

Universidade de Évora - Escola de Ciências e Tecnologia

Mestrado em Biologia da Conservação

Dissertação

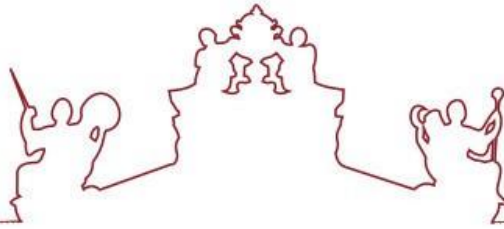
Ardeu a Mata da Margarça! - efeito e consequências do fogo nos macrofungos florestais

Bruno Alexandre Fragoso Natário

Orientadora / Celeste Maria Martins Santos e Silva

Évora 2019





Universidade de Évora - Escola de Ciências e Tecnologia

Mestrado em Biologia da Conservação

Dissertação

**Ardeu a Mata da Margarça! - efeito e consequências
do fogo nos macrofungos florestais**

Bruno Alexandre Fragoso Natário

Orientadora / Celeste Maria Martins Santos e Silva

Évora 2019



Constituição do júri

Presidente: Professor Doutor Paulo Sá Sousa, Universidade de Évora

Arguente: Professora Doutora Anabela Martins, Instituto Politécnico de Bragança

Orientadora: Professora Doutora Celeste Santos e Silva, Universidade de Évora

Agradecimentos

A realização desta dissertação não teria sido possível sem a intervenção das seguintes pessoas às quais estou eternamente agradecido:

Agradeço à minha orientadora Prof.^a Dr.^a Celeste Santos-Silva pelas valiosas sugestões e correções, bem como por todo o tempo, esforço, apoio e dedicação despendido ao longo deste trabalho.

Agradeço ao meu colega e amigo Rogério Louro pela ajuda, empenho e valiosos ensinamentos oferecidos durante o processo laboratorial de identificação dos macrofungos.

Agradeço aos meus pais, Lurdes Natário e Paulo Natário, por todo o apoio, paciência e incentivo que me prestaram ao longo deste trabalho.

Agradeço à minha namorada, Ana Silva, por todo o apoio, paciência, encorajamento e pelos ouvidos gastos durante esta aventura.

Agradeço aos meus colegas e amigos Francisco Barreto, João Alves, Mário Saramago e Nuno Gomes pela paciência e apoio que me deram e em especial pela companhia durante as campanhas de campo.

Por fim, gostaria de agradecer a todas as pessoas aqui não mencionadas, mas que de algum modo contribuíram para a realização desta dissertação.

*“I just wish the world was twice as big and
half of it was still unexplored.”*

(David Attenborough)

Índice

Agradecimentos	1
Organização da dissertação	4
Resumo	5
Abstract	5
Enquadramento geral	6
Os macrofungos e o Homem	6
O papel dos macrofungos nos ecossistemas	8
Os macrofungos, as florestas e fogo	13
Objectivos da dissertação	16
Área de estudo	17
Capítulo I:	
Macrofungi of Mata da Margaraça (Portugal), a relic from the Tertiary age	20
Capítulo II:	
Effects of fire on macrofungal communities of the Mata da Margaraça Laurisilva forest ..	37
Considerações Finais	59
Referências	60

Organização da dissertação

Esta dissertação encontra-se dividida em quatro componentes principais: Enquadramento geral, Capítulo I, Capítulo II e Considerações finais, antecidos de um resumo e abstract.

No enquadramento geral é extensamente explorada a temática dos macrofungos e a sua importância para os ecossistemas florestais, com foco principal nas interações ecofisiológicas macrofungo-ambiente e macrofungo-planta. É ainda explorada a temática do fogo e de que forma este agente afecta os macrofungos florestais, de modo a introduzir a problemática geral que está no cerne desta dissertação.

O Capítulo I consiste no artigo “Macrofungi of Mata da Margaraça (Portugal), a relic from the Tertiary Age”, publicado na revista Biodiversity Data Journal, como tal a sua estrutura encontra-se de acordo com as regras da revista e difere da restante dissertação. Neste capítulo é elaborada uma ampla descrição das características topográficas, geológicas e edafoclimáticas da Mata Nacional da Margaraça, assim como uma descrição da diversidade macrofúngica pré e pós fogo de 2017.

O Capítulo II apresenta o estudo efectuado com o objectivo de compreender o efeito do fogo nas comunidades macrofúngicas da Mata Nacional da Margaraça. Neste capítulo é comparada a riqueza, diversidade e abundância macrofúngica em áreas sujeitas a diferentes graus de severidade do fogo.

Por fim, nas Considerações Finais, os resultados dos dois estudos são apreciados de uma forma global, visando responder à questão: quais os efeitos e consequências do fogo nos macrofungos florestais.

Resumo

A Mata Nacional da Margarça é uma floresta da Laurisilva situada numa área de distinta influência atlântica no seio de uma zona marcadamente mediterrânica. Em 2017, 90% desta Mata ardeu, pondo em risco a sua biodiversidade. Este estudo, elaborado entre 2018-2019, representa a primeira checklist de macrofungos da Mata da Margarça e o primeiro estudo sobre a interação macrofungos-fogo na Laurisilva. Foram registadas 272 espécies, das quais 74 são novas para Portugal e 116 são novas para a Beira Litoral. Os índices de diversidade macrofúngica diminuíram entre as áreas não queimadas e as queimadas. A riqueza de espécies micorrízicas e a proporção micorrízicos/sapróbios provaram ser bons indicadores da ocorrência de fogo, mostrando diferenças significativas entre as áreas não queimadas e queimadas. Considerando a abundância de espécies de macrofungos, foram encontradas diferenças significativas entre as áreas não queimadas e queimadas, mas não entre as áreas queimadas com diversos graus de severidade.

Palavras chave: Fogo; Macrofungos; Floresta; Fungos pós-fogo; Severidade do fogo.

Mata Da Margarça burned down – fire effects and consequences on forest macrofungi

Abstract

Mata Nacional da Margarça is a patch of laurel forest that prevails confined in a vale with a distinct Atlantic influence surrounded by a marked Mediterranean climate. A fire occurred in 2017 burning 90% of this area and putting at risk its biodiversity. The present work represents the first macrofungal species list to Mata da Margarça and the first study on macrofungal-fire interactions on laurel forest. The surveys occurred between 2018-2019. A total of 272 species were documented, being 74 new records to Portugal and 116 to Beira Litoral. The macrofungal diversity indexes decreased from unburned to burned plots. The mycorrhizal richness and mycorrhizal/saprotrophic proportion proved to be good indicators of fire events, since all showed significant differences between unburned and burned plots. Overall, a clear dissimilarity in macrofungal abundance was found between unburned and burned plots, but no clear distinction was observable between low to high fire severity plots.

Keywords: Fire; Macrofungi; Forest; Post-fire fungi; Fire severity.

Enquadramento Geral

Os macrofungos e o Homem

As florestas representam, no nosso planeta, 30% a 40% da área terrestre (Waring & Running, 2007) sendo por isso fácil de entender a importância destes ecossistemas. Contudo, a exploração de madeira e a abertura de clareiras, prolongadas ao longo dos séculos, ocasionou a perda de mais de 50% da cobertura florestal original. Estes sistemas, de complexidade imensurável, apresentam uma vasta seleção de recursos naturais, os quais desde muito precocemente na história do Homem se tornaram indispensáveis. O Homem iniciou a sua passagem neste planeta como habitante da floresta, estando dependente dos seus recursos para sobreviver (alimentação e abrigo). Mais recentemente, a importância da floresta tomou outros contornos. Deixou de ser essencial para a alimentação, uma vez que o ser humano passou a cultivar/produzir o seu próprio alimento. A floresta tornou-se essencial para a obtenção de matérias primas (madeira, resina, celulose, cortiça) e implementação de atividades lúdicas, como a cinegética e a colheita de cogumelos e frutos.

Os macrofungos (fungos produtores de cogumelos) são parte integrante dos ecossistemas florestais e desde os primórdios da civilização humana que é conhecida a sua potencialidade para o quotidiano do Homem. Uma das evidências mais antigas do uso de cogumelos pelo Homem remonta ao Paleolítico (Power et al., 2005), contudo os primeiros registos figurativos surgiram muito mais tarde, entre 1450 a.C. e 1200 a.C. Um destes registos data de 1200 a.C. na cidade de Herculaneum, numa pintura em azulejo na qual foi identificado o cogumelo da espécie *Lactarius deliciosus* (L.) Gray (Moreno & Manjón, 2010) (Fig. 1). Esta pintura ilustra um “armazém” onde é possível distinguir uma espécie de tordo (*Turdus philomelos* Brehm) e o cogumelo mencionado anteriormente, que possivelmente estariam armazenados para posterior consumo. Mais tarde, entre os séculos II d.C. e IV d.C., é citado na obra “Storia della Micologia Italiana”, de Giacomo Lazari, um método para cultivar macrofungos, que consiste em colocar estrume de equinos debaixo de uma figueira e regar abundantemente (Moreno & Manjón, 2010). Posto isto, é perceptível que um dos mais antigos usos dos macrofungos se prende com a sua colheita (cogumelos silvestres) e produção para consumo humano.

Atualmente, são bem conhecidas as propriedades que tornam os cogumelos um “alimento dos deuses” como acreditavam os romanos. Estas frutificações dos macrofungos possuem elevado teor em água (80 a 90 %), são ricas em proteínas e fibras e possuem um baixo teor em gorduras, hidratos de carbono assimiláveis e sódio, sendo, portanto, um alimento de baixo valor calórico. Conhecem-se aproximadamente 2.000 espécies de fungos produtores de cogumelos comestíveis (p. ex. *Amanita ponderosa* Malençon & R. Heim, *Boletus edulis* Bull., *Lactarius deliciosus* (L.) Gray e *Terfezia* spp.)

entre as quais 25 são cultivadas (p. ex. *Agaricus bisporus* (J.E. Lange) Imbach, *Lentinula edodes* (Berk.) Pegler, *Pleurotus* spp.). Visto que grande parte dos cogumelos comestíveis são silvestres, é importante mencionar que existem cogumelos silvestres que podem conter micotoxinas e são passíveis de ser confundidos com os comestíveis. Alguns dos casos mais notáveis são a confusão que ocorre entre *Amanita ponderosa* Malençon & R. Heim (espécie comestível) e *Amanita boudieri* Barla (espécie tóxica) ou entre *Tricholoma equestre* (L.) P. Kumm. (espécie comestível em quantidades moderadas) (Fig. 2) e *Amanita phalloides* (Vaill. ex Fr.) Link (espécie mortal) (Fig. 2).



Figura 1 – "Tordos e cogumelos" – pintura na parede da Casa do Veado em Herculaneum (Nápoles, Itália), Museu de Arqueologia (Raso, 2018).

Os cogumelos não possuem só valor nutricional, mas também medicinal. As propriedades medicinais dos cogumelos são conhecidas há tanto tempo quanto o seu potencial nutricional, sendo utilizados na medicina asiática há mais de 10.000 anos. Estes macrofungos foram associados à saúde, recuperação, longevidade, proezas sexuais, sabedoria e felicidade. O seu potencial medicinal passa por melhorar a resistência física, curar constipações, reduzir o colesterol no sangue (*Lentinula edodes*), estancar hemorragias e cauterizar ferimentos (*Fomitopsis betulina* (Bull.) B.K. Cui, M.L. Han & Y.C. Dai, *Fomes fomentarius* (L.) Fr.). Atualmente, conhecem-se cerca de 270 espécies de cogumelos com propriedades medicinais. Estas constituem uma vasta e ainda inexplorada fonte de compostos activos benignos, com aplicações sobretudo como potenciadores do sistema imunitário e com acção anti-tumoral. A maioria destes compostos activos são polissacarídeos, também conhecidos por β -glucanos, que interagem com o sistema imunitário, regulando aspectos específicos da nossa resposta imunológica, aumentando as defesas do organismo contra agentes patogénicos e tendo

efeitos citotóxicos sobre as células cancerígenas.

Apesar dos usos acima mencionados serem os mais comuns e de maior valor, estes fazem parte dos infindáveis usos possíveis para os cogumelos. Em épocas passadas, os cogumelos eram utilizados para colorir vestuário, preparar pinturas corporais, para usos recreativos e culturais. Mais recentemente, alguns usos mais alternativos têm sido revelados, como o uso para materiais de construção, embalagens degradáveis e como substituto do poliestireno extrudido.

É, portanto, palpável a importância dos macrofungos para o cotidiano e evolução do ser humano como civilização e espécie.



Figura 2 – *Amanita phalloides* (Vaill. ex Fr.) Link (Archenzo, 2012) (lado esquerdo) e *Tricholoma equestre* (L.) P. Kumm. (David Braird, 2007) (lado direito).

O papel dos macrofungos nos ecossistemas

No tópico anterior foi perceptível a importância dos macrofungos para o Homem. Uma vez que estes são membros integrantes das florestas, datando a sua origem a uma época muito anterior ao aparecimento do *Homo sapiens sapiens* L., qual será o seu papel ecológico e funcional como “sócios” das comunidades florestais?

Para entender a magnitude do papel dos macrofungos nas florestas é preciso perceber a sua fisionomia/fisiologia. Os macrofungos são organismos eucarióticos, constituídos por filamentos de células justapostas com paredes quitinosas. O conjunto destes filamentos (hifas), que formam o corpo vegetativo destes organismos, denomina-se micélio. Estes organismos produzem estruturas reprodutivas denominadas carpóforos (cogumelo) onde ocorre a produção de esporos. Dado que estes não produzem o seu próprio alimento, são heterotróficos por absorção, desenvolveram diferentes estratégias tróficas para obter os nutrientes de que necessitam para sobreviver. Podemos descrever três estratégias tróficas para os macrofungos: micorrízicos (mutualistas com plantas), sapróbios

(decompositores de matéria orgânica) e parasitas (de fungos [*Tremella* spp.], plantas [*Armillaria* spp.] e animais [*Cordyceps* spp.]), podendo desenvolver-se no solo (micorrízicos e terrícolas), material lenhoso (lenhícolas), excrementos (coprófilos), húmus (humícolas), cadáveres animais (necrófagos) entre outros.

O solo é o substrato com maior representatividade de macrofungos, sendo possível encontrar 13 km de micélio em 2,54 cm³ de solo. Tendo em conta que em 2013 a área florestal intacta era de cerca de 12 milhões de km², fazendo alguns cálculos minimalistas, se a camada orgânica do solo do nosso planeta possuísse somente 1 cm de profundidade e se só existisse micélio em florestas intactas, estaríamos a falar de 60 milhões de km de micélio no solo. Se considerarmos todos os restantes ecossistemas, excluindo desertos e massas de água, é quase inconcebível a quantidade de micélio que habita o solo do nosso planeta. Wallander et al. (2001) e Nilsson et al. (2005) estimaram que a quantidade total de micélio ectomicorrízico produzido por ano pode atingir 600 kg/ha em florestas mistas de *Picea abies* (L.) H. Karst. e *Quercus robur* L. Em conjunto, os fungos do solo ocupam uma área e representam um valor da biomassa total bastante consideráveis, existindo casos excepcionais a nível do indivíduo. Na Suíça, um indivíduo da espécie *Armillaria ostoyae* (Romagn.) Herink (cogumelo do mel) foi descrito como tendo mais de 1000 anos e ocupar cerca de 500 m². Outro caso ilustre ocorre no estado norte-americano de Oregon, onde foi descrito um macrofungo com 600 toneladas, 2400 anos e 8 km² de extensão.

Assim sendo, o impacto destes organismos na dinâmica e composição do solo é proporcional à sua representatividade. A componente inorgânica dos solos, que por norma é incorporada no mesmo por ação de elementos abióticos, também é fortemente modificada pela ação dos macrofungos. Foi demonstrada a capacidade dos macrofungos, neste caso ectomicorrízicos, de dissolver e transformar vários minerais como clorite, apatite, mica, moscovite, biotite e microclina (Wallander et al., 2002; Arocena et al., 2004; van Schöll et al., 2006). Os fungos também alteram as propriedades físicas do solo, à medida que o micélio se expande cria cavidades e túneis que aumentam o arejamento do solo, a incorporação de água e nutrientes e criam habitat para uma variedade imensa de formas de vida. Caeser-TonThat (2002) descreve a capacidade de produção de polissacarídeos por parte de um *Basidiomycota* que funciona como agente de “soil-binding”, prevenindo a erosão do solo. Os micélios são ainda responsáveis pela filtração do solo, destruindo agentes patogénicos como vírus, protozoários e bactérias e degradando compostos poluentes que resultam da ação humana. Mais ainda, enriquecem o substrato envolvente com substâncias que resultam do seu metabolismo como polissacarídeos, glicoproteínas, enzimas, hormonas, tendo um papel fulcral no ciclo de nutrientes do solo.

O relevante papel dos fungos nos processos físicos e químicos da formação dos solos atesta a sua importância para a sobrevivência e manutenção das comunidades florestais. Contudo, a sua

influência mais directa na vegetação está na formação de micorrizas que, no caso dos macrofungos, são maioritariamente ectomicorrizas. Esta interação planta-macrofungo resulta da ligação - penetração intercelular das hifas que constituem o macrofungo - às raízes de uma planta parceira e tem como objetivo a troca de compostos entre os intervenientes. As ectomicorrizas aumentam exponencialmente a disponibilidade de água e nutrientes essenciais, como carbono, azoto e fósforo, para a planta. Este fenómeno ocorre a nível físico, pois a ectomicorriza aumenta a área útil de absorção das raízes na rizosfera; a nível químico, dado que o fungo consegue captar e disponibilizar à planta nutrientes que esta sozinha não absorveria do solo; a nível biológico, pois o fungo mutualista protege a planta de possíveis infecções de agentes patogénicos. A vasta gama de necessidades fisiológicas, tanto das plantas como dos macrofungos, variam com a ontogenia, fenologia e as condições abióticas, ocasionando uma sucessão no estabelecimento de diferentes parcerias que dão origem a uma intrincada rede de micélios formada por diversas espécies de fungos e plantas. Contudo, as diversas espécies de macrofungos ectomicorrízicos têm estratégias diversas, podendo ser generalistas (formando micorrizas com várias espécies de plantas hospedeiras) ou especialistas (formando micorrizas exclusivamente com uma espécie ou género de planta) (Bruns et al., 2002; Selosse et al., 2006), facto que abre um mundo de possibilidades funcionais complementares que oferecem à planta mais resiliência e uma maior capacidade de produção de biomassa (Simard & Durrall, 2004; Courty et al., 2010).

Newman (1988) sugeriu que, em sistemas florestais, várias plantas micorrízicas poderiam estar ligadas por uma rede de micélio, a qual denominou de “Common Mycorrhizal Network” (CMN), com implicações relevantes para o funcionamento dos ecossistemas. Apesar de à época a maior parte dos estudos que corroboravam esta teoria estarem a ser desenvolvidos em laboratório, mais recentemente os avanços ao nível da biologia molecular permitiram comprová-la em áreas florestais (He et al., 2003). Ainda assim, à data era conhecido um exemplo muito comum desta interação: o caso das plantas micoheterotróficas obrigatórias de algumas famílias de orquídeas, como as *Orchidaceae* e *Montropaceae*. Estas são plantas não fotossintéticas que adquirem hidratos de carbono (até 85%) por intermédio do fungo, e visto que o fungo é, ele próprio, incapaz de produzir matéria orgânica, é expectável que este composto provenha de uma planta fotossintética (Gebauer & Meyer, 2003; Leake et al., 2004; Bidartondo et al., 2005; Leila et al., 2013). A troca/ facilitação de nutrientes planta-macrofungo atinge outras proporções quando se assume a existência de um CMN: no caso das *Orchideaceae* indica a existência de troca de hidratos de carbono entre duas plantas. McKendrick et al. (2000) concluiu que quando orquídeas da espécie *Corallorhiza trifida* Châtel. não se encontravam ligadas a uma CMN com plantas autotróficas, perdiam aproximadamente 13% da sua biomassa.

É teorizado que a CMN adquire extrema importância quando as plantas estão com défice de hidratos de carbono. Nas referidas circunstâncias, a CMN permite mobilizar hidratos de carbono de

plantas bem nutridas para as mais carentes, mas também transportar hidratos de carbono resultantes da degradação da matéria orgânica do solo. Isto porque se sabe que alguns fungos micorrízicos têm a capacidade de produzir enzimas decompositoras e tem sido verificado um aumento da produção destes compostos em épocas em que as plantas hospedeiras se encontram com défice de hidratos de carbono (Courty et al., 2007; Cullings et al., 2008). A transferência de hidratos de carbono entre plantas poderá ser um fenómeno para explicar o facto de plantas jovens, fortemente ensombradas por plantas mais velhas e mais capazes, conseguirem vingar. Read et al. (1984) comprovou que existe transferência de hidratos de carbono de plantas “de sol” para plantas “de sombra”, no sentido de promover o desenvolvimento das últimas (Read et al., 1985 em Simard & Durall, 2004). Situações similares foram constatadas para a nutrição mineral, maioritariamente para o azoto (N) e em menor escala para o fósforo (P) (Simard et al., 1997; Fellbaum et al., 2014). Isto porque, a transferência de P entre plantas só parece ser verdadeiramente importante quando existe deficit de P no solo (Tibbett et al., 1998; Jentschke et al., 2001; Wilson et al., 2006), ocorrendo igualmente a translocação de P, viabilizada por fungos micorrizicos, de raízes em decomposição para as plantas vivas (Johansen & Jensen, 1996). Resumindo, a quantidade de nutrientes que as plantas hospedeiras fornecem aos fungos são variáveis de planta para planta e a forma como esses fungos redistribuem os nutrientes por outras plantas hospedeiras também o é (Selosse et al., 2006; Courty et al., 2010), podendo deixar, em casos extremos, ao fungo a função de “decidir” quem sobrevive.

