1A and 5D). However, a collection from France (HKAS80856), already attributed to this taxon by Zhao et al. (2014a), and the newly generated collection EF61012B from Greece, may be equally claimed to represent this binomial. Deeper investigations, including type studies of "*Boletus radicans*" and satellite taxa are necessary, to clarify the full range of diversity and fix the nomenclature within this species complex (Assyov et al. in prep.).

A collection represented by a single basidiocarp morphologically resembling *R. persicolor*, has nested in a distinct clade, sister to that of *R. armeniacus* (Figs. 1B and 5K). This clade likely represents an undescribed species and is currently the subject of a separate study (Simonini et al., in prep.). Cypriot collections of *Ru. lupinus* on the other hand, are morphologically indistinguishable from continental collections of this taxon, but their ITS sequence analysis supports a phylogenetic isolate to have evolved on the island (Figs. 1C and 5L). More sequences from Greece, Turkey and other east Mediterranean localities will be necessary, before deciding which taxonomic rank, if any, should be assigned to Cypriot populations. Similarly, all sequenced Cypriot collections morphologically identified as *Bu. fechtneri*, nest, together with a collection from Bulgaria and a Cypriot collection previously identified as "*Boletus appendiculatus*" (Loizides et al., 2011), in a basal position relative to continental sequences of *Bu. fechtneri* (Figs. 1D and 5C). The paraphyly of the basalmost sequences in relation to the pan-European subclade, reflects the apparent lack of synapomorphy for "*Bu. fechtneri* aff.", and careful analysis of polymorphic positions within the lineage, and in particular three heterozygocities found in the ITS sequence of coll. ML61972BF, indicates that none of them segregate the two groups (Fig. 1, Loizides et al., 2019). Such finding, together with the presence of a second Bulgarian collection within the pan-European subclade, points to a single species with extensive gene flow between genetically polymorphic populations, rather than two reproductively isolated species. However, ongoing speciation with



**Fig. 4. Precipitation correlations to Boletaceae fruitings.** Yearly numbers of annual rainfall levels (blue bars, scale on left) and boletoid collections (red curves, scale on right) during the period 2008–2016, using Pearson's product-moment tests. From top to bottom: Annual, August, December.

incomplete haplotype sorting may take place in this lineage and a subspecies or variety rank for the Cypro-Bulgarian haplotype might be justified, following wider sampling in the future.

The generic placement of *E. permagnificus* has gone through controversial treatments in recent years. Vizzini et al. (2014a,b) erected the genus *Exsudoporus* to accommodate species with distinct morphological traits shared by this European taxon and the North American taxa *Boletus floridanus* and *Boletus frostii*. However, due to lack of sufficient sequences and convincing phylogenetic data, Wu et al. (2016) was reluctant to accept the newly proposed genus and considered *Exsudoporus* to be a synonym of *Butyriboletus*. Our well-sampled analysis unambiguously supports the monophyly of *Exsudoporus*, but also its sister-clade relationship with *Butyriboletus*; therefore, both a narrow generic treatment with the three species placed in *Exsudoporus*, or a more inclusive one with them placed in *Butyriboletus*, are in principle possible. Considering, nonetheless, (1) the intraspecific phylogenetic distances within *Butyriboletus sensu stricto* and comparatively much longer distance separating *Butyriboletus* from *Exsudoporus*; (2) the markedly pronounced, elongated and often 'sculpted' (raised) stipe reticulation shared by all three concerned species; (3) their predominantly reddish-orange hymenial colours; and (4) the exuding pores, features which are not seen in *Butyriboletus sensu stricto*, a distinct genus seems justified to accommodate these species, and

*Exsudoporus* is thus retained in the present study.