O material lenhoso de uma floresta representa a maior porção de biomassa da mesma, e a sua produção consome quantidades consideráveis de C e de nutrientes. Muitos desses nutrientes encontram-se retidos nos detritos vegetais, em particular na madeira morta, tendo Pan et al. (2011) estimado que, anualmente, no lenho caído encontram-se sequestrados 73×10^{12} kg de C. Nas florestas, os fungos sapróbios são os responsáveis pela reciclagem de grandes quantidades de carbono e outros nutrientes, funcionando como decompositores primários, secundários e terciários, mas é como decompositores primários (lenhícolas) que assumem um papel crucial. A lenhina é um complexo de biopolímeros recalcitrantes que representa 10 a 40 % dos tecidos das plantas lenhosas (Hobbie et al., 1999) e somente os fungos a conseguem degradar de forma eficaz (Boddy et al. 2008), como é o caso da espécie *Trametes versicolor* (L.) Lloyd (Fig. 3). Outros compostos vegetais mais fáceis de degradar - celulose, hemicelulose, etc. - inicialmente decompostos por insectos e bactérias, também são uma fonte de C explorada pelos fungos florestais (maioritariamente decompositores secundários). Os fungos não decompõem apenas detritos vegetais, mas todas as substâncias passíveis de lhes fornecer energia, como húmus (fungos humícolas, um exemplo de decompositores terciários), dejetos (fungos coprófilos), quitina, etc.

Contrastante aos fungos sapróbios, os parasíticos obtêm os seus nutrientes através de organismos vivos, penetrando as suas defesas e por vezes causando doenças ou até mesmo a morte

do hospedeiro. Estes organismos funcionam como estruturadores ecológicos das comunidades florestais, “predando” plantas e animais que, na sua maioria, não possuem outros “predadores” naturais. Alguns exemplos notórios destes organismos são os géneros *Armillaria* (Fr.) Staude, *Cordyceps* Fr. e fungos nematófagos. O género *Armillaria* caracteriza-se por parasitar a área radicular de espécie vegetais lenhosas, e, dependendo da sua virulência, podem dizimar florestas inteiras. As espécies do género *Cordyceps* (Fig. 4), por outro lado, são fungos parasitas de *Elaphomyces* T. Nees e maioritariamente de artrópodes. Neste último caso, o fungo desenvolve o seu micélio no interior do invertebrado, absorvendo os nutrientes e frutificando assim que for favorável, ocorrendo sempre a morte do hospedeiro. Por fim, os fungos nematófagos (*Coprinus comatus* (O.F. Müll.) Pers.) (Luo et al., 2004) são fungos que se especializaram em predar nemátodes através de armadilhas, endoparasitismos, etc. Estes podem ser bastante importantes para controlar populações de nemátodes infestantes de algumas espécies vegetais.



Figura 3 – *Trametes versicolor* (Scheibner, 2013).

O papel dos macrofungos nas florestas não se limita às suas acções directas que derivam do seu nicho trófico. Assumem ainda extrema importância no funcionamento dos ecossistemas florestais devido às suas capacidades de modelar o habitat e constituírem uma importante fonte de alimento. Muitos macrofungos são responsáveis pela criação de microhabitats, que originam através de processos de decomposição, criando fendas e cavidades que são essenciais para muitas aves, mamíferos, artrópodes e plantas epífitas (Fritz & Heilmann-Clausen, 2010; Remm & Lohmus, 2011; Cockle et al., 2012). Estes organismos estão ainda na base da cadeia trófica da microfauna (p. ex. pequenos mamíferos e invertebrados). O micélio, por exemplo, faz parte da dieta de muitos

invertebrados que habitam o solo, como diversos nemátodes e espécies da subordem *Collembola* e da ordem *Haploutaxida* (Klironomos & Moutoglis, 1999; Tuffen et al., 2002). Por sua vez, os carpóforos (cogumelo) desempenham funções de abrigo e alimento para vários animais. São habitat particularmente importante para insetos, especialmente para espécies das ordens *Diptera* e *Coleptera*, podendo albergar mais de 260 espécies da ordem *Coleoptera* (Nikitsky & Schigel, 2004).

Afora o exposto, é necessário aprofundar o conhecimento sobre a ecofisiologia dos macrofungos por forma a descrever plenamente a sua importância para os ecossistemas. Apesar do muito que falta conhecer, é perceptível a necessidade de conservar estes organismos, de modo a manter os ecossistemas saudáveis. Ameaças como o fogo, má gestão dos solos e práticas agrícolas e florestais incorretas põem em causa a sobrevivência destes seres e consequentemente a dos ecossistemas e dos restantes grupos biológicos que os habitam.



Figura 4 – *Cordyceps militaris* (Pato, 2008).

Os macrofungos, as florestas e o fogo

A exploração das áreas florestais tem aumentado de modo a responder às necessidades da crescente população humana. O aumento da exploração tem sido acompanhado por um conjunto de más práticas e má gestão dos recursos. A introdução de espécies exóticas, a sobre-exploração de recursos, processos descontrolados de desflorestação, aumento das áreas agrícolas, mobilização dos solos, uso de pesticidas, entre outros afetam as comunidades florestais e resultam na perda de biodiversidade, disrupção dos ciclos biogeoquímicos e sobretudo, à escala global, no que hoje é denominado de alterações climáticas. Nos últimos anos, devido às alterações climáticas, tem-se

verificado um aumento da ocorrência de catástrofes naturais como fogos, tornados, tempestades, terremotos e cheias. Estes acontecimentos têm consequências devastadoras não só para as comunidades humanas, mas também para as restantes comunidades bióticas.

O fogo representa uma das perturbações naturais mais assoladoras para as comunidades florestais. Só em 2017, o California Department of Forestry and Fire Protection registou para o estado da Califórnia 500 mil hectares queimados. Em Portugal, segundo o Instituto para a Conservação da Natureza e das Florestas (ICNF) (2017) ardeu, em 2017, um total de 420 mil hectares até 16 de outubro desse ano. Estes incêndios florestais dizimaram uma vasta área e provocaram alterações bruscas quer na fisionomia da paisagem (Fig. 7 D), quer no funcionamento dos ecossistemas, tendo como consequências: a perda de vegetação, o aumento da temperatura do solo, a combustão da camada orgânica do solo, a libertação para a atmosfera de nitrogénio e carbono e a deposição de carvão e cinza (Monleon & Cromack, 1996; Nearya et al., 1999). Estes eventos afetam os macrofungos florestais de forma direta, através da combustão ou aquecimento da camada orgânica do solo (Hart et al., 2005), que resulta na morte dos organismos, ou de forma indireta através da perda de plantas mutualistas, disponibilidade de substratos, nutrientes e água (Hart et al., 2005; Vázquez-Gabise et al., 2011).

Várias têm sido as tentativas de explicar os efeitos do fogo nas populações de macrofungos. Hart et al. (2005) teorizou que as respostas a longo prazo das comunidades microbianas do solo ocorrerão, primariamente, devido a alterações na composição da flora e vegetação, devido à forte relação entre as plantas e os microrganismos do solo. Alguns estudos correlacionaram índices de intensidade, frequência ou severidade do fogo com índices de diversidade de macrofungos, taxas de micorrização, entre outros (Smith et al., 2005; Kipfer et al., 2010). De entre os três índices do fogo mencionados anteriormente, a severidade do fogo é a que melhor descreve o efeito do fogo nos ecossistemas (Keley, 2009). Ryan & Noste (1985) desenvolveram este índice que utiliza a matriz vegetal e os impactos no solo para refletir o grau de matéria orgânica consumida. Na maioria dos estudos este índice está dividido em 5 categorias: “Unburned” (1), “Scorched” (2), “Light” (3), “Moderate” (4), “Deep burning” (5) (Keley, 2009; Ryan & Noste, 1985). Quando aplicados índices com semelhante categorização do impacto do fogo, os resultados são díspares para ecossistemas semelhantes como, por exemplo, em florestas de *Pinus pinaster* Aiton. Jonsson et al. (1999), Kennedy et al. (2010) e Rincón & Pueyo, (2010) verificaram que a severidade do fogo não afetou significativamente a riqueza e diversidade das comunidades macrofúngicas. Contudo, Dahlberg et al. (2001), Dahlberg (2002) e Smith et al. (2005) reportaram o declínio da diversidade de macrofungos no mesmo tipo de ecossistema. As taxas de micorrização evidenciam o mesmo padrão dos índices acima mencionados, pois enquanto Barker et al. (2013) afirmou que as taxas de micorrização, durante o primeiro ano após o fogo, não são perturbadas pela severidade do mesmo, já Gassibe et al. (2011)

verificou a diminuição das taxas de micorrização em áreas com níveis de severidade 4 e 5, tendo ambos os estudos sido realizados em florestas dominadas por *Pinus pinaster*.

Apesar dos resultados sobre o impacto do fogo na comunidade de macrofungos serem dissemelhantes, são evidentes as alterações a nível da composição do micobiota. Após o fogo, observavam-se carpóforos de macrofungos que anteriormente eram inexistentes ou pouco frequentes (maioritariamente *Ascomycota*). Por exemplo, o género *Morchella* (*Ascomycota*) (Fig. 5) é amplamente conhecido pelo aumento de produtividade de carpóforos após ocorrência de incêndios (Greene et al., 2010; Larson et al., 2016). Embora as causas específicas para este aumento de produtividade ainda estejam por clarificar, os norte-americanos utilizam incêndios controlados, *in situ*, para induzirem a produção destes cogumelos.



Figura 5 – *Morchella angusticeps* (Harnisch, 2009)

As espécies de macrofungos que se caracterizam por produzirem carpóforos essencialmente após a ocorrência de um incêndio, são denominadas “Fungos pós-fogo”. O aumento de temperatura, da radiação incidente e do teor de cinza no solo são as principais causas deste fenómeno (Peay et al., 2009). Em particular, as propriedades do solo sofrem uma alteração profunda, com a subida significativa do pH, devido essencialmente à libertação de cátions alcalinos (Ca, Mg, K, Na) (Ferreira et al., 2010). Os fungos pós-fogo produzem carpóforos, por norma, após as primeiras chuvas que sucedem a perturbação, que não resultam da germinação de esporos formados nessa mesma época (Claridge et al., 2009), indicando que estes organismos possuem mecanismos de resistência ao fogo. Baar et al. (1999) demonstrou que na camada mineral do solo, localizada abaixo da camada orgânica, existiam estruturas resistentes que permitiam a recolonização da camada orgânica pós-fogo. Espécies

do género *Rhizopogon* Fr. e indivíduos da espécie *Alpova diplophloes* (Zeller & C.W. Dodge) Trappe & A.H. Sm. possuem esporos dormentes na camada inorgânica do solo (Baar et al., 1999; Peay et al., 2009). Outras espécies como *Wilcoxina mikolae* (Chin S. Yang & H.E. Wilcox) Chin S. Yang & Korf e *Thelephora wakefieldiae* Zmitr., Shchepin, Volobuev & Myasnikov produzem, respectivamente, clamidósporos e propágulos resistentes à dessecação (Baar et al., 1999). Por fim, Baar et al. (1999) observou micorrizas em plântulas de *Pinus muricata* D. Don inoculadas a partir de micélio existente nas raízes de *Pinus* L. mortos numa área ardida.

A sucessão ecológica pós-fogo depende de inúmeros factores, sendo fundamentais as características do incêndio e a existência de propágulos viáveis. Numa primeira fase, caracterizada pela elevada deposição de cinza, aumento de temperatura e aumento do pH do solo, as espécies de macrofungos cujos propágulos (esporos sexuais, clamidósporos, micorrizas, etc.) resistiram ao incêndio colonizaram o espaço afectado. Entre as primeiras contam-se as espécies pós-fogo (geralmente sapróbias), cuja germinação dos esporos existentes na camada inorgânica do solo, é induzida pela passagem do fogo. Seguidamente, surgem outras espécies, em particular micorrízicas, que acompanham e auxiliam o desenvolvimento das suas plantas hospedeiras. A inoculação destas advém de micorrizas que resistiram ao fogo (Baar et al., 1999), de esporos resistentes ou ainda de esporos produzidos por macrofungos presentes em áreas não ardidas. Sem a existência de macrofungos numa área ardida seria impossível a sobrevivência da maioria das espécies vegetais, isto porque muitas delas dependem da relação mutualista para a sua sobrevivência, e outras necessitam de nutrientes sob a forma assimilável, cuja presença pode ser assegurada pelos macrofungos sapróbios.

A gestão de áreas florestais ardidas deve basear-se no conhecimento multidisciplinar, ou seja, não só perceber a dinâmica da vegetação ou do microbiota pós-fogo, mas antes a dinâmica da vegetação-microbiota pós-fogo, de modo a implementar medidas adequadas à recuperação destas áreas.

Objectivos da dissertação

O objectivo geral desta dissertação é responder à questão: quais os efeitos e consequências do fogo nos macrofungos florestais, tendo por caso de estudo a Mata da Margarça.

Os objectivos específicos são:

Compreender a importância dos macrofungos para a manutenção e recuperação dos ecossistemas florestais;

Salientar a importância da Mata Nacional da Margarça como floresta relíquia da Era Terciária em

Portugal e contribuir para listar o elenco do seu micobiota;

Compreender de que forma o fogo alterou as comunidades de macrofungos da Mata da Margaraça, identificando os *taxa* e os grupos tróficos mais afectados;

Perceber de que forma os diferentes graus de severidade do fogo afectam a diversidade e abundância de macrofungos da Mata da Margaraça e identificar *taxa* de macrofungos que sejam indicadores de graus de severidade do fogo;

Área de estudo

A Mata da Margaraça (MM) está localizada na Serra do Açor (Arganil, Coimbra), próxima da aldeia de Pardieiros e representa um dos raros exemplos nacionais onde um clima de influência atlântica vinga no seio de uma paisagem nitidamente mediterrânea. Em 1982, de modo a preservar, em grande parte, as características singulares da MM, a Serra do Açor foi constituída como Paisagem Protegida (APPSA). A MM engloba hoje a Rede de Reservas Biogenéticas do Conselho da Europa e é considerada um Sítio de Importância Comunitária (SIC), do Complexo do Açor (PTCON00051), no âmbito da Rede Natura 2000.

Esta Mata Nacional ocupa 68 ha (Fig. 6) de uma encosta com exposição N-NO, entre os 450-850 m de altitude. A MM está posicionada no Maciço Hespérico, no limite das três Beiras e condicionada entre duas falhas de grande dimensão (falha da Lousã e falha da Sobreira Formosa). Esta floresta é dominada por xisto, fazendo parte do Complexo Xisto-Grauváquico, do período geológico do Câmbrico ou Pré-câmbrico (xisto-arenito-porfiroide), que conferem a acidez dos seus solos.

De entre as comunidades vegetais mais importantes da MM sobressai a associação *Rusco aculeati-Quercetum roboris*, sub-associação *Viburnetosum tini*, que se insere taxonomicamente na classe *Querco-Fagetea*, na ordem *Quercetalia roboris* e na aliança *Quercion robori-pyrenaicae* (Alves et al., 1998). Na sua maioria, a floresta é ocupada por espécies arbóreas atlânticas e eurosiberianas como *Quercus robur* L e *Castanea sativa* Mill. As formações de *Quercus robur* representam o carvalhal primitivo que cobrira grande parte das encostas com exposição NO de influência mais atlântica desta serra, sendo uma raridade regional e nacional. Os castiçais abandonados ocupam, também, grande parte do interior do bosque. Por oposição, espécimes de *Quercus suber* L. são menos frequentes e encontram-se na periferia da MM. O coberto arbustivo apresenta uma particular dominância de espécies lauróides, que representam, em Portugal, uma rara formação da Laurissilva (Anexo B-I da Diretiva Habitats, 5230), relíquia do Terciário Português. *Viburnum tinus* L., *Ilex aquifolium* L., *Laurus nobilis* L., e o endemismo português *Prunus lusitanica* L. subsp. *lusitanica*, são as espécies mais emblemáticas que constituem esta formação. *Prunus*

lusitanica subsp. *lusitanica*, espécie abrangida pelo Livro vermelho da flora vascular de Portugal continental, apresenta nesta região a maior população de toda a sua área de distribuição (Silveira, 2001). No coberto arbustivo predominam ainda espécies não lauróides como *Cytisus* spp., *Erica* spp., *Calluna vulgaris* L., *Ulmus minor* Mill., *Prunus cerasus* L., *Prunus avium* L., *Corylus avellana* L. e *Arbutus unedo* L (Fig. 7 A, B, C).



Figura 6 – Mapa de Portugal dividido em províncias. Árvore - Mata Nacional da Margarça.

Apesar das diminutas dimensões da MM, esta apresenta um vasto elenco de espécies macrofúngicas. Segundo Natario et al. (2019), conhecem-se mais de duas centenas de espécies de macrofungos, associadas maioritariamente aos povoamentos florestais dominantes, representadas pelas Divisões *Ascomycota* (Fig. 7 F) e *Basidiomycota* (Fig. 7 E, G, H), com claro predomínio da última. As famílias de *Basidiomycota* mais representadas são: *Russulaceae*, *Mycenaceae*, *Agaricaceae* e *Inocybaceae*, sendo que *Pyronemataceae* e *Pezizaceae* são as famílias de *Ascomycota* que apresentam mais espécies (Natario et al., 2019).



Figura 7 – A – Entrada este da estrada M518 da Mata Nacional da Margaraça (Noticias de Coimbra, 2018); B – Mata da Margaraça (Rica de Bela Mata da Margaraça, 2010); C – Ribeira da Mata da Margaraça (Alves, 2019); D – Souto ardido na Mata da Margaraça (Natário, 2018); E – *Cortinarius balteatocumatilis* (Gianluigi, 2012); F – *Peziza praetervisa* (Lindsey, 2004); G - *Leucoagaricus crystallifer* (First Nature); H – *Cortinarius caperatus* (Esmith, 2011).



Macrofungi of Mata da Margaraça (Portugal), a relic from the Tertiary Age

Bruno Alexandre Fragoso Natário[‡], Rogério Louro[‡], Celeste Santos-Silva[‡]

[‡] Biology Department, Macromycology Laboratory, Instituto de Ciências Agrárias e Ambientais Mediterrânicas, University of Évora, 7002-554, Évora, Portugal

Corresponding author: Bruno Alexandre Fragoso Natário (bafn@uevora.pt)

Academic editor: Dmitry Schigel

Received: 11 Jul 2019 | Accepted: 01 Oct 2019 | Published: 03 Oct 2019

Citation: Natário BAF, Louro R, Santos-Silva C (2019) Macrofungi of Mata da Margaraça (Portugal), a relic from the Tertiary Age. Biodiversity Data Journal 7: e38177. <https://doi.org/10.3897/BDJ.7.e38177>

Abstract

Mata Nacional da Margaraça represents a rare example where the Atlantic climate influences the perpetuity of a small enclave of a previously widespread laurel forest. The higher relative humidity values (> 80%), which are almost constant all year long and the mild temperatures, rarely exceeding 30°C, even in the dry season (June to September), create an insular-like effect. The biological communities of Margaraça exhibit a transitory character. The forest is dominated by *Quercus robur* and *Castanea sativa*, yet *Quercus suber*, although less frequent, can also be found. The laurel species, such as *Viburnum tinus*, *Ilex aquifolium*, *Laurus nobilis* and the Portuguese endemic *Prunus lusitanica* ssp. *lusitanica*, relics from the ancient Portuguese Tertiary, comprise the understorey. The present work represents, to the best of our knowledge, the first regional macrofungal species list of the Mata da Margaraça published to date. The recent fires that occurred in the area have provided the opportunity to study the post-fire communities. The surveys were carried out in 2004 and later in 2018-2019. A total of 271 species were registered as belonging to Basidiomycota (≈ 80%) and Ascomycota (≈ 20%). The most represented Basidiomycota families were Russulaceae, Mycenaceae and Agaricaceae and the most represented Ascomycota families were Pyrenomataceae and Pezizaceae. The new records to Portugal add up to a total of 88 species and another 116 species are new records to the province of Beira Litoral. Post-fire fungi account for 17 of the total of 271 species registered in these studies and most of these species are new to Portugal.

Keywords

Ascomycota, Basidiomycota, Beira Litoral, Portugal, Laurisilva, post-fire

Introduction

Continental Portugal's unique location – eastern border of the Atlantic Ocean – allows for the co-existence of two biogeographic regions (the Eurosiberian region and the Mediterranean region) with distinct bioclimatic features (Costa et al. 1998). Besides the predominant Mediterranean climatic influence in the country, there are, nevertheless, rare locations where the Atlantic influence supports the establishment and continuity of different plant communities, some of which are relics of ancient forests, dating back to the Miocene and Pliocene periods. In that context, the Mata Nacional da Margaraça (M.M.) represents a rare example where the Atlantic climate influences the perpetuity of a small enclave of a previously widespread laurel forest called Laurisilva within the landscape of the Serra do Açor, which largely has a Mediterranean climate. Hence, in 1982, the Serra do Açor became a protected landscape area (A.P.P.S.A.) to protect the M.M. Nowadays, the M.M. is included in the European Network of Biogenetic Reserves and is a Site of Community Importance (SCI) under the Nature 2000 network (PTCON00051). With a total area of 68 ha, the M.M. is a unique reserve of biodiversity and an important conservation site in Central Portugal.

M.M. is situated in the Iberian fold belt (Lourenço 1996), between two large faults and several small ones and it is mainly occupied by acidic soils, originating from granite and schist rocks. The M.M. is located between 450 and 800 m above sea level and has an N-NW orientation. These topographic, geomorphologic and geographic characteristics are unique compared to other mountain regions with Atlantic climate influence in North and Central Portugal. For instance, the higher relative humidity values (> 80%), which are almost constant all year long and the mild temperatures, rarely exceeding 30°C, even in the dry season (June to September), create an insular-like effect, that is translated into the isolation of the ecosystems and species of the M.M. from the surrounding areas of the Serra do Açor (Neves 2005).

The biological communities of M.M. exhibit a transitory character, with a diverse flora comprised of Atlantic, Eurosiberian and Mediterranean species. However, given its dominance, the *Rusco aculeati-Quercetum roboris* association, sub-association *Viburnetosum tini*, class *Quercio-Fagetea*, order *Quercetalia roboris* and alliance *Quercion robori-pyrenaicae*, best describe the flora of the M.M. (Alves et al. 1998). As such, in its majority, the forest is dominated by the Atlantic and Eurosiberian arboreal species. *Quercus robur* L. and *Castanea sativa* Mill. occupy most of the inner part of M.M., yet *Quercus suber* L., although less frequent, can be found on the outskirts of the M.M. The understorey is comprised mainly of laurel species (e.g. *Viburnum tinus* L., *Ilex aquifolium* L., *Laurus nobilis* L. and the Portuguese endemic *Prunus lusitanica* L. ssp. *lusitanica*) which are relics from the ancient Portuguese Tertiary Laurisilva forests (Habitats Directive

Annex B-I, 5230). Furthermore, *Prunus lusitanica* ssp. *lusitanica*, contained in the Red List of Vascular Flora of Portugal, has, in the M.M., the largest number of individuals within its distribution range. Other shrub species, such as *Cytisus* spp., *Erica* spp., *Calluna vulgaris* (L.) Hull, *Ulmus minor* Mill., *Prunus cerasus* L., *Prunus avium* L., *Corylus avellana* L. and *Arbutus unedo* L., are also present in the understorey of these woods. In M.M., some of them can reach far greater sizes than in the rest of their distribution range. The M.M. herbaceous stratum accounts for many of the endemic species and the majority is listed in the Habitats Directive (H.D.) for this SCI, such as *Eryngium duriaei* Gay ex Boiss, *Lavandula stoechas* L. ssp. *luisieri* (Rozeira) Rozeira, *Antirrhinum meonanthum* Hoffmans. & Link, *Veronica micrantha* Hoffmans. & Link (in H.D. Annex II) and *Murbeckiella sousae* Rothm. (in H.D. Annex IV). The Bryoflora on the site is particularly well represented, with more than 150 species described. Some of these species, like *Cephaloziella elegans* (Heeg) Schiffn., *Campylopus pyriformis* Brid., *Hypnum revolutum* (Mitt.) Lindb., *Plagiothecium nemorale* (Mitt.) A. Jaeger and *Plagiothecium succulentum* (Wilson) Lindb., are restricted to M.M. in the Portuguese territory. Moreover, the reduced distribution of the above-mentioned *Plagiothecium* species in the national territory highlights the importance of M.M. as a preclimatic forest system.

Until the 1960s, the A.P.P.S.A. suffered profound human-induced landscape changes: 1) Massive deforestation was undertaken in order to create pastures, agricultural lands and for edification; 2) Replacement of the main forest with *Pinus pinaster* Ainton. monocultures. However, the M.M. area was preserved in order to produce wood (*Castanea sativa* coppice stands) and to harvest the forest surplus production. Later, rural desertification led to a decrease in agricultural land and pastures, which greatly contributed to shrub encroachment and forest regeneration (Moreira et al. 2011), by favouring the ecological succession and promoting the natural values of A.P.P.S.A. and particularly of M.M. However, the cumulative organic matter deposited on the forest floor increased the risk of high-intensity fires (Pausas et al. 2008) and culminated in the forest fires of 1987 and 2017 which burned 90% of the M.M. area and threatened its biodiversity, particularly in the upper limit of the M.M. and in its outskirts where non-native species (*Pinus* spp. and *Acacia* spp.) are more frequent. The fire had almost no effect in the lower limit of M.M. where the main forest remained untouched and the M.M. recover capability was preserved.

To the best of our knowledge, the present work represents the first regional macrofungal species list of M.M. published so far and one of the few available for Portugal (e.g. Louro et al. 2009). Due to its singularity, M.M. is a remarkable location for examining and documenting the macrofungal communities, as a unique relic of the ancient forests that previously occupied most of the national territory. Additionally, the recent fires that occurred in the area have provided the opportunity to observe the post-fire communities which, before the fire (undisturbed period), were less likely to be detected. The addition of these species to the list is particularly important since little is known about post-fire macrofungi communities in Laurel forests.

Material and methods

The survey was conducted in the Mata Nacional da Margaraça (40°12.9781' N, 7°55.1349' W) (Fig. 1), between May 2018 and May 2019, with sampling occurring in the most favourable months, Spring (March-May) and Autumn (October-December). After the most recent wildfire (October 2017), 75 × 25 m² plots were randomly distributed, within a fire severity range of values (Botella-Martínez and Fernández-Manso 2017). From the 75 preliminary plots, only 66 were surveyed due to topographic constraints. All the specimens within the plot area were harvested, stored under 4°C and processed within twenty-four hours. These specimens were then preserved and deposited in Évora University herbarium (UEVH- FUNGI). Macrofungi nomenclature follows the Catalogue of Life (2019) and Kirk (2019). Current species distribution areas were consulted in Calonge (1998), Centro de Micologia da Universidade de Lisboa (2002), Global Biodiversity Information Facility Data Portal (2019) and other local publications and follows Castroviejo et al. (1986) usage of Iberian territory division into provinces.



Figure 1. [doi](#)

Map of the Portuguese territory. Map of the Portuguese territory divided by province. Mata da Margaraça located as a tree symbol.

Complementarily, a preliminary unpublished study, conducted by the Instituto para a Conservação da Natureza e das Florestas, was consulted. The study occurred in 2004, fortnightly, except for the months of July and August, in 10 × 100 m transects scattered throughout the 3 different biotopes, dominated respectively by *Quercus robur*, *Castanea sativa* and *Prunus lusitânica* ssp. *lusitânica*. All the specimens were collected and deposited in an exsiccatae personal herbarium (Gama 2004).

The species are arranged alphabetically, according to the higher taxonomic placement Phylum, Order, Family. For each species, the respective trophic group, putative host species (for mycorrhizal and parasitic species) and deposit number of UEVH- FUNGI were assigned. The species, referred to as novelties, were divided into species new to Portugal

and new to the Beira Litoral province (B.L.) (Fig. 1). The post-fire species were identified according to Dix and Webster (1995), Sumorok (2001), Robinson et al. (2008) and Claridge et al. (2009) (Suppl. material 1).

Results and Discussion

A total of 272 macrofungal species, representing 127 genera and 59 families, were recorded during these two studies, belonging to Basidiomycota ($\approx 80\%$) and Ascomycota ($\approx 20\%$) (Suppl. material 1). Considering the trophic groups, saprophytic species slightly outnumber the mycorrhizal species (1.36:1). The most represented Basidiomycota families were Russulaceae, Mycenaceae and Agaricaceae, accounting for 30% of all Basidiomycota species (Fig. 2), all well speciose families. *Russula* and *Lactarius* are mycorrhizal genera, well represented in Fagaceae dominated forest (Sarnari 2007). Mycenaceae and Agaricaceae comprise many species growing on decaying hard wood, such as *Quercus* spp. and *Castanea sativa* or associated with moss (Aronsen and Læssøe 2016). The most numbered Ascomycota families were Pyrenomataceae and Pezizaceae, accounting for $\approx 50\%$ of all Ascomycota species (Fig. 2). These species are greatly associated with forest ecosystems and some of them are post-fire species, such as *Anthracobia macrocystis* (Cooke) Boud., *Peziza praetervisa* Bres. and *Pyronema omphalodes* (Bull.) Fuckel.

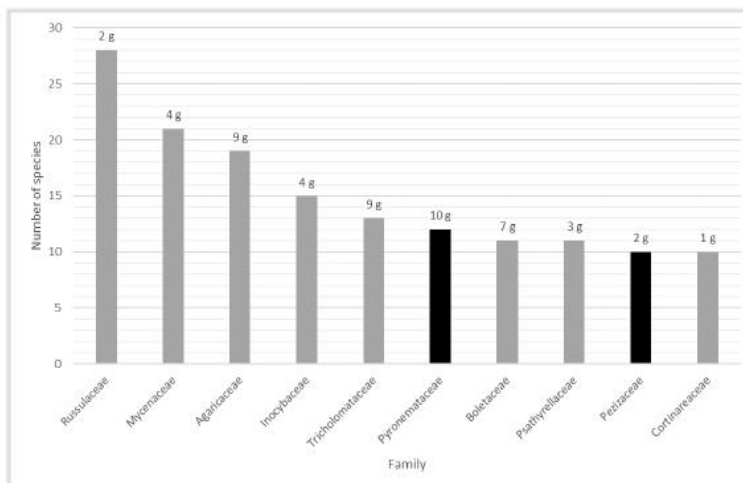


Figure 2. [doi](#)

The ten most speciose families. Number of species of the ten most numerous families and number of genera (g) from each family. Grey bars refer to Basidiomycota families and black bars refer to Ascomycota families.

Parasitic species were the least represented trophic group, with only six species, *Desarmillaria tabescens* (Scop.) R.A. Koch & Aime, *Rhizina undulata* Fr., *Thyronectria aquifolii* (Fr.) Jaklitsch, *Cordyceps militaris* (L.) Fr., *Phaeotremella foliacea* (Pers.) Wedin J.C. Zamora & Millanes and *Tremella mesenterica* Retz. Except for *C. militaris* (insect

parasite) and *P. foliacea* and *T. mesenterica* (both fungal parasites), the other species are plant parasites. These species occurred frequently during sampling periods, except for Tremellaceae species.

The new records for Portugal add up to a total of 74 species and another 116 species are new records to B.L. (Suppl. material 1). The phylum Ascomycota is the least studied worldwide and even less so in Portugal. This fact is reflected in the number of novel Ascomycota species described in this study in which 44 are new records to B.L. and 22 of these are new records to Portugal. Due to the inconspicuous nature of most of these species (small dimensions and ephemerality of the carpophores) (e.g. *Bisporella citrina* (Batsch) Korf & S.E. Carp., *Lanzia echinophila* (Bull.) Korf and *Rutstroemia firma* (Pers.) P. Karst.), they are often overlooked and uncommon in species lists. The *Morchella* genus, in contrast, is well studied in most countries but represents an important novelty to B.L. Post-fire conditions were important for the development of some species (Dix and Webster 1995, Sumorok 2001, Robinson et al. 2008 and Claridge et al. 2009), such as *Anthracobia macrocystis* (Cooke) Boud., *Ascobolus carbonarius* P. Karst., *Morchella* spp., *Peziza* spp., *Plicaria endocarpoides* (Berk.) Rifai, most of which are novelties to Portugal.

Fifty-two novel Basidiomycota species were registered to Portugal and 94 to B.L. *Leucoagaricus crystallifer* Vellinga is especially worthy of mention since it is an extremely uncommon species in Europe, yet its rare observations are documented all over Europe (Vellinga 2000). In addition to *Leucoagaricus crystallifer*, species like *Cortinarius balteatocumatilis* Rob. Henry ex P.D. Orton, *Conocybe vestita* (Fr.) Kühner, *Cortinarius caperatus* (Pers.) Fr., *Crepidotus autochthonus* J.E. Lange, *Marasmius cohaerens* (Pers.) Cooke & Quél., *Marasmius epiphylloides* (Rea) Sacc. & Trotte, *Mycena pearsoniana* Dennis ex Singer, *Mycena pseudocorticola* Kühner, *Typhula quisquiliaris* (Fr.) Henn., *Pseudocraterellus subundulatus* (Peck) D.A. Reid and *Hymenochaetopsis tabacina* (Sowerby) S.H. He & Jiao Yang are representative of M.M. singular features. These species are associated with more humid and less variable climates, like the conditions found in M.M., which are uncommon in the rest of the country. Other species, such as *Boletus reticulatus* Schaeff., *Bovista plumbea* Pers., *Clitocybe costata* Kühner & Romagn., *Coprinellus domesticus* (Bolton) Vilgalys, Hopple & Jacq. Johnson, *Cortinarius trivialis* J.E. Lange, *Hygrocybe russocoriacea* (Berk. & T.K. Mill.) P.D. Orton & Watling, *Lycoperdon excipuliforme* (Scop.) Pers., *Mycena abramsii* (Murrill) Murrill, *Russula cyanoxantha* (Schaeff.) Fr., *Tremella mesenterica* Retz. and *Xylaria hypoxylon* (L.) Grev., are novelties to B.L. and reflect the lack of macrofungi studies in this area. These species are very common in the rest of the country but have not been documented for B.L. until now.

The post-fire fungi account for 17 of the total 271 species registered in these studies (e.g. *Ascobolus carbonarius* P. Karst., *Morchella elata* Fr., *Peziza praetervisa* Bres., *Pholiota brunnescens* A.H. Sm. & Hesler.) (Suppl. material 1). The addition of these species was an important enrichment to this checklist, since 7 of them represent novelties to Portugal (e.g. *Morchella eximia* Boud., *Pholiota brunnescens*, *Plicaria endocarpoides* (Berk.) Rifai) and were unlikely to be recorded otherwise.

Conclusions

FUNGI comprise one of the most megadiverse biological groups and one of the most understudied and misunderstood. In a period where biodiversity loss is one of the main environmental challenges facing the planet, halting the loss of biodiversity and the degradation of ecosystem services by 2020 seems to be, nowadays, a more and more impossible task. The panorama seems even grimmer as climate change is deeply altering the geographical redistribution of plant and animal species and causing extinctions in the profoundly fragmented world of today. Under these premises, undertaking biological surveys that summarise the latest information on the status and trends of biodiversity, especially in areas of high biodiversity value in Natura 2000 sites and encouraging the publication of regional checklists on such high nature value areas, is of the utmost importance for the maintenance and preservation of biodiversity. In that context, the present work represents a contribution to the mycological knowledge of one of the most singular protected areas in Portugal, that harbours almost three hundred macrofungal species in a relatively small area. The wildfires that occurred in this area highly threatened the mycological diversity and subsequently their host species (Natario et al. unpublished data), most of which are obligatory mycorrhizal species. Continuous post-fire work should be undertaken in order to evaluate the long-term fire effects, on both flora and mycobiota diversity.

Acknowledgements

We wish to thank Instituto para a Conservação da Natureza e das Florestas for the authorisation to harvest macrofungi specimens in A.P.P.S.A.

Hosting institution

Évora University

Author contributions

All authors contributed equally to the development of this paper.

References

- Alves JM, Espírito-Santo MD, Costa JC, Gonçalves JH, Lousã MF (1998) Habitat naturais e seminaturais de Portugal continental. Assírio & Alvim, 251 pp.
- Aronsen A, Læssøe T (2016) The genus *Mycena* the fungi of Northern Europe 5. Svampetryk, 373 pp.

- Botella-Martinez MA, Fernández-Manso A (2017) Estudio de la severidad post-incendio en la Comunidad Valenciana comparando los índices dNBR, RdNBR y RBR a partir de imágenes Landsat 8. *Revista de Teledetección* 49: 33-47. <https://doi.org/10.4995/raet.2017.7095>
- Calonge FD (1998) *Flora Mycologica Iberica*. Real Jardín Botánico, Consejo superior de Investigaciones Científicas, 271 pp.
- Castroviejo S, Lainz M, López-González C, Montserrat P, Muñoz Garmendia F, Paiva J, Villar L (1986) *Flora Iberica*. Madrid: Real Jardín Botánico
- Catalogue of Life (2019) Species 2000 & ITIS, 25th March 2019. <http://www.catalogueoflife.org/col>. Accessed on: 2019-3-08.
- Centro de Micologia da Universidade de Lisboa (2002) Listagem preliminar de fungos agaricoides de Portugal. Centro de Micologia da Universidade de Lisboa, 70 pp.
- Claridge AW, Trappe JM, Hansen K (2009) Do fungi have a role as soil stabilizers and remediators after forest fire? *Forest Ecology and Management* 257: 1063-1069. <https://doi.org/10.1016/j.foreco.2008.11.011>
- Costa JC, Aguiar C, Capelo J, Lousã M, Neto C (1998) Biogeografia de Portugal continental. *Biogeografia de Portugal continental*.
- Dix NJ, Webster J (1995) Phoenicoid fungi. *Fungal Ecology* 303-321. https://doi.org/10.1007/978-94-011-0693-1_11
- Gama A (2004) Quantificação da Diversidade de Macrofungos em Alguns Habitats da Serra do Açor. Relatório elaborado para o Instituto da Conservação da Natureza. ICNF.
- Global Biodiversity Information Facility Data Portal (2019) <http://www.gbif.net>. Accessed on: 2019-5-12.
- Kirk PM (2019) Index Fungorum. <http://www.speciesfungorum.org/Index.htm>. Accessed on: 2019-3-08.
- Lourenço L (1996) Serras de Xisto do Centro de Portugal-Contribuição para o seu conhecimento geomorfológico e geo-ecológico. Universidade de Coimbra
- Louro R, Calado M, Pinto B, Santos-Silva C (2009) Epigeous macrofungi of the Parque de Natureza de Noudar in Alentejo (Portugal). *Mycotaxon* 107: 49-52. <https://doi.org/10.5248/107.49>
- Moreira F, Viedma O, Arianoutsou M, Curt T, Koutsias N, Rigoloff E, Barbati A, Corona P, Vaz P, Xanthopoulos G, Mouilloti F, Bilgili E (2011) Landscape-wildfire interactions in southern Europe: Implications for landscape management. *Journal of Environmental Management* 92: 2389-2400. <https://doi.org/10.1016/j.jenvman.2011.06.028>
- Neves S (2005) Alargamento e reclassificação da Área de Paisagem Protegida da Serra do Açor – Nota justificativa. Documento interno do ICN. ICNF.
- Pausas JG, Llovet J, Rodrigo A, Vallejo R (2008) Are wildfires a disaster in the Mediterranean basin? *International Journal of Wildland Fire* 17: 713-723. <https://doi.org/10.1071/WF07151>
- Robinson RM, Mellican AE, Smith RH (2008) Epigeous macrofungal succession in the first five years following a wildfire in karri (*Eucalyptus diversicolor*) regrowth forest in Western Australia. *Austral Ecology* 33: 807-820. <https://doi.org/10.1111/j.1442-9993.2008.01853.x>
- Samari M (2007) Monografia illustrate del genere *Russula* in Europa–Tomo Primo. Associazione Micologia Bresadola - Fondazione Centro Studi Micologici, 799 pp.
- Sumorok B (2001) Post-fire macrofungi in the burnt area in the Jelonka reserve (Bialowieza region). *Acta Mycologica* 36: 149-158. <https://doi.org/10.5586/am.2001.010>

- Vellinga EC (2000) Notulae ad floram agaricinamneerlandicam–XXXVIII. *Leucoagaricus* subgenus *Sericeomyces*. *Persoonia* 17: 473-480.

Supplementary material

Suppl. material 1: Ascomycota and Basidiomycota macrofungi recorded in Mata da Margarça [doi](#)

Authors: Natario B., Louro R. and Santos-Silva C.

Data type: Ecology, Occurrences, Trophic group, Taxonomy

Brief description: Species are arranged alphabetically according to higher taxonomic placement (Filo, Order and Family). Trophic group; P: parasitic; S: saprophytic; M: mycorrhizal. Host species (putative host); C: *Castanea sativa*; E: *Eucalyptus* spp.; H: *Stereum* spp.; I: *Ilex aquifolium* P: *Pinus pinaster*; Q: *Quercus robur*; T: *Thaumatophoea pityocampa*; Z: *Peniophora* spp. Novelities; N: novelties to Portugal; n: novelties to Beira Litoral. Occurrence; 1: recorded only in one of the two studies; 2: recorded in the two studies.

[Download file](#) (610.09 kb)

Supplementary material 1: Table S1

Table S1 – Macrofungi of Mata da Margarça (Portugal), a relic from the Tertiary Age, Supplementary material 1: *Ascomycota* and *Basidiomycota* macrofungi recorded in Mata da Margarça. Species are arranged alphabetically according to higher taxonomic placement (Filo, Order and Family). Trophic group; P: parasitic; S: saprophytic; M: mycorrhizal. Host species (putative host); C: *Castanea sativa*; E: *Eucalyptus* spp.; H: *Stereum* spp.; I: *Ilex aquifolium* P: *Pinus pinaster*; Q: *Quercus robur*; T: *Thaumatophoea pityocampa*; Z: *Peniophora* spp. Novelities; N: novelties to Portugal; n: novelties to Beira Litoral. Occurrence; 1: recorded only in one of the two studies; 2: recorded in the two studies.