The most frequently encountered and consistently occurring bolete in Cyprus is *L. lepidum*, a typically Mediterranean species which nonetheless fruits late in the season in low temperatures (Fig. 2A). Preliminary phylogenetic inferences by Binder and Besl (2000) and Den Bakker and Noordeloos (2005) suggested that *L. lepidum* and *Leccinellum corsicum* are distinct species, but the two taxa suffered from insufficient sampling and were subsequently placed in synonymy by Bertolini (2014), on the basis of morphology. Nevertheless, our observations and analyses of several collections from Cyprus, Greece, Croatia and Corsica, confirm the presence of two phylogenetically, ecologically and phenologically distinct species (Figs. 1E, 5I–J): *L. lepidum*, a large (up to 20 cm in diameter), late autumn or winter species exclusively associated with evergreen oaks (*Q. alnifolia*, *Q. coccifera*, *Q. coccifera* subsp. *calliprinos*, *Quercus ilex*); and *L. corsicum*, a medium-sized (up to 10 cm in diameter), late winter or early spring species exclusively associated with rockroses (*Cistus ladanifer*, *C. monspeliensis*, *C. salviifolius*). Conversely, our analysis has failed to delineate between the widespread *Boletus aereus* and *Boletus mamorensis*, in concordance with Dentinger et al. (2010). Since neither phylogenetic, nor morphological, ecological or biogeographical data appear to segregate the two taxa, they should be regarded as synonyms, with the name *B. aereus* taking priority over the Moroccan taxon.

#### 4.2. Strict ecological niches and intimate relationships

At least fourteen putative ectomycorrhizal associations documented in this survey are reported for the first time, with the two evergreen oak species, *Q. alnifolia* and *Q. coccifera* subsp. *calliprinos*, revealed to be by far the most prolific hosts. Notably, out of the twenty-five Boletaceae taxa confirmed to be present on the island, nineteen are broadly or strictly associated with the narrow-endemic golden oak (*Q. alnifolia*), with seven of them exclusively documented under this host. Eight of the nineteen species recorded under *Q. alnifolia* were also found with *Q. coccifera* subsp. *calliprinos* (Fig. 3), while for four species found in mixed habitats (*Ch. amarellus* (Fig. 5E), *R. persicolor* aff., *X. cisalpinus* and the poorly known *S. adonis*), the exact ectomycorrhizal symbiont remains uncertain.

One of the most surprising results of this study has been the dearth of boletoid fungi documented under the semi-deciduous *Q. infectoria* subsp. *veneris*, with just a single collection of *X. sarnii* so far linked to this host. The reasons behind this 'fungal drought' in association with the gall oak are not quite clear, but may be related to a degree of host-specialization among boletes in the eastern Mediterranean, most of which appear to be associated with evergreen oaks of the ilicoid group rather than deciduous oaks (Binyamini and Avizohar-Hershenson, 1973; Biketova and Wasser, 2015). Alternatively, the scarcity of ectomycorrhizal fungi found under this host could merely reflect a particularly poor ectomycorrhizal community associated with this tree, or even highly erratic fruiting patterns in low elevation xeric ecosystems, where the gall oak currently survives as scattered trees or within relict, heavily fragmented stands.

In addition to highly specific plant associations, most boletes on the island appear to be confined within specific regions and exhibit very particular preferences with regard to substrate, altitude and climatic conditions. For instance, *Ru. rhodoxanthus* (Fig. 5N) can be locally frequent in years with early rainfall, but appears to be confined to serpentine and acidic substrates at the higher elevations of Troodos, where it is found exclusively in association with *Q. alnifolia*. *Xerocomus subtomentosus* (Fig. 5Y), apparently more versatile in its plant partners and equally frequent under pine and oak, is widespread at elevations above 1000 m, but also appears to be predominantly acidophilous. *Xerocomellus redeuilhii*, a



**Fig. 5. Diversity of Boletaceae fungi in Cyprus.** (A) *Alessioporus ichnusanus*, (B) *Boletus aereus*, (C) *Butyriboletus fechtneri* s.l., (D) *Caloboletus radicans* s.l., (E) *Chalciporus amarellus*, (F) *Exsudoporus permagnificus*, (G) *Hemileccinum impolitum*, (H) *Imperator luteocupreus*, (I) *Leccinellum corsicum*, (J) *Leccinellum lepidum*, (K) *Rheubarbariboletus persicolor* aff., (L) *Rubroboletus lupinus* s.l., (M) *Rubroboletus pulchrotinctus*, (N) *Rubroboletus rhodoxanthus*, (O) *Rubroboletus satanas*, (P) *Suillellus adonis*, (Q) *Suillellus comptus*, (R) *Suillellus luridus*, (S) *Suillellus mendax*, (T) *Suillellus queletii*, (U) *Xerocomellus chrysenteron*, (V) *Xerocomellus cisalpinus*, (W) *Xerocomellus redeuilhii*, (X) *Xerocomellus sarnarii*, (Y) *Xerocomus subtomentosus*.