Filo	Order	Family	Species	Trophic group	Host species	UEVH-FUNGI	Novelties	Post-fire spp.	Occurrence	
Ascomycota	<i>Incertae sedis</i>	<i>Incerta sedis</i>	<i>Thyronectria aquifolii</i> (Fr.) Jaklitsch & Voglmayr	P	I	2004687	N		1	
	<i>Geoglossales</i>	<i>Geoglossaceae</i>	<i>Geoglossum umbratile</i> Sacc.	S			N		1	
	<i>Helotiales</i>	<i>Leotiaceae</i>	<i>Leotia lubrica</i> (Scop.) Pers.		S			n		1
		<i>Helotiaceae</i>	<i>Bisporella citrina</i> (Batsch) Korf & S.E. Carp.		S		2004460	N		2
		<i>Rutstroemiaceae</i>	<i>Lanzia echinophila</i> (Bull.) Korf		S			n		1
			<i>Rutstroemia firma</i> (Pers.) P. Karst.		S		2004527	n		2
	<i>Sclerotiniaceae</i>	<i>Moellerodiscus lentus</i> (Berk. & Broome) Dumont		S		2004148	N		1	
	<i>Hypocreales</i>	<i>Cordycipitaceae</i>	<i>Cordyceps militaris</i> (L.) Fr.	P	T	2004214	n		1	
<i>Leotiales</i>	<i>Bulgariaceae</i>	<i>Bulgaria inquinans</i> (Pers.) Fr.	S		2004450	N		1		

Pezizales	Ascobolaceae	<i>Ascobolus carbonarius</i> P. Karst.	S		2004096	N	X	1	
	Helvellaceae	<i>Helvella elastica</i> Bull.	M	C, P, Q		n		1	
		<i>Helvella fibrosa</i> (Wallr.) Korf	M	C, P, Q	2004127	N		1	
		<i>Helvella lacunosa</i> Afzel.	M	C, P, Q	2004457	n		1	
		<i>Helvella leucomelaena</i> (Pers.) Nannf.	M	P	2004699	n		1	
		<i>Helvella leucopus</i> Pers.	M	C, Q	2004109	n		1	
		<i>Helvella macropus</i> (Pers.) P. Karst.	M	C, P, Q	2004130	N		1	
		Morchellaceae	<i>Disciotis venosa</i> (Pers.) Arnould	S		2004046	N		1
	<i>Morchella elata</i> Fr.		S		2004153	n	X	1	
	<i>Morchella esculenta</i> (L.) Pers.		S		2004206	n	X	2	
	<i>Morchella eximia</i> Boud.		S		2004183	N	X	1	
	<i>Verpa conica</i> (O.F. Müll.) Sw.		S		2004689	N		1	
	Pezizaceae	<i>Peziza arvernensis</i> Roze & Boud.	M	C, Q	2004218	n		1	
		<i>Peziza echinospora</i> P. Karst.	M	C, Q	2004175	N	X	1	
		<i>Peziza granularis</i> Donadini	M	C, Q	2004181	N		1	
		<i>Peziza lobulata</i> (Velen.) Svrček	M	C, Q	2004140	N		1	
		<i>Peziza michelii</i> (Boud.) Dennis	M	C, Q	2004219	N		1	
		<i>Peziza phyllogena</i> Cooke	M	C, Q	2004227	n		1	
		<i>Peziza praetervisa</i> Bres.	M	C, Q	2004176	n	X	1	
		<i>Peziza queletii</i> Medardi, Lantieri & Cacialli	M	C, Q	2004128	N		1	
		<i>Peziza septiata</i> Cooke	M	C, Q	2004143	n		1	
		<i>Plicaria endocarpoides</i> (Berk.) Rifai	M	C, Q	2004180	N	X	1	
		Pyronemataceae	<i>Anthracobia macrocystis</i> (Cooke) Boud.	S		2004241		X	1
	<i>Cheilymenia granulata</i> (Bull.) J. Moravec		S		2004746	N		1	
	<i>Geopora arenosa</i> (Fuckel) S. Ahmad		M	C, P, Q	2004126	N		1	
	<i>Humaria hemisphaerica</i> (F.H. Wigg.) Fuckel		M	C, Q		n		1	
	<i>Lamprospora trachycarpa</i> (Curr.) Seaver		S		2004137	N		1	
	<i>Otidea alutacea</i> (Pers.) Massee		M	C, P, Q		n		1	
	<i>Otidea bufonia</i> (Pers.) Boud.		M	C, Q	2004463	n		1	
	<i>Pyronema omphalodes</i> (Bull.) Fuckel		S		2004137	N	X	1	
	<i>Scutellinia scutellata</i> (L.) Lambotte		S			N		1	
	<i>Tarzetta catinus</i> (Holmsk.) Korf & J.K. Rogers		M	C, Q	2004686	n		1	
	<i>Tarzetta cupularis</i> (L.) Svrček		M	C, Q	2004149	n		2	
	<i>Trichophaea woolhopeia</i> (Cooke & W. Phillips) Boud.		M	C, Q	2004744	n	X	1	
	Rhizinaceae		<i>Rhizina undulata</i> Fr.	P	P	2004097		X	1
	Sarcoscyphaceae		<i>Sarcoscypha coccinea</i> (Gray) Boud.	S		2004447	n		2
	Xylariales		Xylariaceae	<i>Xylaria hypoxylon</i> (L.) Grev.	S		2004435	n	2
	Basidiomycota	Incertae sedis	Incerta sedis	<i>Cotylidia undulata</i> (Fr.) P. Karst.	S	C, Q	N	1	

<i>Incertae sedis</i>	<i>Incerta sedis</i>	<i>Loreleia marchantiae</i> (Singer & Clémençon) Redhead, Moncalvo, Vilgalys & Lutzoni	S			N		1	
<i>Agaricales</i>	<i>Amanitaceae</i>	<i>Amanita citrina</i> Pers.	M	C, P, Q	2004345			2	
		<i>Amanita gemmata</i> (Fr.) Bertill	M	C, P, Q	2004690			2	
		<i>Amanita mairei</i> Foley	M	P	2000322	n		1	
		<i>Amanita muscaria</i> (L.) Lam.	M	C, P, Q	2004343			2	
		<i>Amanita pantherina</i> (DC.) Krombh.	M	C, P, Q	2004225			2	
		<i>Amanita phalloides</i> (Vail. ex Fr.) Link	M	C, P, Q	2004390			2	
		<i>Amanita rubescens</i> Pers.	M	C, Q	2004215			2	
		<i>Amanita vaginata</i> (Bull.) Lam.	M	C, P, Q	2004237			2	
	<i>Agaricaceae</i>	<i>Agaricus amanitiformis</i> Wasser	S				N		1
		<i>Agaricus cappellianus</i> Hlaváček	S				N		1
		<i>Bovista aestivalis</i> (Bonord.) Demoulin	S			2004451	n		1
		<i>Bovista cunninghamii</i> Kreisel	S			2004402	n		1
		<i>Bovista delicata</i> Berk. & M.A. Curtis	S			2004309	n		1
		<i>Bovista plumbea</i> Pers.	S			2004208	n		1
		<i>Bovista promontorii</i> Kreisel	S			2004222	n		1
		<i>Calvatia candida</i> (Rostk.) Hollós	S			2004351	n		1
		<i>Cyathus striatus</i> (Huds.) Willd.	S			2004430	n		1
		<i>Cystolepiota adulterina</i> (F. H. Møller) Bon	S						1
		<i>Lepiota castanea</i> Quéf.	S						1
		<i>Lepiota clypeolaria</i> (Bull.) P. Kumm.	S				n		1
		<i>Leucoagaricus crystallifer</i> Vellinga	S			2004392	N		1
		<i>Leucoagaricus serenus</i> (Fr.) Bon & Boiffard	S				n		1
		<i>Lycoperdon excipuliforme</i> (Scop.) Pers.	S			2004352	n		1
		<i>Lycoperdon perlatum</i> Pers.	S				n		1
		<i>Macrolepiota mastoidea</i> (Fr.) Singer	S			2004332	n		2
		<i>Macrolepiota procera</i> (Scop.) Singer	S			2003044			2
		<i>Macrolepiota venenata</i> Bom	S			2004459	N		1
		<i>Bolbitiaceae</i>	<i>Conocybe vestita</i> (Fr.) Kühner	S				N	
	<i>Clavariaceae</i>	<i>Clavaria flavipes</i> Pers.	S			2004513	N		1
	<i>Cortinariaceae</i>	<i>Cortinarius acutus</i> (Pers.) Fr.	M	P			N		1
		<i>Cortinarius anomalus</i> (Fr.) Fr.	M	C, Q			n		1
		<i>Cortinarius balteatocumatilis</i> Rob. Henry ex P.D. Orton	M	C, P, Q	2004321		N		1
		<i>Cortinarius caperatus</i> (Pers.) Fr.	M	C, P, Q			N		1
<i>Cortinarius flexipes</i> (Pers.) Fr.		M	P	2004747		N		1	
<i>Cortinarius rigens</i> (Pers.) Fr.		M	C, P, Q					1	

	<i>Cortinarius saniosus</i> (Fr.) Fr.	M	C, Q		n		1
	<i>Cortinarius stillatitius</i> Fr.	M	P		N		1
	<i>Cortinarius trivialis</i> J.E. Lange	M	C, Q	2004472	n		2
	<i>Cortinarius vernus</i> H. Lindstr. & Melot	M	C, Q		N		1
<i>Entolomataceae</i>	<i>Clitopilus prunulus</i> (Scop.) P. Kumm.	S		2004400			2
	<i>Entoloma hirtipes</i> (Schumach.) M.M. Moser	S		2004092	n		2
	<i>Entoloma papillatum</i> (Bres.) Dennis	S		2004696	n		2
	<i>Entoloma sericeum</i> Quéf.	S			n		1
<i>Fistulinaceae</i>	<i>Fistulina hepatica</i> (Schaeff.) With.	S		2004549	n		2
<i>Hydnangiaceae</i>	<i>Laccaria amethystina</i> Cooke	M	C, P, Q	2004540	n		2
	<i>Laccaria fraterna</i> (Sacc.) Pegler	M	C, P, Q	2004138	n		1
	<i>Laccaria laccata</i> (Scop.) Cooke	M	C, P, Q	2004697			2
<i>Hygrophoraceae</i>	<i>Cuphophyllus pratensis</i> (Fr.) Bon	S					1
	<i>Cuphophyllus virgineus</i> (Wulfen) Kovalenko	S			n		1
	<i>Hygrocybe acutoconica</i> (Clem.) Singer	S		2004691			1
	<i>Hygrocybe conica</i> (Schaeff.) P. Kumm.	S					1
	<i>Hygrocybe chlorophana</i> (Fr.) Wünsche	S					1
	<i>Hygrocybe miniata</i> (Fr.) P. Kumm.	S		2004521			1
	<i>Hygrocybe russocoriacea</i> (Berk. & T.K. Mill.) P.D. Orton & Watling	S		2004519	n		1
<i>Hymenogastraceae</i>	<i>Deconica crobula</i> (Fr.) Romagn.	S		2004199			1
	<i>Galerina clavata</i> (Velen.) Kühner	S		2003983	N		1
	<i>Galerina marginata</i> (Batsch) Kühner	S			N		1
	<i>Gymnopilus odini</i> (Fr.) Bon & P. Roux	S		2004291	N		1
	<i>Gymnopilus penetrans</i> (Fr.) Murrill	S			n		1
	<i>Hebeloma crustuliniforme</i> (Bull.) Quéf.	M	C, Q	2004692			1
	<i>Hebeloma leucosarx</i> P. D. Orton	M	C, Q		N		1
	<i>Hypholoma fasciculare</i> (Huds.) P. Kumm.	S		2004467			2
<i>Inocybaceae</i>	<i>Crepidotus applanatus</i> (Pers.) P. Kumm.	S		2004364	N		1
	<i>Crepidotus autochthonus</i> J.E. Lange	S		2004516	N		1
	<i>Crepidotus mollis</i> (Schaeff.) Staude	S		2004546			1
	<i>Crepidotus variabilis</i> (Pers.) P. Kumm.	S					1
	<i>Inocybe assimilata</i> Britzelm.	M	C, P, Q	2004110	n		1
	<i>Inocybe calida</i> Velen.	M	C, Q	2004541	n		1
	<i>Inocybe dulcamara</i> (Pers.) P. Kumm.	M	P	2004226	n		1
	<i>Inocybe geophylla</i> (Bull.) P. Kumm.	M	C, Q	2003374			1
	<i>Inocybe lacera</i> (Fr.) P. Kumm.	M	C, P, Q	2004228			1

	<i>Inocybe pallida</i> Velen.	M	P	2004694	N		1
	<i>Inocybe rimosa</i> (Bull.) P. Kumm.	M	P	2004529			2
	<i>Inocybe rufoalba</i> Sacc.	M	C, P, Q	2004141	N		1
	<i>Inocybe splendens</i> R. Heim	M	C, Q	2004112	n		1
	<i>Phaeomarasmium erinaceus</i> (Fr.) Scherff. ex Romagn.	S		2004441			1
	<i>Simocybe centunculus</i> (Fr.) P. Karst.	S		2004561	N		1
<i>Lyophyllaceae</i>	<i>Ossicaulis lignatilis</i> (Pers.) Redhead & Ginns	S			N		1
	<i>Tephrocycbe anthracophila</i> (Lasch) P.D. Orton	S		2004307	N	X	1
<i>Marasmiaceae</i>	<i>Marasmius cohaerens</i> (Pers.) Cooke & Quél.	S			n		1
	<i>Marasmius epiphyllodes</i> (Rea) Sacc. & Trotte	S			n		1
	<i>Marasmius oreades</i> (Bolton) Fr.	S		2003975			1
	<i>Marasmius rotula</i> (Scop.) Fr.	S					1
	<i>Marasmius torquescens</i> Quél.	S			n		1
<i>Mycenaceae</i>	<i>Hemimycena lactea</i> (Pers.) Singer	S		2004426			1
	<i>Mycena abramsii</i> (Murrill) Murrill	S		2004436	n		2
	<i>Mycena acicula</i> (Schaeff.) P. Kumm.	S					1
	<i>Mycena aetites</i> (Fr.) Quél.	S		2004305	n		1
	<i>Mycena arcangeliana</i> Bres.	S					1
	<i>Mycena cinerella</i> (P. Karst.) P. Karst.	S			n		1
	<i>Mycena erubescens</i> Höhn.	S			n		1
	<i>Mycena flavescens</i> Velen.	S		2004542	n		1
	<i>Mycena galericulata</i> (Scop.)	S					1
	<i>Mycena galopus</i> (Pers.) P. Kumm.	S		2004306			1
	<i>Mycena inclinata</i> (Fr.) Quél.	S					1
	<i>Mycena maculata</i> P. Karst.	S		2004745	N		1
	<i>Mycena pearsoniana</i> Dennis ex Singer	S			N		1
	<i>Mycena pseudocorticola</i> Kühner	S		2004489	N		1
	<i>Mycena renati</i> Quél.	S			N		1
	<i>Mycena rosea</i> Gramberg	S		2003607			1
	<i>Mycena seynii</i> Quél.	S		2004356			2
	<i>Mycena vitilis</i> (Fr.) Quél.	S		2004453			1
	<i>Mycena stipata</i> Maas Geest. & Schwöbel	S			N		1
	<i>Roridomyces roridus</i> (Fr.) Rexer	S			N		1
	<i>Xeromphalina campanella</i> (Batsch) Kühner & Maire	S		2004198	N		1
<i>Omphalotaceae</i>	<i>Gymnopus androsaceus</i> (L.) Della Maggiora & Trassin.	S			n		1
	<i>Gymnopus dryophilus</i> (Bull.) Murrill	S		2004231			1
	<i>Gymnopus erythropus</i> (Pers.) Antonín, Halling & Noordel.	S		2004427			1

	<i>Gymnopus foetidus</i> (Sowerby) P. M. Kirk	S			n		1
	<i>Gymnopus fusipes</i> (Bull.) Gray	S			N		1
	<i>Rhodocollybia butyracea</i> (Bull.) Lennox	S		2003912			1
<i>Physalacriaceae</i>	<i>Desarmillaria tabescens</i> (Scop.) R.A. Koch & Aime	P	C, Q	2004344	n		1
<i>Pluteaceae</i>	<i>Pluteus cervinus</i> (Schaeff.) P. Kumm.	S		2004234			2
	<i>Pluteus salicinus</i> (Pers.) P. Kumm.	S			n		1
	<i>Volvopluteus gloiocephalus</i> (DC.) Vizzini, Contu & Justo	S		2003990			1
<i>Psathyrellaceae</i>	<i>Coprinellus angulatus</i> (Peck) Redhead, Vilgalys & Moncalvo	S		2004414	n	X	1
	<i>Coprinellus domesticus</i> (Bolton) Vilgalys, Hopple & Jacq. Johnson	S		2002732	n		1
	<i>Coprinellus micaceus</i> (Bull.) Vilgalys, Hopple & Jacq. Johnson	S					1
	<i>Coprinopsis lagopides</i> (P. Karst.) Redhead, Vilgalys & Moncalv	S		2004517	n		2
	<i>Psathyrella corrugis</i> (Pers.) Konrad & Maubl.	S		2004394			1
	<i>Psathyrella hirta</i> Peck	S		2004173	n		1
	<i>Psathyrella multipedata</i> (Peck) A.H. Sm.	S		2004290	n		2
	<i>Psathyrella murcida</i> (Fr.) Kits van Wav.	S		2004401	N		1
	<i>Psathyrella pennata</i> (Fr.) A. Pearson & Dennis	S		2004469	n	X	1
	<i>Psathyrella piluliformis</i> (Bull.) P. D. Orton	S			n		1
	<i>Psathyrella spadiceogrisea</i> (Schaeff.) Maire	S		2004293	n		1
<i>Schizophyllaceae</i>	<i>Schizophyllum commune</i> Fr.	S		2004434			2
<i>Strophariaceae</i>	<i>Agrocybe praecox</i> (Pers.) Fayod	S		2004695			1
	<i>Cyclocybe aegerita</i> (V. Brig.) Vizzini	S					1
	<i>Pholiota brunnescens</i> A.H. Sm. & Hesler	S		2004333	N	X	1
	<i>Pholiota carbonaria</i> (Fr.) Singer	S		2004437		X	1
	<i>Pholiota lenta</i> (Pers.) Singer	S		2004367	N		1
<i>Tricholomataceae</i>	<i>Arrhenia griseopallida</i> (Desm.) Watling	S		2000601	N		1
	<i>Clitocybe costata</i> Kühner & Romagn.	S		2004503	n		1
	<i>Clitocybe gibba</i> (Pers.) P. Kumm.	S		2004346			1
	<i>Clitocybe odora</i> (Bull.) P. Kumm.	S					1
	<i>Clitocybe subspadicea</i> (J. E. Lange) Bon & Chevassut	S			n		1
	<i>Collybia tuberosa</i> (Bull.) P. Kumm	S		2004303			1
	<i>Lepista nuda</i> (Bull.) Cook	S					1
	<i>Paralepista flaccida</i> (Sowerby) Vizzini	S		2004439	n		1
	<i>Sphagnurus paluster</i> (Peck) Redhead & V. Hofst.	S			N		1

		<i>Tricholoma acerbum</i> (Bull.) Quél.	M	C, Q			1
		<i>Tricholoma fulvum</i> (DC.) Bigeard & H. Guill.	M	C, Q		n	1
		<i>Tricholoma sulphureum</i> (Bull.) P. Kumm.	M	C, Q			1
		<i>Tricholomopsis rutilans</i> (Schaeff.) Singer	S		2004375		2
	<i>Tubariaceae</i>	<i>Tubaria furfuracea</i> (Pers.) Gillet	S		2004295		1
		<i>Tubaria romagnesiana</i> Arnolds	S		2004433	n	1
	<i>Typhulaceae</i>	<i>Typhula quisquiliaris</i> (Fr.) Henn.	S		2004537	N	1
<i>Boletales</i>	<i>Boletaceae</i>	<i>Boletus edulis</i> Bull.	M	C, P, Q		n	1
		<i>Boletus reticulatus</i> Schaeff.	M	C, P, Q		n	1
		<i>Boletus subtomentosus</i> L.	M	C, P, Q		n	1
		<i>Caloboletus calopus</i> (Pers.) Vizzini	M	C, P, Q		n	1
		<i>Caloboletus radicans</i> (Pers.) Vizzini	M	Q		n	1
		<i>Hortiboletus rubellus</i> (Krombh.) Simonini, Vizzini & Gelardi	M	C, Q	2004384	n	1
		<i>Leccinum molle</i> (Bon) Bon	M	C, Q		n	1
		<i>Neoboletus erythropus</i> (Pers.) C. Hahn	M	C, P, Q		n	1
		<i>Phylloporus rhodoxanthus</i> (Schwein.) Bres.	M	C, Q		n	1
		<i>Xerocomellus chrysenteron</i> (Bull.) Šutara	M	C, Q	2004514		2
			<i>Xerocomellus porosporus</i> (Imler ex Watling) Šutara	M	Q		N
	<i>Diplocystidiaceae</i>	<i>Astraeus hygrometricus</i> (Pers.) Morgan	M	C, P, Q	2004357		2
	<i>Gyroporaceae</i>	<i>Gyroporus cyanescens</i> (Bull.) Quél.	M	C, Q		n	1
	<i>Hygrophoropsidaceae</i>	<i>Hygrophoropsis aurantiaca</i> (Wulfen) Maire	S		2004557		2
	<i>Paxillaceae</i>	<i>Paxillus involutus</i> (Batsch) Fr.	M	C, P, Q	2004349		2
	<i>Rhizopogonaceae</i>	<i>Rhizopogon luteolus</i> Fr.	M	P	2004072	n	1
	<i>Sclerodermataceae</i>	<i>Pisolithus arhizus</i> (Scop.) Rauschert	M	C, E, Q			1
		<i>Scleroderma cepa</i> Pers.	M	C, P, Q			1
		<i>Scleroderma citrinum</i> Pers.	M	C, Q	2004524		2
	<i>Suillaceae</i>	<i>Suillus bovinus</i> (L.) Roussel	M	P		n	1
<i>Cantharellales</i>	<i>Cantharellaceae</i>	<i>Cantharellus pruinosis</i> Peck	M	C, Q	2004230	n	1
		<i>Craterellus lutescens</i> (Fr.) Fr.	M	C, Q	2004520		1
		<i>Craterellus tubaeformis</i> (Fr.) Quél.	M	C, Q			1
		<i>Pseudocraterellus subundulatus</i> (Peck) D.A. Reid	S		2004535	N	1
	<i>Clavulinaceae</i>	<i>Clavulina coralloides</i> (L.) J. Schröt.	M	C, P, Q		n	1
		<i>Clavulina rugosa</i> (Bull.) J. Schröt.	S		2004216	n	1
	<i>Hydnaceae</i>	<i>Hydnum repandum</i> L.	M	C, P, Q		n	1
		<i>Hydnum rufescens</i> Pers.	M	C, Q	2004363	n	2
<i>Dacrymycetales</i>	<i>Dacrymycetaceae</i>	<i>Calocera cornea</i> (Batsch) Fr.	S			N	1

		<i>Calocera viscosa</i> (Pers.) Fr.	S		2004446	N		2
<i>Gomphales</i>	<i>Gomphaceae</i>	<i>Ramaria stricta</i> (Pers.) Quél.	M	C, P, Q		n		1
<i>Hymenochaetales</i>	<i>Hymenochaetaceae</i>	<i>Coltricia perennis</i> (L.) Murrill	M	C, P, Q	2004372			2
		<i>Hymenochaetopsis tabacina</i> (Sowerby) S.H. He & Jiao Yang	S		2004748			1
		<i>Inonotus hispidus</i> (Bull.) P. Karst.	S		2004445			1
		<i>Phellinus pomaceus</i> (Pers.) Maire	S		2004693			1
	<i>Schizoporaceae</i>	<i>Xylodon flaviporus</i> (Berk. & M.A. Curtis ex Cooke) Riebesehl & Langer	S		2004393	N		1
<i>Polyporales</i>	<i>Fomitopsidaceae</i>	<i>Laetiporus sulphureus</i> (Bull.) Murrill	S		2004998			2
		<i>Daedalea quercina</i> (L.) Pers.	S		2004158			1
	<i>Polyporaceae</i>	<i>Cerrena unicolor</i> (Bull.) Murrill	S		2004391			1
		<i>Faerberia carbonaria</i> (Alb. & Schwein.) Pouzar	S		2004407	n	X	1
		<i>Panus conchatus</i> (Bull.) Fr.	S		2004461	N		1
		<i>Trametes pubescens</i> (Schumach.) Pilát	S		2004308	n		1
		<i>Trametes versicolor</i> (L.) Lloyd	S		2004449			1
<i>Russulales</i>	<i>Russulaceae</i>	<i>Lactarius acerrimus</i> Britzelm.	M	C, Q	2004558			1
		<i>Lactarius aurantiacus</i> (Pers.) Gray	M	C, Q	2004523	n		1
		<i>Lactarius chrysorrheus</i> Fr.	M	C, Q	2003107			1
		<i>Lactarius controversus</i> Pers.	M	C, Q	2004382	n		1
		<i>Lactarius lacunarum</i> Romagn. ex Hora	M	C, Q	2003343	n		1
		<i>Lactarius pergamenus</i> (Sw.) Fr.	M	C, Q		n		1
		<i>Lactarius piperatus</i> (L.) Pers.	M	C, Q	2004210			1
		<i>Lactarius vellereus</i> (Fr.) Fr.	M	C, P, Q	2004320	n		1
		<i>Russula acrifolia</i> Romagn.	M	C, P, Q		N		1
		<i>Russula amoena</i> Quél.	M	C, Q	2004235	n		1
		<i>Russula anthracina</i> Romagn.	M	C, P, Q		N		1
		<i>Russula aurea</i> Pers.	M	C, Q		n		1
		<i>Russula brunneoviolacea</i> Crawshay	M	C, Q		N		1
		<i>Russula cyanoxantha</i> (Schaeff.) Fr.	M	C, P, Q		n		1
		<i>Russula delicata</i> Fr.	M	C, P, Q	2004423			2
		<i>Russula foetens</i> Pers.	M	C, P, Q	2004289			1
		<i>Russula fragilis</i> Fr.	M	C, P, Q	2003331	n		1
		<i>Russula graveolens</i> Romell	M	C, Q	2004525	n		1
		<i>Russula grata</i> Britzelm.	M	C, P, Q	2004428	n		1
		<i>Russula intermedia</i> P. Karst.	M	C, Q		N		1
		<i>Russula ionochlora</i> Romagn.	M	C, Q		N		1
		<i>Russula melitodes</i> Romagn.	M	C, Q	2004239	N		1
		<i>Russula odorata</i> Romagn.	M	C, P, Q	2004223	n		1
<i>Russula parazurea</i> Jul. Schäff.	M	C, Q		n		1		

			<i>Russula pelargonica</i> Niolle	M	C, Q	2004429	n		2
			<i>Russula praetervisa</i> Samari	M	C, P, Q	2004233	N		1
			<i>Russula risigallina</i> (Batsch) Sacc.	M	C, P, Q	2004688	n		1
			<i>Russula virescens</i> (Schaeff.) Fr.	M	C, Q		n		1
		<i>Stereaceae</i>	<i>Aleurodiscus amorphus</i> (Pers.) J. Schröt.	S		2004312	n		1
			<i>Stereum hirsutum</i> (Willd.) Pers.	S		2004313			1
			<i>Stereum subtomentosum</i> Pouzar	S		2004311	n		1
	<i>Tremellales</i>	<i>Tremellaceae</i>	<i>Phaeotremella foliacea</i> (Pers.) Wedin, J.C. Zamora & Millanes	P	H	2004373	n		2
			<i>Tremella mesenterica</i> Retz.	P	Z	2004462	n		2

Capítulo II

Effect of fire on macrofungal communities of Mata da Margarça Laurisilva forest

Bruno A. F. Natário¹, Rogério F. A. Louro¹, Celeste M. M. Santos-Silva¹

¹Macromycology Laboratory, Institute of Mediterranean Agricultural and Environmental Sciences
Biology Department, University of Évora, Apartado 94
7002-554 ÉVORA, Portugal

Keywords: Fire; macrofungi; laurel forest; bioindicators; diversity indexes.

Abstract:

Laurel forests are one of the rarest ecosystems on Earth. Mata Nacional da Margarça, in Portugal, is a patch of laurel forest that prevails imprisoned in a vale with a distinct Atlantic influence surrounded by a marked Mediterranean climate. A fire, in 2017, burned 90% of the Mata Nacional da Margarça area, putting at risk its biodiversity. This study represents the first study on macrofungal-fire interactions on laurel forest and aims to compare macrofungal richness and abundance of areas subjected to different fire severity levels (unburned; burned: low, moderate and high severity) and suggest bioindicators. Fire severity had a high explanatory value for the variance of our plots, being highly correlated with hypsometry and negatively correlated with the topographic wetness index. A decreased in richness, Shannon and Margalef indexes values throughout fire severity groups was remarked. The mycorrhizal and mycorrhizal/saprotrophic proportion, for both richness and abundance, proved to be good indicators of fire events, since all showed significant differences between unburned plots and the others. *Amanita muscaria* was the most remarkable case where a demarked decrease in abundance was observable from unburned to burned plots. Concerning the saprotrophic species, *Pholiota brunnescens*, *Psathyrella pennata* and *Tephrocybe anthracophila*, also seem to be good indicatives of fire severity, since their abundances increase systematically from unburned to burned plots. Furthermore, fire severity proved to be the variable that explained the most variance of species abundance, with a clear distinction between unburned and burned plots and no clear distinction within burned plots. As so, is of the utmost importance to follow the post-fire macrofungal succession to evaluate the ecosystems sanity and ensure the proper management to secure a healthy post-fire succession and development of the ecosystems.

Introduction

Laurel forests are one of the rarest ecosystems on Earth, being very similar to the laurel forest of Southern Europe and Northern Africa from the Tertiary period, millions of years ago. The biggest area of Laurel forest measures 15000 ha and is located in Madeira island (Portugal). Nevertheless, several other laurel areas are distributed through all five continents. The European portion of the Mediterranean have some unique locations where laurel forests still thrives, such as Mata Nacional da Margaraça, in Portugal. This patch of laurel forest prevails imprisoned in a vale with a distinct Atlantic influence surrounded by a marked Mediterranean climate. Although, an enrichment in species, such as *Quercus suber* L., is provided by the adjacent Mediterranean ecosystem, a higher risk of forest fire, which are usual in Mediterranean ecosystem, is also transposed. Wildfires are one of the most catastrophic natural events and imposes a strong selection pressure in the ecosystems (Johnson, 1992; Dahlberg, 2002; Martín-Pinto et al., 2006). In Mediterranean ecosystems this event is considered the main natural disturbance noticeably shaping the landscape and ecosystems (Keeley, 2011; Mediavilla et al., 2014).

Macrofungal communities are well represented in most ecosystems and consequently are one of the biological groups most aggrieved by wildfires. The impact on macrofungal communities is strongly dependent on the fire intensity, duration and periodicity, and influences the after-fire succession. These factors are translated to severe changes in soil physical, chemical and biochemical properties, that are very detrimental to most macrofungal species (Peay et al., 2009; Kurtoga 2012). Several studies showed a decrease and shift of species richness (Martín-Pinto, 2006; Olsson and Jonsson, 2010; Kutorga et al., 2012; Hernández-Rodríguez et al., 2013; Franco-Manchón et al., 2019) after-fire, with a clear decrease of mycorrhizal species. The shift in plant communities greatly promoted the decrease in mycorrhizal species, due to host mortality (Dahlberg, 2002). Nevertheless, mycorrhizal species, like *Laccaria laccata* (Scop.) Cooke and *Rhizopogon* spp., are common in after-fire scenarios because they are multi-host species or primary mycorrhizal, respectively, which can benefit from the growth of new seedlings (Buscardo et al., 2012; Franco-Manchón et al., 2019). The soil spore bank is very important for after-fire macrofungal succession, since most species, common immediately after fires, grow from fire resistant structures preserved in soil (Martín-Pinto et al., 2006; Carney and Bastias, 2007; Claridge et al., 2009; Gassibe et al., 2011; Franco-Manchón 2019). Some of this species are post-fire species (Dix and Webster, 1995; Sumorok, 2001; Robinson et al., 2008; Claridge et al., 2009), that greatly benefit from after-fire conditions, since spore germination may result from soil heating or pH and C/N changes. These species are very important in after-fire succession since they colonize disturbed substrates, such as burned wood debris and soil high ashes content (Claridge et al., 2009), and promote after-fire succession. Furthermore, these species are

indicators of after-fire conditions, has mention above, and are important factor to consider in forest management approaches in after-fire scenarios. Other species, like *Stereum hirsutum* (Willd.) Pers. and *Tremella mesenterica* Retz., are very common and widespread in both burned and unburned areas (Mediavilla et al., 2014; Franco-Manchón et al., 2019), independently of the fire characteristics. Their multistage ecological and physiological features are the explanation why they cannot be considered good indicators of pre and/or post-fire succession stages.

To our best knowledge, the scarce fire events that occurred in Laurisilva forest were not object of macrofungal communities after-fire studies. This ecosystem is, theoretically, more vulnerable to fire events in comparison, for example, to Mediterranean ecosystem and management is key for a healthy after-fire recovery of the ecosystem. Mata Nacional da Margarça was severely burned in 2017 fire and is now target of management, that includes salvage logging and reforestation. This may later add up to the disturbance and shift the ecosystem response to this disturbance. Post-fire macrofungal communities are very important to the ecosystem recover in unmanaged area, since mycelial networks may improve soil aeration and water infiltration into deeper soil layers, by binding soil particles into aggregates, and may have a major role in capturing and concentrating nutrients in the post-fire soil, contrasting to managed areas where mycelium may work as a water repellent (Claridge et al., 2009).

This study aims to characterize the macrofungal community in burned areas of Mata Nacional da Margarça, with special focus on richness, composition and abundance of species. Our specific objective is to compare macrofungal richness and abundance of areas subjected to different fire severity levels and, if possible, suggest bioindicators.

Methodology

Study area

The survey was conducted in Mata Nacional da Margarça (MM), Paisagem Protegida da Área da Serra do Açor (40°13'00.2"N 7°55'08.6"W) (Fig. 1). This region has an Atlantic climate influence with a three month long dry season (July to September), a mean annual precipitation of 1440 mm and mean temperatures ranging from 7.9 to 22.6 °C (Silveira, 2001), these climatic data were provided by the closest meteorological station (Pampilhosa da Serra, 591503.791 Latitude-UTM, 4444687.287 Longitude-UTM and 890 m above the sea level, Instituto do Português do Mar e da Atmosfera). This protected landscape is situated 450-800 m above the sea level in the Iberian fold belt (Lourenço, 1996), between Lousã fault and Sobreira Formosa fault, and has a N-NW orientation. The soil is classified as a Cambisol and Leptisol.

The forest as a clear dominance of the *Rusco aculeati-Quercetum roboris* association,

subassociation *Viburnetosum tini*, class *Quercio-Fagetea*, order *Quercetalia roboris* and alliance *Quercion robori-pyrenaicae*. *Quercus robur* L. and *Castanea sativa* Mill. abandoned coppice stands, occupy the inner part of the MM *Quercus suber* L., although less frequent, can be found on the outskirts of the MM. The understory is composed mainly of laurel species (e.g *Viburnum tinus* L., *Ilex aquifolium* L., *Laurus nobilis* L. and *Prunus lusitanica* L. ssp. *lusitanica*), *Cytisus* spp., *Erica* spp., *Calluna vulgaris* (L.) Hull, *Ulmus minor* Mill., *Prunus cerasus* L., *Prunus avium* L., *Corylus avellane* L. and *Arbutus unedo* L.

By the early 1960s all the economic activities derived from the MM natural sources were ceased. The cumulative organic matter deposited on the forest floor culminated in the forest fires of 1987 and 2017. The 2017 fire burned 90 % of the MM area, except for the location near the river which delimits lower section of the MM.

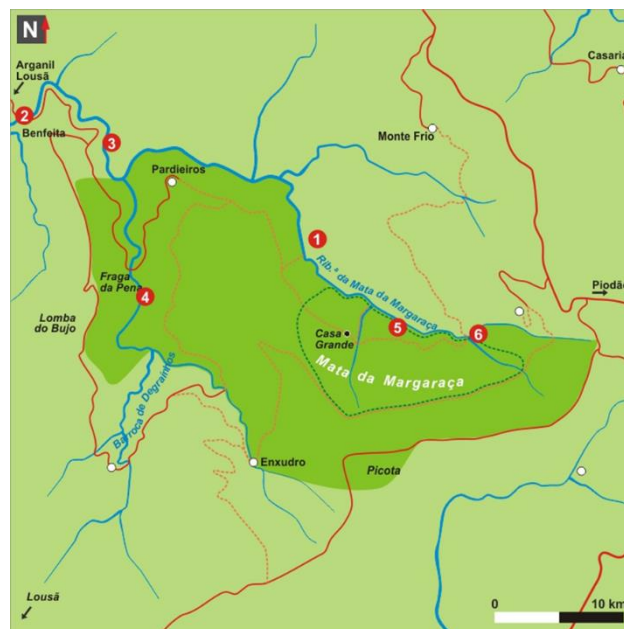


Figure 1 - Mata Nacional da Margaraça (ICNF)

Sampling

Seventy-five 25 m² non-overlapping plots were randomly distributed, within a fire severity range of values (varying from 20 to 1200) (Botella-Martínez & Fernández-Manso, 2017). From the seventy-five preliminary plots, only sixty-six were surveyed due to topographic constraints. The survey was conducted after the most recent wildfire (October 2017), between May 2018 and May 2019, with samplings occurring in the most favourable months, Spring (March-May) and Autumn (October-December). Four surveys were conducted, two in the Spring and two in the Autumn.

Specimens Determination

All the specimens within the plot area were harvested, stored under 4 °C and processed within

twenty-four hours. All the sporocarps were identified at species level whenever possible. The specimens were then preserved and deposited in Évora University herbarium (UEVH- FUNGI). Macrofungal nomenclature follows Catalogue of Life (2019) and Kirk (2019). The post-fire species were classified according to Dix and Webster (1995), Sumorok (2001), Robinson et al. (2008) and Claridge et al. (2009).

Independent variables

The fire severity values, for each plot, were calculated using ArcGis 10.X, based on the Normalize Burn Index (NBR), which uses radiation reflection information, namely the near-infrared (NIR) and mid-infrared bands (also known as short-wave infrared (SWIR)) from the Sentinel-2 satellite sensor. In order to assess the occurrence of differences between fire severity and vegetation cover, an ordinal variable with four classes (SEVER_4) was created, based on the original fire severity values per plot. As such, each class corresponded to a distinct fire severity range as observed in the field: 1 - unburned or slightly burned, 2 - low fire severity, 3 - moderate fire severity and 4 - high fire severity (Botella-Martínez & Fernández-Manso, 2017).

ASTER-derived digital elevation model (DEM) was used to compute several surface metrics. The original DEM was resampled to a resolution of 30 m through a bilinear interpolation method in ArcGIS 10 (ESRI 2011). Surface complexity, temperature and moisture DEM derived metrics, were calculated, within and without a specific window (5, 15, 25 cells). This set of surface metrics were obtained through Geomorphometry and Gradient Metrics (version 1.0) (Evans et al., 2013), DEM Surface Tools (Jenness, 2011) and Land Facet Corridor Tools (Jenness et al. 2013) toolboxes for ArcGIS 10 (ESRI 2011) (Supp. File Table S1).

Data analysis

The data was organized on different matrix according to taxonomic level (specie, genus and family), trophic group (mycorrhizal and saprotrophic) and harvest season (Spring and Autumn). Species with a wide representation throughout the points in all four severity groups and species represented a single time were removed from the data matrix, upon submitting it to statistical analysis and diversity, uniformity and richness calculations.

Shannon's H' (Shannon & Weaver, 1949) Margalef d (Margalef, 1958) diversity indexes were calculated. Species Evenness J' (Pielou, 1969) and Richness (S) were also analysed. These variables were calculated using the following formulas:

$$H' = \sum p_i [\log_e (p_i)]$$

$$d = (S - 1) / \log (N)$$

$$J' = H' / \log(S)$$

S = number of species

where coefficient P_i indicates the relative importance of each fungal species and N is the total number of individuals in the sample.

Normality and homoscedasticity of the data were evaluated to select the appropriated statistical methods. Since none of the abovementioned assumptions were verified, the Spearman's correlation coefficient was chosen to select significant correlations between environmental variables and biological data. Furthermore, pairwise correlations between the chosen environmental variables were made, in order to exclude highly correlated ($r > 0.70$) variables. The Kruskal-Wallis test was used to compare the shape and spread of the trophic groups proportions variables, richness and diversity indexes across the four groups (fire severity). When appropriate the chi-squared test was used to analyse the association between dependent and independent variables. The Mann-Whitney test was used to make pairwise comparisons between groups where an overall significant difference was found.

The selected environmental variables and biological data were submitted to multivariate statistical analysis. Prior to the multivariate statistical analysis, a transformation to square root (\sqrt{x}) was conducted for all the environmental variables, due to the skewed distribution, with exception of topographic position index, which was not transformed, and aspect, which was transformed to sine ($\sin x$). Finally, the set of variables was normalized in order to proceed with principal component analysis (PCA), that computes principal components (new variables) which account for as many variance as possible, based on the original data (Clarke & Gorley, 2015).

All biological data was firstly transformed (square root) and then submitted to a Bray-Curtis resemblance measure, to convert data into dissimilarity triangular matrices (Clarke & Warwick, 2001). Afterword, a canonical analysis of principal coordinates (CAP) was preformed (Anderson & Willis, 2003), to better visualize the differences between sample groups in a multidimensional space, based on severity factor. Additionally, a PERMANOVA design was conducted to test global and pairwise significant differences based on severity factor (SEVER_4). Similarity percentage analysis routine (SIMPER) was ran to analyse the contributions of individual species to similarities and dissimilarities within and between groups according to factor severity.

Finally, a distance-based linear model (DistLM) was performed to analyse and model (regression and multiple regression models) relationships between biological data and environmental variables. The multiple regression model will sequentially select the variables, that together, better explain the biological data and produce the best fitted model, using AIC model selection criterion.

All calculations were carried out using IBM SPSS statistics 22 for Windows (SPSS Inc, Chicago, IL, United States) and PRIMER-e v.7 with Permanova+.

Results

General Data

A total of 138 species were recorded during this survey, representing 78 genera and 47 families, belonging to the phyla *Basidiomycota* and *Ascomycota*. Twenty-six specimens were only amenable of determination to the genus (e.g. *Agrocybe* sp., *Bovista* sp. and *Collybia* sp.). From the 138 species 56 can be classified as mycorrhizal, 78 as saprotrophic and 4 as parasitic, with an overall mycorrhizal/saprophytic (m/s) proportion of 1/1.4. Twelve species were classified as post-fire.

One hundred and one species were found in the severity group 1 (m/s = 1/1.08) and 63 of those were exclusive to this group (e.g. *Amanita muscaria* (L.) Lam., *Hebeloma crustuliniforme* (Bull.) Qué., *Laccaria amethystina* Cooke, *Russula pelargonica* Niolle) (Fig. 2; Fig. 3). This group as the most species and exclusive species of all severity groups. In group 2 (m/s = 1/2.3) were recorded 44 species and 12 of these were exclusive to this group (Fig. 2; Fig. 3) (e.g. *Arcyria denudata* (L.) Wettst., *Trametes versicolor* (L.) Lloyd and *Coprinopsis lagopides* (P. Karst.) Redhead, Vilgalys & Moncalvo). Fourty-one were found in the severity group 3 (m/s = 1/4.6), 13 of those were exclusive to this group (Fig. 2; Fig. 3) (*Gymnopus dryophilus* (Bull.) Murrill, *Crepidotus mollis* (Schaeff.) Staude and *Hygrocybe russocoriacea* (Berk. & T.K. Mill.) P.D. Orton & Watling). In group 4 (m/s = 1/5) were recorded 32 species and 12 of these were exclusive to this group (Fig. 2; Fig. 3) (e.g. *Simocybe centunculus* (Fr.) P. Karst., *Faerberia carbonaria* (Alb. & Schwein.) Pouzar and *Lamprospora trachycarpa* (Curr.) Seaver).