Mediterranean species usually associated with oaks (Simonini et al., 2016), is most frequently seen under pines in Cyprus (*P. brutia*, *P. halepensis*), in low-elevation thermomediterranean matorral extending as far as the dunal zone. *Rubroboletus lupinus* s.l., *S. comptus* and *S. luridus* are fairly widespread under both evergreen oaks, but their fruiting is also highly dependent on early rainfall and were seen in significant numbers only once. The widespread *B. aereus* (Fig. 5B), a typically southern species reported from several Mediterranean islands such as Corsica (Dentinger et al., 2010), Naxos (Polemis et al., 2012), Sardinia (Brotzu, 2004) and Sicily (Venturella and Rocca, 2001), is curiously uncommon in Cyprus, where it is restricted to the highest peaks of the Troodos ophiolite, sparingly appearing between August and November. So far, it has been found on serpentine and igneous substrates under *Q. alnifolia*, *C. creticus* and *A. andrachne* (Loizides, 2011, 2016; Loizides et al., 2011), but was never seen on calcareous soil under *Q. coccifera* subsp. *calliprinos* or *Q. infectoria* subsp. *veneris*.

#### 4.3. An uncertain future unfolding

Based on the spatio-temporal frequency of their fruiting, eleven out of the twenty-five species documented in Cyprus (*A. ichnusanus*, *C. amarellus*, *E. permagnificus*, *I. luteocupreus*, *R. persicolor* s.l., *Ru. pulchrotinctus*, *S. adonis*, *S. mendax*, *S. queletii*, *X. chrysenteron* (Fig. 5U), *X. cisalpinus*) appear to be rare or very rare. In addition, four of the species present in Cyprus (*E. permagnificus*, *Ru.*

*pulchrotinctus*, *S. adonis*, *S. comptus*), appear to be regionally or globally rare (Simonini, 1998; Assyov, 2005; Muñoz, 2005; Gyosheva et al., 2006; Galli, 2007; Karadelev and Rusevska, 2013). For these species, complementary information regarding below-ground distribution of their mycelia is urgently needed, in order to confirm their status as endangered species (IUCN 2012). As can be seen in Fig. 4, the frequency of boletoid fruitings is highly correlated with above-average annual, late summer (August), autumn and, for spring species, early winter (December) rainfall, suggesting that most boletoid species on the island are highly restricted by low soil moisture and particularly depend on above-average late summer or early autumn rainfall episodes to produce sporocarps.

During the studied decade (2007–2016), the most productive seasons were 2009, 2012 and 2016, when exceptional weather conditions and above-average rainfall between August and October had occurred. In 2009, an average of 37.8 mm and 40.3 mm in precipitation was recorded in September and October (or 78.1 mm combined), which corresponds to 840% and 123% of average precipitation values, respectively. Similarly, in 2012, precipitation in October was 53.4 mm, accounting to 162% of the average precipitation for this month, while in 2016 precipitation in September and October was 8.1 and 23.5 respectively, although locally increased precipitation of 28.6 mm (or 286%) was recorded at the highest peaks of Troodos in September, correlating to increased boletoid fruitings in that area (Department of Meteorology official database

and Table 3, Loizides et al., 2019). Average rainfall, however, has been steadily decreasing over the past 30 y in Cyprus, with precipitation expected to further decrease by an additional 8–15% by 2030 (Michaelides and Pashiardis, 2008; Hadjinicolaou et al., 2010). These forecasts are congruent with a multitude of studies predicting increases in temperature, a decrease in annual precipitation and increases of the length and frequency of drought spells throughout the Mediterranean region (Giorgi, 2006; IPCC 2007; Giorgi and Lionello, 2008; Mariotti, 2010; Hoerling et al., 2012; Kelley et al., 2012; Zittis et al., 2014). More pessimistic outlooks predict an increase in temperature up to 5.5 °C in Cyprus, accompanied by a decrease in precipitation up to 30% by the end of the century (Lelieveld et al., 2012; Shoukri and Zachariadis, 2012). Under this scenario, the studied ecosystems are facing profound changes, including direct responses to both host-trees and associated mycota (Richard et al., 2011), as well as complex interaction shifts through soil feedbacks (Aponte et al., 2010; Bardgett and Wardle, 2010). Increased atmospheric evaporative demand due to climate warming might further lead to decreases in mycorrhizal fungi fruiting, which under some models are predicted to drop by as much as 40% (Ágreda et al., 2015). Such an outcome, could be detrimental for many of the species reported here, shown to rely on a delicate balance of mild temperatures and above-average early rainfall to produce sporocarps, fruiting within a very narrow window of opportunity several years apart.