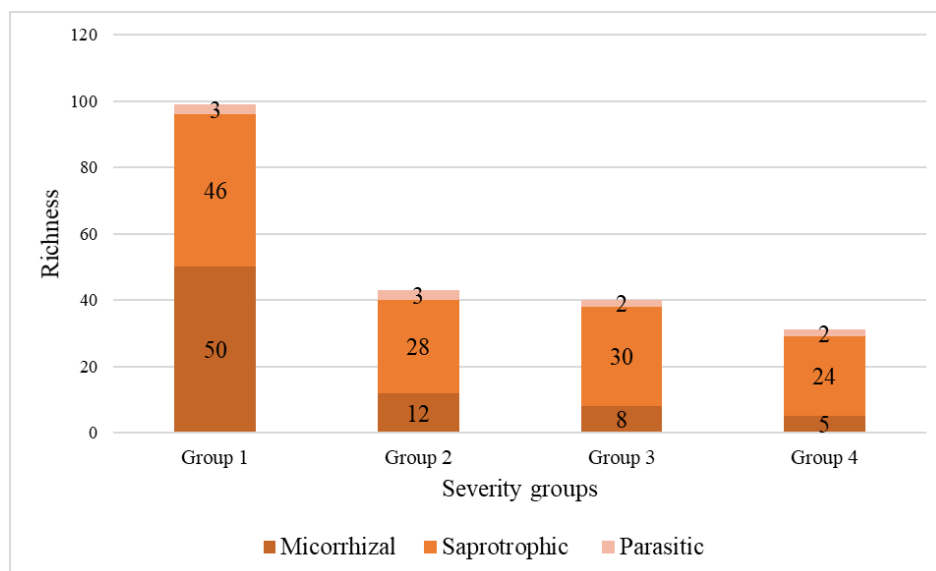


Figure 2 - Richness of mycorrhizal, saprotrophic and parasitic species per severity group.

The number of harvested sporocarps was higher in the severity group 1 than in the rest of the groups (Fig. 4). Diminutive difference was found between group 2, 3 and 4 (Fig. 4), with group 3

being the one with the less collected sporocarps. Although the number of sporocarps of saprotrophic species had less noticeably differences between severity groups, it follows the same pattern as the total of harvested sporocarps, with the severity group 1 having the most sporocarps collected of all groups and group 3 having the lower number of collected sporocarps (Fig. 4). The total number of collected sporocarps of mycorrhizal species was lower from group to group (Fig. 4).

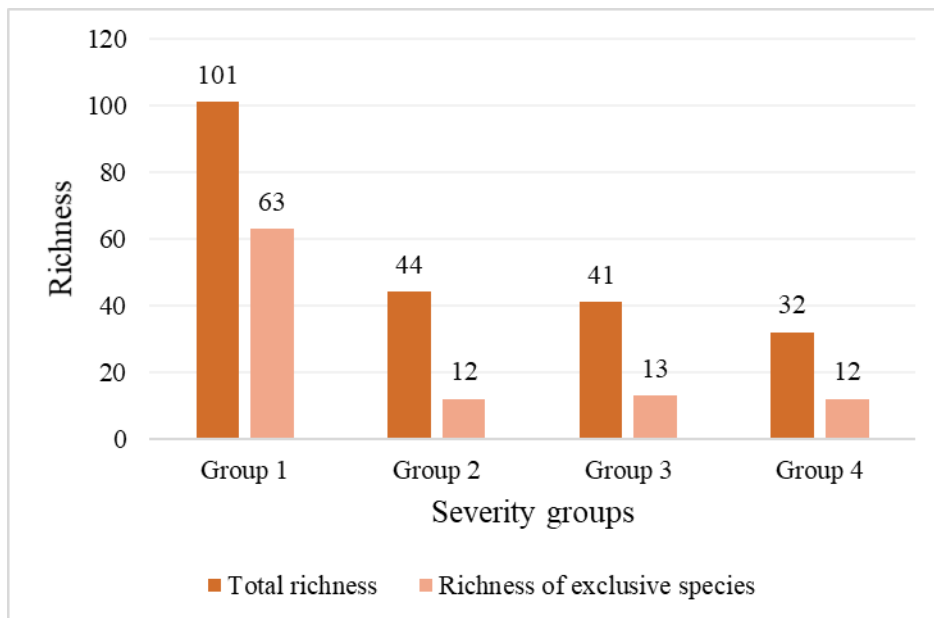


Figure 3 - Richness of total and exclusive species per severity group.

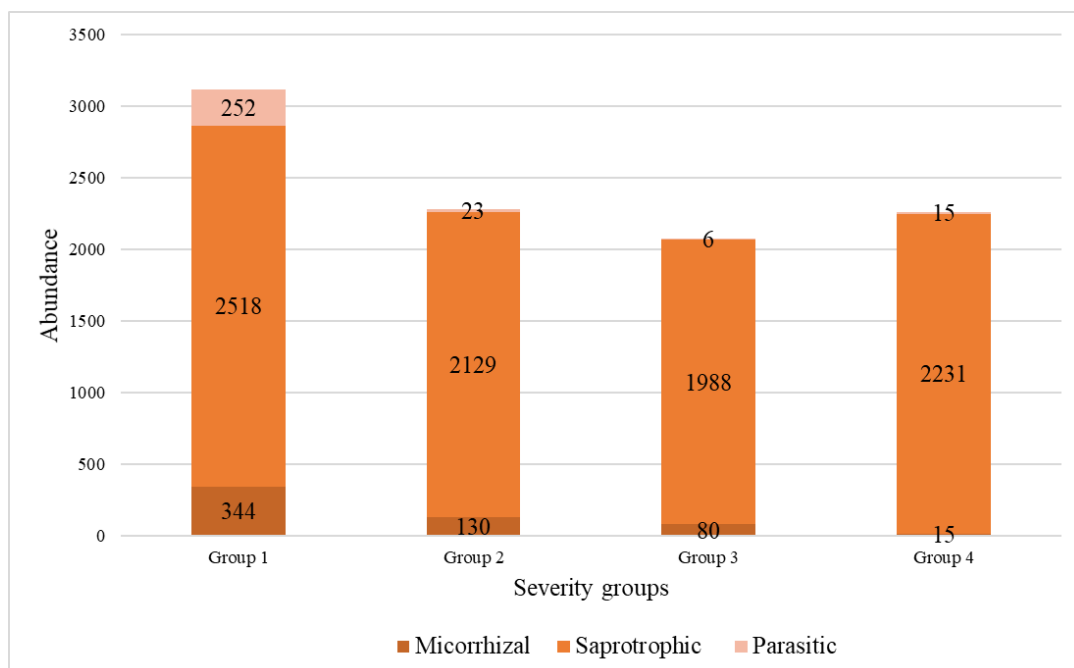


Figure 4 - Abundance of mycorrhizal and saprotrophic sporocarps per severity group.

There were statistically significant differences ($p < 0.05$) between the fire severity groups in

terms of mycorrhizal richness, mycorrhizal abundance, mycorrhizal/saprotrophic species proportion and mycorrhizal/saprotrophic abundance proportion, in all cases only between group 1 and the other groups.

Richness and Diversity

Evenness J' showed values superior to 0.5 in $\approx 84\%$ of the samples and did not reveal any significant correlation with the environmental data used. In contrast, richness was highly negatively correlated with fire severity and had a substantial negative correlation with hypsometry (Table 1). Margalef d showed the same patterns as richness for fire severity and hypsometry, but not for aspect, with which it had a substantial positive correlation (Table 1). Furthermore, Shannon's H' was highly negatively correlated with fire severity (Table 1). There were no statistically significant differences ($p < 0.05$) between the fire severity groups in terms of richness and diversity indexes.

Tabela 1 – Correlation values between richness, Margalef (d), Evenness (J') and Shannon's (H') indexes and hypsometry (HIP), aspect (ASP) and fire severity (SEV). ns - not significant; significant: * - p - value ≤ 0.05 , ** - p - value ≤ 0.01 .

	Richness	d	J'	H'
HIP	-0.286*	-0.312*	0.051 ^{ns}	-0.152 ^{ns}
ASP	0.147 ^{ns}	0.284*	0.147 ^{ns}	0.135 ^{ns}
SEV	-0.433**	-0.561**	-0.093 ^{ns}	-0.387**

Data analysis

The PCA showed a clear distinction between group 1 and the rest of the groups, with the first three principal components accounting for, respectively, 43.7 %, 23.9 % and 12.5 % (80.2 % cumulative variation) of the total variation. The variables responsible for the patterns showed on the first dimension were vectorial ruggedness measure (0.447), topographic wetness index (0.483), heat load index (-0.421) and topographic position index (-0.421) (Suppl. Files Table. S2 and S3). The positive side of this dimension was mainly occupied by sampling plots belonging to the group 1 and 2, as expected, with rare exception from group 3 (plot 35) and 4 (plots 33 and 40), and the negative side of this dimension was occupied by the bulk of the group 3 and 4 plots and by a considerable portion of the group 1 and 2 plots (Fig. 5). As so, this component separates the sampling plots from areas potentially colder, more capable of retaining water and with a more heterogeneous terrain from

the ones potentially warmer, less capable of retaining water and with a less heterogeneous terrain. The second dimension showed a clear separation between group 1 and the other groups (Fig. 5). The variables fire severity (0.590), hypsometry (0.509) and aspect (-0.500) were responsible for this distinction between the high severity sampling plots and the lower severity sampling plots (Suppl. Files Table. S2 and S3). The group 1 plots were distributed throughout the negative side of this dimension, with exception of the plot 6, and the groups 3 and 4 plots in the positive side of this dimension (Fig. 5). Group 2 showed an overlapping distribution with group 1, 3 and 4. CTI (0.928) (Suppl. Files Table. S2 and Table S3) is responsible for the trends showed on the third dimension, which separates the more humid plots from the drier plots (Fig. 5).

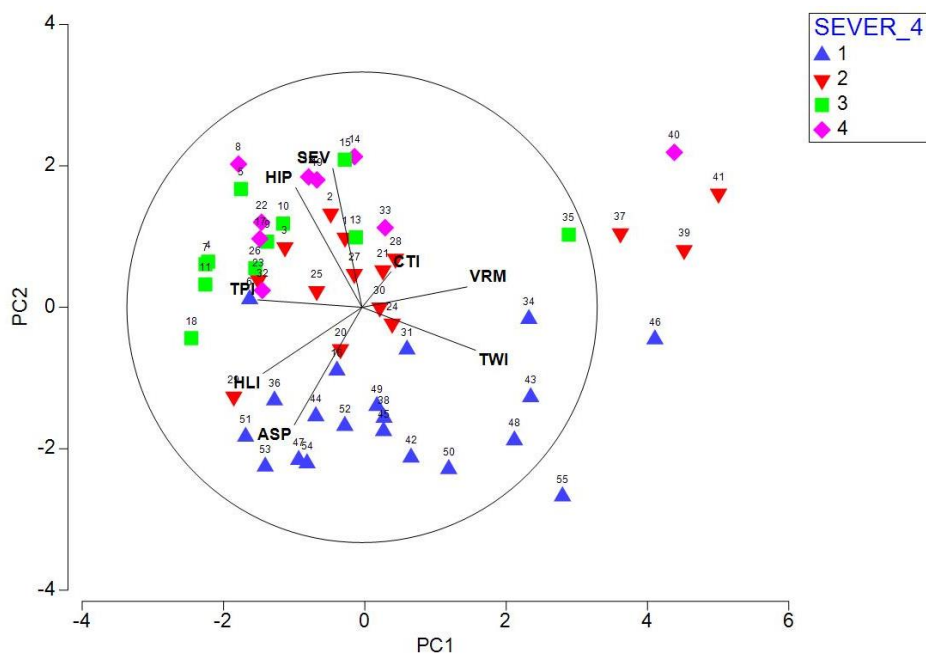


Figure 5 - Principal Component Analysis with eigenvectors. Samples plots are numbered from 1 to 55. Sever_4: fire severity groups. Environmental variables: aspect (ASP), compound topographic index fire severity (CTI), (SEV), hypsometry (HIP), vectorial rudgness measure (VRM), topographic wetness index (TWI), heat load index (HLI) and topographic position index (TPI).

Significant differences among severity groups were shown by one-way Permanova analysis ($p = 0.001$). Furthermore, pair-wise Permanova test revealed significant differences between group 1 and the other three ($p = 0.001$, for the three pairs), and no significant differences among group 2, 3 and 4 (2 & 3: $p = 0.109$; 2 & 4: $p = 0.883$; 3 & 4: $P = 0.856$) (Suppl. Files Table. S4).

CAP ordination revealed a separation of data among severity groups, using $m = 6$ principal coordinate axes (Fig. 6) ($p = 0.0001$, using 9999 permutations). A strong association was seen between the multivariate data and the hypothesis of differences among severity groups, indicated by the large size of their canonical correlations ($m= 1: \delta^1 = 0.8785$; $m = 2: \delta^2 = 0.3749$) (Suppl. Files Table. S5). The first canonical axis (CAP1) showed a clear separation between group 1 and the others,

as observed in Permanova analysis, and the second canonical axis (CAP2) showed a less noticeable marginal distinction between group 2 and group 3 and 4 (Fig. 6). Cross validation of the CAP model showed that $\approx 57\%$ of plots were correctly classified to their severity group. More specifically, group 1, 2, 3 and 4 had, respectively, 80 %, 60 %, $\approx 37\%$ and 0 %, of correctly classified plots (Suppl. Files Table. S6). Group 4 plots were relocated to group 2 (3 plots) and group 3 (6 plots).

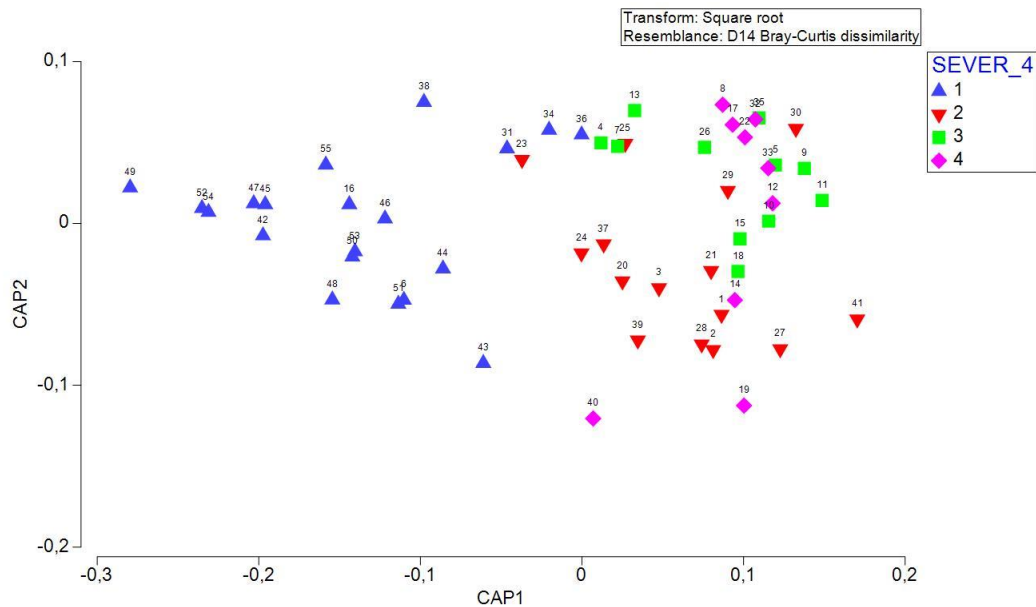


Figure 6 - Canonical Analysis of Principal coordinates. Samples plots are numbered from 1 to 55. Sever_4: fire severity groups.

SIMPER analysis was used in order to determine which genera were responsible for the dissimilarity between severity group. This analysis showed that group 1 is the most different, with average dissimilarity values of 89.55 (1 & 2), 88.73 (1 & 3) and 89.81 (1 & 4). Furthermore, SIMPER analysis revealed that the genera responsible for the dissimilarity between groups were almost the same in every group pair, such as *Hypholoma* (Fr.) P. Kumm., *Laccaria* Berk. & Broome, *Pholiota* (Fr.) P. Kumm. (highest contribution in every group pair), *Psathyrella* (Fr.) Quél. and *Tephrocybe* Donk, accounting for a cumulative contribution of $\approx 40\%$ (Suppl. Files Tables S7, S8, S9, S10, S11 and S12). These genera are represented, in this study, by species associated with post fire conditions (Dix and Webster, 1995, Sumorok, 2001, Robinson et al., 2008; Claridge et al., 2009), like *Hypholoma fasciculare* (Huds.) P. Kumm., *Pholiota brunnescens* A.H. Sm. & Hesler, *Pholiota carbonaria* (Fr.) Singer, *Psathyrella pennata* (Fr.) A. Pearson & Dennis, *Tephrocybe anthracophila* (Lasch) P.D. Orton, and species known to proliferate in early ecological succession stages of forest ecosystems, like *Laccaria laccata*. This analysis further revealed that species belonging to *Amanita* genus are also greatly responsible ($\approx 5\%$) for the dissimilarity of group 1 and the other three. These mycorrhizal species are associated with later stages of ecological succession and well-developed systems (Redecker et al., 2001).

The results of the DISTLM analysis revealed the extent to which the measured environmental variables were responsible for the patterns shown by genera assemblages. Macrofungal genera abundance was significantly influenced by fire severity ($p = 0.001$), hypsometry ($p = 0.001$), aspect ($p = 0.0026$) and topographic wetness index ($p = 0.0042$) (Marginal test), when each variable is considered individually (Suppl. Files Table. S13). The sequential model indicated that fire severity individually accounted for 11.51 % of the total variation (Suppl. Files Table. S13), and no additional variables were accounted for when they were considered simultaneously (Suppl. Files Table. S13), suggesting that the variables overlap in their explanatory capacity.

The dbRDA diagram showed a distinction between severity groups, except for group 3 and 4 which are not distinguishable among themselves. The first dimension of the dbRDA clustering explains 14 % of the total variation (Fig. 7), with the variables fire severity (0.715) and hypsometry (0.545) (Suppl. Files Table. S14) being the ones responsible for this variation. The negative side of this dimension is mainly occupied by group 1 plots, group 2 plots occupy the central area on this dimension (near 0) and the positive side is occupied by plots from group 3 and 4 with no clear distinction in the positioning of these plots. The variables topographic wetness index (-0.591) and heat load index (0.556) (Suppl. Files Table. S14) are responsible for the 2.4 % of total variation observed in the second dimension of the dbRDA clustering (Fig. 7). No clear distinction is observed among plots or severity groups in this dimension, corroborating the patterns observed by the sequential test of the DISTLM analysis that suggested that the variables overlapped in their explanatory capacity (Fig. 7).

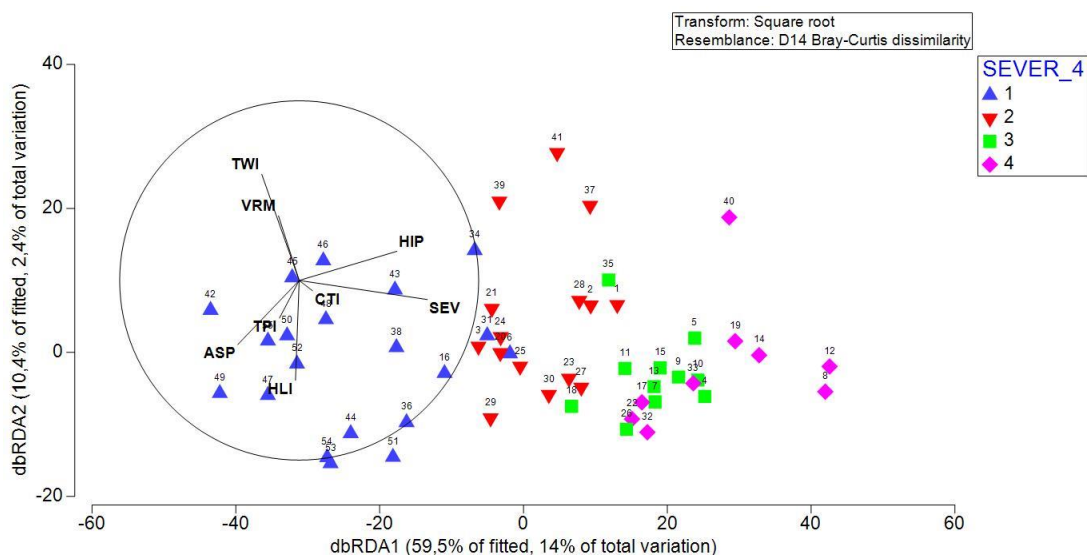


Figure 7 - Distance based redundancy analysis. Samples plots are numbered from 1 to 55. Sever_4 - fire severity groups. Environmental variables - aspect (ASP), compound topographic index fire severity (CTI), (SEV), hypsometry (HIP), vectorial ruggedness measure (VRM), topographic wetness index (TWI), heat load index (HLI) and topographic position index (TPI).

Discussion

To our best knowledge this work represents the first study of macrofungal and fire interactions in a Laurisilva ecosystem. Fires are common events in Mediterranean ecosystems but not in Laurisilva ecosystem, making MM an exceptional area to study this specific interaction, due to its geographic position.

Fungal diversity and productivity are important to describe the general biodiversity in forest ecosystems (Arnolds, 1992; Hawksworth, 2001; Gassibe et al., 2011). Regarding to the total number of fungal taxa, our work showed a very high fungal richness (138 *taxa*), to which the species exclusive to burned plots contributed with 39 *taxa*. The high richness value found shows the same pattern as works done in *Pinus* spp., *Cistus* spp. and *Quercus* spp. stands (Gassibe et al., 2011; Hernández-Rodríguez et al., 2013; Pourreza et al., 2014; Franco-Manchón et al., 2019). However, this pattern is mostly influenced by the values found in group 1 plots, which by themselves account for $\approx 50\%$ of the species found. Despite no significant differences concerning richness and diversity indexes were observed, a decreased in richness, H' and d indexes values through group 1, 2, 3 and 4 was remarked. This pattern is similar to the results found in studies carried on *Pinus* spp., *Cistus* spp. and *Quercus* spp. stands immediately and one year after the fire (Gassibe et al., 2011; Hernández-Rodríguez et al., 2013; Pourreza et al., 2014; Franco-Manchón et al., 2019). On the other hand, the proportion mycorrhizal/saprotrophic (m/s) species proved to be a good indicator of fire events, since all variables (m_richness, m_sporocarps abundance, m/s richness and m/s_sporocarps abundance) showed significant differences between group 1 and the others.

MM ecosystem singular features (topography and edaphoclimatic features) showed low effect explaining the species abundance and distribution after-fire, when compared to fire severity, which was the most important explanatory variable in this study. In fact, the small dimensions and N-NW orientation of MM are translated into the little variation observed within the environmental variables used in this work (Suppl. Files Table. S15), that denote a uniformity of condition throughout all the MM. Hypsometry (HIP) is perhaps the most explanatory environmental variable in this work, as it has the second higher value in PCA analysis (second to fire severity) and is highly correlated with fire severity. Even though, the high correlation with fire severity can be explained by the location of several burned plots that are mostly placed in the upper area of MM, hypsometry by itself condenses a lot of information. The higher hypsometric locations have a higher slope, less humidity and are mainly composed by *Pinus pinaster*, *Castanea sativa* stands and almost no shrub cover, consequently having higher temperatures, more radiation reaching the ground and less organic matter on the soil. In contrast, the lower area of the MM, near the river, is more humid, flatter and has a more complex plant structure, composed mainly by *Quercus robur* and several shrub species, consequently having

lower temperature, less radiation reaching the soil and more organic matter on the soil deriving from the upper areas of the MM. The 2017 fire progressed from the outside of the MM burning primarily and more severely the outskirts of the MM. As so, some high humidity areas were severely burned, like the plots 39 to 41, contrasting with what was expected. Our analysis further exposes this situation, when the group 4 plots were all misclassified and diluted into group 2 and 3, indicating that the high humidity plots that were severely affected may recover fast. Still, there is underlying fire feature that we were not able to consider. To some extent fire severity (fire variable) (Botella-Martínez & Fernández-Manso, 2017) considers the presence/absence of vegetation and fire intensity. In the other hand, some important post-fire feature cannot be extrapolated from fire severity, such as the amount of ashes deposited on soil, temperature reached during the fire, soil erosion factor, soil pH and C:N ratio. Still, relevant patterns were found during this work.

Considering the most frequent species, such as *Mycena galopus* (Pers.) P. Kumm., *Pholiota brunnescens*, *Psathyrella pennata*, and *Tephrocybe anthracophila*, is observable a shift in species abundance from group 1 to 4, which is responsible for the differences between groups noted in SIMPER analysis. This shift is more prominent from group 1 to the rest, with an average increase on abundance from group 1 to 2 of $\approx 59\%$ for *Mycena galopus*, *Pholiota brunnescens*, *Psathyrella pennata*, and *Tephrocybe anthracophila* and a decrease on abundance from group 1 to 2 of $\approx 59\%$ for *Amanita muscaria* (L.) Lam (the most represented species of *Amanita* in this work). The finding is in accordance with Dahnberg (2002) who showed that a change in fungal abundance through unburned and burned sites was more evident than a shift in richness. Even though this is true in this work, a clear change in species abundance is only observed in post-fire species (*Pholiota brunnescens*, *Psathyrella pennata*, and *Tephrocybe anthracophila*), which appear in almost all fire severity group but are more abundant in group 3 and 4. This may be due to the fire-resistant structures (infected root tips, sclerotia and resistant spores) that the post-fire species produce in order to prevail after-fire conditions (soil heating, increment of ashes into the soil and topsoil erosion). These conditions usually result in the death of most of the individuals, destruction of the fire-resistant structures, decrease in root infection rates (Barker et al., 2013; Peay et al., 2009), changing the optimal soil pH and C:N ratio (Kutorga et al., 2012) and reduction of infectivity of fungal propagules (Rashid et al., 1997), that prevent less resilient species to propagate. Most of the other species were rare (collected in less than 5 plots), making them exclusive to a certain severity group (e.g. group 1: *Amanita rubescens* Pers.; group 2: *Coprinopsis lagopides*; group 3: *Psathyrella hirta* Peck; group 4: *Simocybe centunculus*) and as so no clear drop between group was observed. It is important to note that this study was carried on for only one year and, maybe, some major dissimilarities can be observed in the future, or in the opposite, the mycobiota may recover fast.

A big portion of macrofungal communities are composed by mycorrhizal species, as so, the

effect of fire in plant communities has substantial impact on post-fire macrofungal communities. Most of this impact resides on the death of the host plants (Dahlberg et al., 2001) and can be catastrophic for mycorrhizal macrofungal communities when coupled with mycelium death (Dahlberg, 2002) and topsoil erosion (Rashid et al., 1997), leaving the germination of the remaining soil spores as the only survival choice (Vilarino & Arines, 1991). In this study, the mycorrhizal/saprotrophic proportion shows this exact pattern, with the highest m/s being in group 1 (1/1.08) and the lowest in group 4 (1/5). The gradual decrease in m/s through the severity groups shows that the impact of fire was different in all groups. The CAP analysis revealed that some plots from group 2 and 3 were misclassified and allocated, due to the low number and abundance of species, and all plots of group 4 were misclassified. This may be because the mycorrhizal species in this group were composed by pioneer species, such as *Laccaria laccata* and *Plicaria endocarpoides* (Berk.) Rifai, and late succession stage species, such as *Inocybe rufoalba* Sacc. and *Xerocomus* sp., that oppose each other to explain post-fire succession. Buscardo et al. (2012) showed that post-fire condition favoured multi-host species, this may be the case of *Laccaria laccata* and *Plicaria endocarpoides* since they were very common throughout the burned plots. The same study proposed that spores from adjacent unburned areas may colonize the burned area and facilitate the growth of late succession stage species (Buscardo et al. 2010). Furthermore, *Amanita* spp. highly contributed to distinguish group 1 from the others. This genus is also composed, but not exclusively, by multi-host and late succession stage species, with no association with post fire conditions, and its presence/absence may be very important to distinguish impacted areas in ecosystems where the arboreal and shrub cover are themselves multi-species. Further analysis based on tree and shrub pre- and after-fire cover and species presence should highlight differences between plots and severity groups.

The most notorious contribution to the dissimilarity between groups is by saprotrophic species from *Hypholoma*, *Pholiota*, *Psathyrella* and *Tephrocybe* genera, which are mainly formed by post-fire species. These species, naming *Hypholoma fasciculare*, *Pholiota brunnescens*, *Pholiota carbonaria*, *Psathyrella pennata*, *Tephrocybe anthracophila*, fruit as a result of fire, some are carbonicolous, fruiting on charcoal or burned organic debris, others fruit on ash or heated soil. These results are in accordance with Martín-Pinto et al. (2006) Claridge et al. (2009), Gassibe et al. (2011) and Franco-Manchón et al. (2019), who found these macrofungal species in early stages of after-fire succession. Furthermore, the fruiting condition of these species may explain the unclear distinction between group 2, 3 and 4 in our analysis, since the fire aftereffects seem to promote homogenisation of conditions between plots of each burned group (2, 3 and 4), and as so promoting the development of post-fire fungi throughout these three groups. Several studies revealed that effects of fire may be visible in macrofungal communities up to 5 years after the fire (Hernández-Rodríguez et al., 2013; Mediavilla et al., 2014; Franco-Manchón, 2019), the point at which post-fire species and super-

pioneer species give place to late stages species, mostly mycorrhizal. These findings are perhaps important to evaluate the progression and succession of MM macrofungal communities, in the sense that an extended fruiting period, further then the period mention above, with no visible shifting in species may indicate a more sever effect of fire in these areas.

The pattern showed throughout all our analysis lead us to the same conclusion, that there is a clear distinction between unburned/slightly burned and burned areas. The fire severity degree (Botella-Martínez & Fernández-Manso, 2017) does not seem to have further capacity to distinguish post-fire fungal communities, one year after fire, better than an unburned and burned plot methodology (Martín-Pinto et al., 2006). Still, one may hypothesize that the fire severity categorization by Botella-Martínez & Fernández-Manso (2017) might prove to be important in post-fire successional studies, as higher fire severity values reveal a deeper effect of fire in the forest structure, a gradual stabilization (according to groups) of the biological communities and environmental condition should be observed. Several studies point to a higher risk of fire, higher fire intensity and frequency, as climate changes became more prominent (Dale et al., 2001; Krawchuk et al., 2009; Moritz et al., 2012), affecting the stabilization of ecosystems after fire. This risk is higher for already prone to fire ecosystems but is more problematic in ecosystems with little to no fire history, like MM (Moritz et al., 2012). Fire frequency is documented has especially problematic to a healthy regeneration of macrofungal communities and pointed to be extremely devastating to the common mycorrhizal network (Buscardo et al., 2010). Nevertheless, fire occurrence in MM. is close to none, with two documented fire separated 30 years apart. This may in fact be benefit, as occasional fires showed to trickle-down effects of fire in opposition to longer periods of no fire that showed too increase the vulnerability of the ecosystems to fire (Krawchuk et al., 2009).

Taking in consideration these assumptions, is of the utmost importance to follow the post-fire ecosystems succession at all levels, biological communities and environmental conditions, and ensure the proper management in order to evaluate and secure a healthy post-fire succession and development of the ecosystems.

Conclusions

Mata da Margaraça Laurisilva ecosystem displayed very similar pattern to several other studies developed in Mediterranean ecosystems. Mycorrhizal communities proved to be very good indicator to distinguish unburned and burned areas, as showed for other types of disturbances, like lumbering, grazing and agriculture. Furthermore, fire severity showed to be capable of characterizing macrofungal richness and diversity from unburned/low severity (group 1) areas to higher severity areas (group 2 to 4). Post-fire species were very important to distinguish the four severity groups and

Amanita genus revealed to be extremely important to separate group 1 from the others. Therefore, it's of utmost importance to keep track of the successional changes the MM, in order to implement the optimal management solutions.

Acknowledgements

We wish to thank Instituto para a Conservação da Natureza e das Florestas for the authorisation to harvest macrofungi specimens in APPSA.

References

- Anderson, M.J. & Willis, T.J. (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology*, 84 (2): 511-525.
- Arnolds, E. (1988) The changing macromycetes flora in the Netherland. *Trans. Br. Mycol. Soc.*, 90: 391-406.
- Barker, J.S., Simard, S.W., Jones, M.D. & Durall, D.M. (2013) Ectomycorrhizal fungal community assembly on regenerating Douglas-fir after wildfire and clearcut harvesting. *Oecologia*, 172: 1179-1189.
- Botella-Martínez, MA. & Fernández-Manso, A. (2017) Estudio de la severidad post-incendio en la Comunidad Valenciana comparando los índices dNBR, RdNBR y RBR a partir de imágenes Landsat 8. *Revista de Teledetección*, 49: 33-47.
- Buscardo, E., Rodríguez-Echevarría, S., Martín, M.P., de Angelis, P., Pereira, J.S. & Freitas, H. (2010) Impact of wildfire return interval on the ectomycorrhizal resistant propagules communities of a Mediterranean open forest. *Fungal Biol.*, 114: 628-636.
- Buscardo, E., Rodríguez-Echeverría, S., Barrico, L., García, M.A., Freitas, H., Martín, M.P., De Angelis, P. & Muller, L.A.H. (2012) Is the potential for the formation of common mycorrhizal networks influenced by fire frequency? *Soil Biol. Biochem.*, 46: 136-144.
- Cairney, J.W.G. & Bastias, B.A. (2007) Influences of the fire on forest soil fungal communities. *Canadian Journal of Forest Research*, 37: 207-215.
- Catalogue of Life. (2019) Species 2000 & ITIS, 25th March 2019, accessed on: 8 March 2019. <http://www.catalogueoflife.org/col>.
- Claridge, A., Trappe, J. & Hansen, K. (2009) Do fungi have a role as soil stabilizers and remediators after forest fire? *For. Ecol. Manage.* 257: 1063-1069.
- Clarke, K.R. & Warwick, R.M. (2001) Change in marine communities. An Approach to Statistical Analysis and Interpretation, Primer-E, Plymouth.
- Clarke, KR & Gorley, RN. (2015) Getting started with PRIMER v7. PRIMER-E: Plymoth.
- Dahlberg, A. (2002) Effects of fire on ectomycorrhizal fungi in fennoscandian forests. *Sylva Fennica*, 36 (1): 69-80.
- Dahlberg, A., Schimmel, J., Taylor, A.F.S. & Johannesson, H. (2001) Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. *Biol. Conserv.*, 100: 151-161.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M. P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J. & Wotton, M.B. (2001) Climate Change and Forest Disturbances. *BioScience*, 51 (9): 723.
- Dix, N.J. & Webster, J. (1995) Phoenicoid Fungi. *Fungal Ecology*, 302-321.
- Evans, J.S., Oakleaf, J., Cushman, S.A. & Theobald, D. (2016) Geomorphometry and Gradient Metrics Toolbox: a toolbox for surface gradient modeling. *Arcgis*, accessed on: 8 September 2019. <http://evansmurphy.wix.com/evansspatial>.
- Franco-Manchón, I., Salo, K., Oria-de-Rueda, J.A., Bonet, J.A. & Martín-Pinto, P. (2019) Are wildfires a threat to fungi in European Pinus Forests? A case study of boreal and Mediterranean forests. *Forests*, 10 (4): 309.
- Gassibe, P., Fraile-Fabero, R., Hernández-Rodríguez, M., Oria-de-Rueda, J.A. & Martín-Pinto, P. (2011) Fungal community succession following wildfire in a Mediterranean vegetation type dominated by

- Pinus pinaster* in Northwest Spain. *For. Ecol. Manage.* 262: 655-662.
- Hawksworth, D.L. (2001) The magnitude of fungal diversity: the 1.5 million species estimate revisited. *Mycol. Res.*, 105: 1422-1432.
- Hernández-Rodríguez, M., Oria-de-Rueda, J.A. & Martín-Pinto, P. (2013) Post-fire fungal succession in a Mediterranean ecosystem dominated by *Cistus ladanifer* L. *Forest Ecology and Management*, 289: 48-57.
- Instituto para a Conservação da Natureza e das Florestas (ICNF). ICNF, accessed on: 8 September 2019. <http://www2.icnf.pt/portal/ap/resource/img/ppsa/map>
- Jenness, J.S. (2011) DEM Surface Tools: an ArcGIS extension for analyzing raster elevation datasets. *Jennessent*, accessed on 8 September 2019. http://www.jennessent.com/arcgis/surface_area.htm
- Jenness J.S., Brost B. & Beier, P. (2013) Land facet corridor designer. Extension for ArcGIS. *Jennessent*, accessed on 8 September 2019. http://www.jennessent.com/arcgis/land_facets.htm
- Johnson, E. (1992) Fire and Vegetation Dynamics. *Cambridge University Press*, Cambridge.
- Keeley, J.E. (2011) Fire in Mediterranean Climate Ecosystems: Ecology, Evolution and Management. *Israel Journal of Ecology & Evolution*, 58: 123-135.
- Kirk, P.M. (2019) *Index Fungorum*, accessed on: 8 March 2019. <http://www.speciesfungorum.org/Index.htm>
- Krawchuk, M.A., Moritz, M.A., Parisien, M.-A., Van Dorn, J. & Hayhoe, K. (2009) Global Pyrogeography: the current and future distribution of wildfire. *PLoS ONE*, 4 (4): 5102.
- Kutorga, E., Adamonytė, G., Iršėnaitė, R., Juzėnas, S., Kasparavičius, J., Markovskaja, S., Motiejūnaitė, J. & Treigienė A. (2012) Wildfire and post-fire management effects on early fungal succession in *Pinus mugo* plantations, located in Curonian Spit (Lithuania). *Geoderma*, 191: 70-79.
- Margalef, R. (1958) Information Theory in Ecology. *General Systems*, 3: 36-71.
- Martín-Pinto, P., Vaquerizo, H., Peñalver, F., Olaizola, J. & Oria-de-Rueda, J.A. (2006) Early effects of a wildfire on the diversity and production of fungal communities in Mediterranean vegetation types dominated by *Cistus ladanifer* and *Pinus pinaster* in Spain. *Forest Ecology and Management*. 225: 296-305.
- Mediavilla O., Oria-de-Rueda J.A. & Martín-Pinto, P. (2014) Changes in sporocarp production and vegetation following wildfire in a mediterranean forest ecosystem dominated by *Pinus nigra* in Northern Spain. *For. Ecol. Manage.*, 331: 85-92.
- Moritz, M.A., Parisien, M.A., Batllori, E., Krawchuk, M. A., Van Dorn, J., Ganz, D. J. & Hayhoe, K. (2012) Climate change and disruptions to global fire activity. *Ecosphere*, 3 (6): 49.
- Natario, B.A.F., Louro, R. & Santos-Silva, C. (2019) Macrofungi of Mata da Margaraça (Portugal), a relic from the Tertiary Age. *Biodiversity Data Journal*, 7: e38177.
- Olsson, J. & Jonsson, B.G. (2010) Restoration fire and wood-inhabiting fungi in a Swedish *Pinus sylvestris* forest. *For. Ecol. Manage.*, 259: 1971-1980.
- Peay, K.G., Garbelotto, M. & Bruns, T.D. (2009) Spore heat resistance plays an important role in disturbance-mediated assemblage shift of ectomycorrhizal fungi colonizing *Pinus muricata* seedlings. *J. Ecol.*, 97:537-547.
- Pielou, E.C. (1969) An Introduction to Mathematical Ecology. *Wiley*, New York.
- Pourreza, M., Hosseini, S.M., Safari Sinangani, A.A., Matinizadeh, M., & Dick, W.A. (2014) Soil microbial activity in response to fire severity in Zagros oak (*Quercus brantii* Lindl.) forests, Iran, after one year. *Geoderma*, 213: 95-102.
- Rashid, A., Ahmed, T., Ayub, M. & Khan, A.G. (1997) Effect of forest fire on number, viability and post-fire re-establishment of arbuscular mycorrhizae. *Mycorrhiza*, 7: 217-220.
- Redecker, D., Szaro, T.M., Bowman, R.J. & Bruns, T.D. (2001) Small genets of *Lactarius xanthoglaucus*, *Russula cremicolor* and *Amanita francheti* in late-stage ectomycorrhizal successions. *Molecular Ecology*, 10: 1025-1034.
- Robinson, R.M., Mellican, A.E. & Smith, R.H. (2008) Epigeous macrofungal succession in the first five years following a wildfire in karri (*Eucalyptus diversicolor*) regrowth forest in Western Australia. *Austral Ecology*, 33: 807-820.
- Shannon, C.E. & Weaver, W. (1949) The Mathematical Theory of Communication. University of Illinois Press, Urbana.
- Sumorok B. (2001) Post-fire macrofungi in the burnt area in the Jelonka reserve (Białowieża region, NE Poland). *Acta Mycologica*, 36 (1): 149-158.
- Vilarino, A. & Arines, J. (1991) Number and viability of vesicular arbuscular fungal propagules in field soil samples after wildfire. *Soil. Biol. Biochem.* 23: 1083-1087.

Supplementary Files

Table S1 - Full set of environmental variables and fire severity.

Variable code	Description	Reference
TPI ^a	Topographic Position Index	Guisan et al. (1999)
VRM ^a	Vectorial Ruggedness Measure	Sappington et al. (2007)
TWI ^b	Topographic Wetness Index	Beven & Kirkby (1979); Schmidt & Persson (2003)
HIP	Hypsometry	-----
HLI	Heat Load Index	McCune & Keon (2002)
ASP	Aspect (Horn's method) (0-NW; 5-N)	Horn (1981)
CTI	Compound Topographic Index	Moore et al. (1993); Gessler et al. (1995)
SEV	Fire Severity	Botella-Martínez & Fernández-Manso (2017)

^a Computed within a specified window (5 cells)

^b Computed using a smoothing threshold (50). Higher values blur the ridges and should be chosen for low relief (1 means display of all ridges)

Table S2 - Principal Component Analysis eigenvalues. Cum. - Cumulative

PC	Eigenvalues	% Variation	Cum. % Variation
1	3.5	43.7	43.7
2	1.91	23.9	67.7
3	1	12.5	80.2
4	0.519	6.5	86.7
5	0.441	5.5	92.2

Table S3 - Principal Component Analysis eigenvectors.

Variable	PC1	PC2	PC3	PC4	PC5
TPI	-0.444	0.032	-0.044	-0.460	0.272
VRM	0.447	0.087	-0.018	0.413	0.594
TWI	0.483	-0.183	0.064	-0.113	0.150
HIP	-0.282	0.509	-0.093	-0.079	0.581
HLI	-0.421	-0.281	0.228	0.418	-0.036
ASP	-0.288	-0.500	0.225	0.288	0.371
CTI	0.123	0.151	0.924	-0.281	0.040
SEV	-0.124	0.590	0.168	0.512	-0.269

Table S4 - Permutational MANOVA pair - wise test.