Although no long-term data on population dynamics is presently available to directly assess any local or regional declines in the populations of boletoid fungi, several species throughout the Mediterranean basin are probably faced with similar threats. Changes in fungal phenology and fruiting patterns in response to climate warming have already been documented in several countries (Straatsma et al., 2001; Gange et al., 2007; Büntgen et al., 2012b; Kauserud et al., 2012; Boddy et al., 2014). In the Mediterranean region, drought-induced changes including autumnal fruiting delays, reductions in fruit body productivity and diversity, as well as forest growth declines, have in some cases become apparent (Büntgen et al., 2015). This pattern is consistent with previous findings from western North America, documenting a decrease of ectomycorrhizal fungal diversity, as well as reduced growth rates in trees, in areas that had been severely affected by long-term drought (Swaty et al., 2004). Studies from *Q. ilex* ecosystems in southern France, have further evidenced significant shifts in ectomycorrhizal community composition as a result of reduced rainfall, reporting an increase of saprobes and species belonging to drought-tolerant genera (Richard et al., 2011). This could mean boletoid species might be further threatened with increased competition from xerotolerant fungi, such as species of Cortinariaceae and Russulaceae, particularly within mixed pine/oak habitats. Such mixed tree communities compose the vast majority of ecosystems in Cyprus. Taking into account the forecasted increases in temperature and drought, as well as a possible loss of habitat and decline of plant-partners, but especially the high extinction rates seen on islands (up to 40 times higher in birds, for instance, see Whittaker and Fernández-Palacios, 2007), a rather alarming picture for the future of boletoid fungi in Mediterranean and insular ecosystems is unfolding.

#### 4.4. What needs to be done

To effectively conserve fungi, an understanding of their ecological needs and distributional patterns is necessary. Equally importantly, fungal diversity within vulnerable hotspots needs to be thoroughly documented and species accurately identified. The previously undetected diversity and crypticism unravelled in this study from a well-known hotspot of biodiversity, reaffirm that a lot

remains to be done in Mediterranean ecoregions, particularly Mediterranean islands. Considering the dramatic shifts in structure, dynamics and functioning of Mediterranean forests forecasted as a result of climate warming (Allard et al., 2008; Ágreda et al., 2015), understanding fungal diversity and plant-fungi dynamics in Mediterranean ecoregions and vulnerable hotspots, has become an urgent concern (Büntgen et al., 2012a, 2015; Taudiere et al., 2015).

The advent of molecular phylogenetic techniques has revolutionized our ability to detect cryptic speciation and resolve complex species-clusters. Cross-disciplinary studies from a wider geographical range are necessary to resolve species complexes within critical genera, such as *Butyriboletus*, *Caloboletus*, *Rubroboletus*, or *Rheubarbariboletus*. Above-ground inventories, although highly valuable tools, do not always provide a complete overview of plant-fungi interactions and organismic distribution, due to the multitude and complexity of factors influencing fungal fruiting and reproduction (Shahin et al., 2013; Boddy et al., 2014). Carefully targeted below-ground studies, particularly of poorly explored hotspots and neglected ecological niches are also necessary, not just for the purpose of documenting fungal diversity and host-specificities, but also to identify urgent conservation priorities (Myers et al., 2000; Behrens et al., 2010). Fungi with a highly specialized ecology (e.g. narrow host-range or habitat quality-dependent, see Taudiere et al., 2017), but also mutualistic fungi associated with endemic and/or highly vulnerable hosts, are evidently more imminently threatened by climate changes. In this respect, the drafting of regulative legislation regarding the harvest and commercial exploitation of fungi, as well as effective implementation of existing legislation (Art. 33 & 34, Περι Δασών Νόμος, 2012), are of paramount importance (Loizides et al., 2017). Since drought-induced changes are bound to affect fungi and tree-hosts alike, exploring fungal diversity within threatened or endemic habitats in Cyprus, such as *C. brevifolia*, *P. nigra* subsp. *pallasiana*, *Q. alnifolia* and *Q. infectoria* subsp. *veneris* ecosystems (all designated as priority habitats in the Natura 2000 ecological network), should be high priorities. Especially with regard to the latter, below-ground studies should clarify whether the gall oak is indeed a poor ectomycorrhizal host, as suggested by surveys so far, or whether above-ground sightings do not accurately reflect the diversity of associated fungal symbionts on its roots.

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