Pair groups	t	P(perm.)	Unique perms
1, 2	2,0518	0,001	999
1, 3	2,4587	0,001	999
1, 4	2,1661	0,001	998
2, 3	1,2154	0,109	999
2, 4	0,79329	0,833	998
3, 4	0,80017	0,856	994

Table S5 - Canonical analysis of principal coordinates correlations. Corr. – Correlation; Sq. - Square

Eigenvalue	Correlation	Corr. Sq.
1	0.8785	0.7718
2	0.3749	0.1406
3	0.1511	00.0228

Table S6 - Canonical analysis of principal coordinates cross validation.

Origin group	1	2	3	4	Total	% correct
1	16	2	2	0	20	80
2	1	9	3	2	15	60
3	0	4	4	3	11	36
4	0	3	6	0	9	0

Table S7 - SIMPER dissimilarity analysis, the five species that most contribute to dissimilarity between group 1 and 2. Abund. – Abundance; Av. – Average; Contrib. – Contribution; Diss. – Dissimilarity;

Genus	Group 1		Group 2	
	Av. Abund.	Av. Abund.	Av. Diss.	Contrib. %
42	0.94	2.30	9.94	11.10
32	0.88	1.59	8.22	9.18
34	1.96	0.81	8.17	9.12
55	0.46	0.90	4.97	5.56
2	0.90	00.7	4.44	4.96

Table S8 - SIMPER dissimilarity analysis, the five species that most contribute to dissimilarity between group 1 and 3. Abund. – Abundance; Av. – Average; Contrib. – Contribution; Diss. – Dissimilarity;

	Group 1	Group 3		
Genus	Av. Abund.	Av. Abund.	Av. Diss.	Contrib. %
42	0.94	3.49	13.63	15.37
55	0.49	2.19	8.26	9.31
34	1.96	0.50	7.47	8.42
2	0.90	0.09	4.21	4.74
46	0.28	0.73	3.56	4.01

Table S9 - SIMPER dissimilarity analysis, the five species that most contribute to dissimilarity between group 1 and 4. Abund. – Abundance; Av. – Average; Contrib. – Contribution; Diss. – Dissimilarity;

	Group 1	Group 4		
Genus	Av. Abund.	Av. Abund.	Av. Diss.	Contrib. %
42	0.94	3.19	14.61	16.26
34	1.96	0.11	7.86	8.75
32	0.88	0.89	6.42	7.14
55	0.49	1.11	5.02	5.59
2	0.90	0.00	4.78	5.32

Table S10 - SIMPER dissimilarity analysis, the five species that most contribute to dissimilarity between group 2 and 3. Abund. – Abundance; Av. – Average; Contrib. – Contribution; Diss. – Dissimilarity;

	Group 2	Group 3		
Genus	Av. Abund.	Av. Abund.	Av. Diss.	Contrib. %
42	2.30	3.49	12.11	16.10
55	0.90	2.19	9.01	11.98
32	1.59	0.13	.43	9.89
46	0.89	0.73	4.83	6.42
43	0.57	0.76	4.61	6.13

Table S11 - SIMPER dissimilarity analysis, the five species that most contribute to dissimilarity between group 2 and 4. Abund. – Abundance; Av. – Average; Contrib. – Contribution; Diss. – Dissimilarity;

	Group 2	Group 4		
Genus	Av. Abund.	Av. Abund.	Av. Diss.	Contrib. %
42	2.30	3.19	13.49	18.00
32	1.59	0.89	10.14	13.53
55	0.90	1.11	7.00	9.34
46	0.89	0.84	5.85	7.81
43	0.57	0.19	3.56	4.74

Table S12 - SIMPER dissimilarity analysis, the five species that most contribute to dissimilarity between group 3 and 4. Abund. – Abundance; Av. – Average; Contrib. – Contribution; Diss. – Dissimilarity;

Genus	Group 3	Group 4	Av. Diss.	Contrib. %
	Av. Abund.	Av. Abund.		
42	3.49	3.19	11.13	16.75
55	2.19	1.11	9.28	13.96
46	0.73	0.84	5.79	8.71
32	0.13	0.89	5.10	7.67
43	0.76	0.19	3.52	5.30

Table S13 - Distance based linear models marginal test.

Variable	Pseudo – F	p - value
TPI	0,96366	0,4737
VRM	1,1181	0,3136
TWI	2,4869	0,0042
HIP	4,7294	0,0001
HLI	1,2117	0,2377
ASP	2,5329	0,0026
CTI	0,47416	0,9627
SEV	6,8963	0,0001

Table S14 - Distance based redundancy analysis multiple partial correlation.

Variable	dbRDA 1	dbRDA 2
TPI	-0.110	-0.210
VRM	-0.115	0.360
TWI	-0.208	0.591
HIP	0.545	0.162
HLI	-0.020	-0.556
ASP	-0.342	-0.357
CTI	0.075	-0.058
SEV	0.715	-0.107

Table S15 - Maximum, minimum and average values of the environmental variables.

Variable	Maximum	Minimum	Average
TPI	7,08643	-17,3827	-3,29629
VRM	0,029318	0,000645	0,007246
TWI	6,31211	4,56167	5,181463
HIP	771	469	623,9091
HLI	6754	3153	5546,891
ASP	6,256182	0	3,020314
CTI	8,93116	4,05113	6,665265
SEV	1,149226	0,02542	0,452289

Considerações finais

A Mata Nacional da Margaraça representa um remanescente da floresta relíquia da Laurisilva, conhecida por albergar uma vasta diversidade florística e faunística. Actualmente é também reconhecido o seu valor micológico singular, com setenta e quatro novas espécies descritas para Portugal e cento e dezasseis novas espécies para a Beira Litoral. Foi notável o forte impacto que o fogo de 2017 teve nas comunidades macrofúngicas desta área protegida. Com efeito, neste estudo foi possível distinguir claramente as áreas não queimadas das áreas queimadas com base na riqueza e abundância de espécies macrofúngicas. Nomeadamente, as espécies sapróbias *Pholiota brunnescens*, *Psathyrella pennata* e *Tephrocybe anthracophila*, e as espécies micorrízicas do género *Amanita*, mostraram ser boas indicadoras do efeito do fogo. A proporção micorrízicos/sapróbios foi o índice mais adequado para discriminar as áreas sujeitas ao incêndio, com diferenças significativas entre áreas ardidadas e não ardidadas.

A análise da inventariação micológica, pré e pós-fogo, revelou a ausência de frutificações de algumas *Boletaceae* e *Cortinarius* nas áreas amostradas em 2018/2019. Este facto poderá indicar que o impacto do fogo se estendeu para além das áreas directamente afectadas, provocando alterações microambientais desfavoráveis à frutificação dos *taxa* acima referidos. Apenas a prossecução dos estudos micológicos na Mata da Margaraça poderá esclarecer esta questão e clarificar o efeito a longo prazo do incêndio florestal nas comunidades de macrofungos.

Referências

- Archenzo. (2012) *Amanita phalloides*. *Wikimedia*, accessed on: 8 February 2019. https://commons.wikimedia.org/wiki/File:2005-09_Amanita_phalloides_crop.jpg
- Arocena, J.M., Gottlein, A. & Raidl, S. (2004) Spatial changes of soil solution and mineral composition in the rhizosphere of Norway-spruce seedlings colonized by *Piloderma croceum*. *Journal of Plant Nutrition and Soil Science*, 4: 479-486.
- Baar, J., Horton, T.R., Kretzer, A.M. & Bruns, T.D. (1999) Mycorrhizal colonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. *New Phytologist*, 143: 409-418.
- Barker, J.S., Simard, S.W., Jones, M.D. & Durall, D.M. (2013) Ectomycorrhizal fungal community assembly on regenerating Douglas-fir after wildfire and clearcut harvesting. *Oecologia*, 172: 1179-1189.
- Bidartondo, M.I. (2005) The evolutionary ecology of mycoheterotrophy. *New Phytologist*, 167: 335-352.
- Blanchette, R.A. (1991). Delignification by Wood-Decay Fungi. *Annual Review of Phytopathology*, 29 (1): 381-403.
- Bruns, T.D., Bidartondo, M.I. & Taylor, D.L. (2002) Host specificity in ectomycorrhizal communities: what do the exceptions tell us? *Integrative and Comparative Biology*, 42: 352-359.
- Caesar-TonThat, T.C. (2002) Soil binding properties of mucilage produced by a basidiomycete fungus in a model system. *Mycological Research*, 106 (8): 930.
- Claridge, A.W., Trappe, J.M. & Hansen, K. (2009) Do fungi have a role as soil stabilizer and remediators after forest fire. *Forest Ecology and Management*. 257: 1063-1069.
- Cockle, K.L., Martin, K. & Robledo, G. (2012) Linking fungi, trees, and hole-using birds in a Neotropical tree-cavity network: pathways of cavity production and implications for conservation. *Forest Ecology and Management*, 264: 210-219.
- Colpaert, J.V. & Laere, A. (1996) A comparison of the extracellular enzyme activities of two ectomycorrhizal and a leaf-saprotrophic basidiomycete colonizing beech leaf litter. *New Phytologist*, 134 (1): 133-141.
- Courty, P.E., Breda, N. & Garbaye, J. (2007) Relation between oak tree phenology and the secretion of organic matter degrading enzymes by *Lactarius quietus* ectomycorrhizas before and during bud break. *Soil Biology & Biochemistry*, 39: 1655-1663.
- Courty, PE., Buée, M., Diedhiou, A.G., Frey-Klett, P., Le Tacon, F., Rineau, F., Turpault, M.P., Uroz, S. & Garbaye, J. (2010) The role of ectomycorrhizal communities in forest ecosystem processes: New perspectives and emerging concepts. *Soil Biology & Biochemistry*, 42: 679-698.
- Cullings, K., Ishkhanova, G. & Henson, J. (2008) Defoliation effects on enzyme activities of the ectomycorrhizal fungus *Suillus granulatus* in a *Pinus contorta* (lodgepole pine) stand in Yellowstone National Park. *Oecologia*, 158(1): 77-83.
- Dahlberg, A., Shimmel, J., Taylor, A.F.S. & Johannesson, H. (2001) Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. *Biological Conservation*, 100: 151-161.
- Dahlberg, A. (2002) Effects of fire on ectomycorrhizal fungi in Fennoscandian boreal forest. *Sylva Fennica*, 36 (1): 69-80.
- Baird, D. (2007) *Tricholoma flavovirens* - geograph.org.uk - 596869.jpg. *Wikimedia*, accessed on: 8 February 2019. https://commons.wikimedia.org/wiki/File:Tricholoma_flavovirens_-_geograph.org.uk_-_596869.jpg
- De Reu, J., Bourgeois, J., Bats, M., Zwertvaegher, A., Gelorini, V., De Smedt, P., Chu, W., Antrop, M., De Maeyer, P., Finke, P. Van Meirvenne, M., Verniers, J., & Crombé, P. (2013) Application of the topographic position index to heterogeneous landscapes. *Geomorphology*, 186:39-49.
- Fellbaum, C.R., Mensah, J.A., Cloos, A.J., Strahan, G.E., Pfeffer, P.E., Kiers, E.T. & Bücking, H. (2014) Fungal nutrient allocation in common mycorrhizal networks is regulated by the carbon source strength of individual host plants. *New Phytologist*, 203(2), 646-656.

- Ferreira, A.D., Coelho, C., Silva, J.S. & Esteves, T. (2010) Efeito do fogo no solo e no regime hidrológico In Moreira, F., Catry, F.X., Silva, J.S., Rego, F. (eds), *Ecologia do fogo e gestão de áreas aridas*. ISA Press. Lisboa.: 21-49.
- Fritz, O. & Heilmann-Clausen, J. (2010) Rot holes create key microhabitats for epiphytic lichens and bryophytes on beech (*Fagus sylvatica*). *Biological Conservation* 143:1008-1016.
- Gassibe, P., Fraile-Fabero, R., Hernández-Rodríguez, M., Oria-de-Rueda, J.A. & Martín-Pinto, P. (2011) Fungal community succession following wildfire in a Mediterranean vegetation type dominated by *Pinus pinaster* in Northwest Spain. *For. Ecol. Manage.* 262: 655-662.
- Gebauer, G. & Meyer, M. (2003) ^{15}N and ^{13}C natural abundance of autotrophic and mycohetero-trophic orchids provides insight into nitrogen and carbon gain from fungal association. *New Phytologist*, 160, 209-223.
- Gessler, P.E., Moore, I.D., McKenzie, N.J. & Ryan, P.J. (1995) Soil-landscape modelling and spatial prediction of soil attributes. *International Journal of GIS*, 9(4):421-432.
- Greene, D.F., Hesketh, M. & Pouden, E. (2010) Emergence of morel (*Morchella*) and pixie cup (*Geopyxis carbonaria*) ascocarps in response to the intensity of forest floor combustion during a wildfire. *Mycologia*, 102(4): 766-773.
- Harnisch, J. (2009) *Morchella elata* group 38336.jpg. Wikimedia, accessed on: 8 February 2019. https://commons.wikimedia.org/wiki/File:Morchella_elata_group_38336.jpg
- Hart, S.C., DeLuca, T.H., Newman, G.S., MacKenzie, M.D. & Boyle, S.I. (2005) Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. *Forest Ecology and Management*, 220: 166-184.
- He, X.H., Critchley, C. & Bledsoe, C. (2003). Nitrogen transfer within and between plants through common mycorrhizal networks (CMNs). *Critical Reviews in Plant Sciences*, 22 (6): 531-567.
- Hobbie, E.A., Macko, S.A. & Shugart, H.H. (1999) Insights into nitrogen and carbon dynamics of ectomycorrhizal and saprotrophic fungi from isotopic evidence. *Oecologia*, 118 (3): 353.
- Horn, B.K.P. (1981) Hill-shading and the reflectance map. *Proceedings of the IEEE*, 69: 14-47.
- Jentschke, G., Brandes, B., Kuhn, A.J., Schröder, W.H. & Godbold, D.L. (2001) Interdependence of phosphorus, nitrogen, potassium and magnesium translocation by the ectomycorrhizal fungus *Paxillus involutus*. *New Phytologist*, 149: 327-337.
- Johansen, A. & Jensen, E.S. (1996) Transfer of N and P from intact or decomposing roots of pea to barley interconnected by an arbuscular mycorrhizal fungus. *Soil Biology and Biochemistry*, 28: 73-81.
- Jonsson, L., Dahlberg, A., Nilsson, M.C., Zackrisson, O. & Karen, O. (1999) Ectomycorrhizal fungal communities in late-successional Swedish boreal forests, and their composition following wildfire. *Molecular Ecology*, 8: 205-215.
- Kennedy, N. & Egger, K.N. (2010) Impact of wildfire intensity and logging on fungal and nitrogen-cycling bacterial communities in British Columbia forest soils. *Forest Ecology and Management*, 260: 787-794.
- Kipfer, T., Egli, S., Ghazoul, J., Moser, B. & Wohlgemuth, T. (2010) Susceptibility of ectomycorrhizal fungi to soil heating. *Fungal Biology*, 114(5-6), 467-472.
- Klironomos, J.N. & Moutoglis, P. (1999) Colonization of nonmycorrhizal plants by mycorrhizal neighbours as influenced by the collembolan, *Folsomia candida*. *Biology and Fertility of Soils*, 29: 277-281.
- Larson, A.J., Cansler, C.A., Cowdery, S.G., Hiebert, S., Furniss, T.J., Swanson, M.E. & Lutz, J.A. (2016) Post-fire morel (*Morchella*) mushroom abundance, spatial structure, and harvest sustainability. *Forest Ecology and Management*, 377: 16–25.
- Leake, J.R. (2004) Myco-heterotroph/epiparasitic plant interactions with ectomycorrhizal and arbuscular mycorrhizal fungi. *Current Opinion in Plant Biology*, 7(4): 422-428.
- Leila, A., Pereira, M., Valadares, R., Filippi, M., Tadeu Sibov, S., Sousa, K., Pereira Luzini, A. & Campos Borba Carvalho, J. (2013) Fungos micorrízicos: conservação de orquídeas e biocontrole de fitopatógenos.

- Luo, H., Mo, M., Huang, X., Li, X., Zhang, K. (2004) *Coprinus comatus*: A basidiomycete fungus forms novel spiny structures and infects nematode. *Mycologia*, 96(6): 1218-1224.
- McCune, B & Keon, D. (2002) Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science*, 13: 603-606.
- McKendrick, S.L., Leake, J.R. & Read, D.J. (2000) Symbiotic germination and development of myco-heterotrophic plants in nature: transfer of carbon from ectomycorrhizal *Salix repens* and *Betula pendula* to the orchid *Corallorhiza trifida* through shared hyphal connections. *New Phytologist*, 145: 539-548.
- Monleon, V.J. & Cromack, K. (1996) Long-term effects of prescribed underburning on litter decomposition and nutrient release in ponderosa pine stands in central Oregon. *Forest Ecology and Management*, 81: 143-152.
- Moore, I.D., Gessler, P.E., Nielsen, G.A., & Petersen, G.A. (1993) Terrain attributes: estimation methods and scale effects. In *Modelling Change in Environmental Systems*, edited by A.J. Jakeman, M.B. Beck & M. McAleer (London: Wiley), 189 - 214.
- Moreno, G., Manjón, J. L. (2010) Historia de la micología. In Ediciones Omega (eds), *Guía de hongos de la Península Ibérica*. Ediciones Omega.
- Nearya, D.G, Klopatek, C.C., DeBano, L.F. & Ffolliott, P.F. (1999) Fire effect on belowground sustainability: a review and synthesis. *Forest Ecology and Management*, 122 (1-2): 51-71.
- Newman, E.I. (1988) Mycorrhizal links between plants: their functioning and ecological significance. *Advances in Ecological Research*, 18: 243-270.
- Nikitsky, N.B. & Schigel, D.S. (2004) Beetles in polypores of the Moscow region: checklist and ecological notes. *Entomologica Fennica*.
- Nilsson, L.O., Giesler, R., Bååth, E. & Wallander, H. (2005). Growth and biomass of mycorrhizal mycelia in coniferous forests along short natural nutrient gradients. *New Phytologist*, 165: 613-622.
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A. & Hayes, D. (2011) A large and persistent carbon sink in the world's forests. *Science*, 333(6045): 988-993.
- Pato, J.R. (2008) 2008-12-14 Cordyceps militaris 3107128906.jpg. *Wikimedia*, accessed on: 8 February 2019. https://commons.wikimedia.org/wiki/File:2008-12-14_Cordyceps_militaris_3107128906.jpg.
- Peay, K.G., Garbelotto, M., Bruns, T.D. (2009) Spore heat resistance plays an important role in disturbance-mediated assemblage shift of ectomycorrhizal fungi colonizing *Pinus muricata* seedlings. *Journal of Ecology*, 97(3): 537-547.
- Power R, Salazar-García D, Straus L, Morales M & Henry A. (2015) Microremains from El Mirón Cave human dental calculus suggest a mixed plant-animal subsistence economy during the Magdalenian in Northern Iberia. *Journal of Archaeological Science*, 60: 39-46.
- Raso, G. (2018) "Thrushs and mushrooms" - wall painting from House of the Deer at Herculaneum, buried by Vesuvius' eruption on 79 AD - Naples, Archaeological Museum. *Flickr*, accessed on: 8 of February 2019. <https://www.flickr.com/photos/70125105@N06/39653769114>
- Remm, J., Lohmus, A. (2011) Tree cavities in forests – The broad distribution pattern of a keystone structure for biodiversity. *Forest Ecology and Management*, 262: 579-585.
- Rincón, A., Pueyo, J.J. (2010) Effect of fire severity and site slope on diversity and structure of the ectomycorrhizal fungal community associated with post-fire regenerated *Pinus pinaster* Ait. Seedlings. *Forest Ecology and Management*, 260: 361-369.
- Ryan, K. & Noste, N. (1985) Evaluating prescribed fires. In Lotan, J.E. et al. (tech. coord.) *Proceedings-Symposium and Workshop on Wilderness Fire*. USDA Forest Service Intermountain Forest and Range Experiment Station, General Technical Report INT, 182: 230-238;
- Sappington, J.M., Longshore, K.M. & Thompson, D.B. (2007) Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management*, 71: 1419 - 1426.
- Scheibner, HM. (2012) Schmetterlingstramete (Trametes versicolor) - hms(1).jpg. *Wikimedia*, accessed on: 8 February 2019.

[https://commons.wikimedia.org/wiki/File:Schmetterlingstramete_\(Trametes_versicolor\)_-_hms\(1\).jpg](https://commons.wikimedia.org/wiki/File:Schmetterlingstramete_(Trametes_versicolor)_-_hms(1).jpg)

- Schmidt, F. & Persson, A. (2003) Comparison of DEM data capture and topographic wetness indices. *Precision Agriculture*, 4: 179-192.
- Selosse, M.A., Richard, F., He, X. & Simard, S.W. (2006) Mycorrhizal networks: des liaisons dangereuses? *Trends in Ecology and Evolution*, 21 (11): 621-628.
- Simard, S.W., Perry, D.A., Jones, M.D., Myrold, D.D., Durall, D.M. & Molina, R. (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* (Lond.), 388: 579-582.
- Simard, S.W. & Durall, D.M. (2004) Mycorrhizal networks: a review of their extent, function and importance. *Canadian Journal of Botany*, 82 (8): 1140-1165.
- Smith, J.E., McKay, D., Brenner, G., McIver, J. & Spatafora, J.W. (2005) Early impacts of forest restoration treatments on the ectomycorrhizal fungal community and fine root biomass in a mixed conifer forest. *Journal of Applied Ecology*, 42: 526-535.
- Sørensen, R. & Seibert, J. (2007) Effects of DEM resolution on the calculation of topographical indices: TWI and its components. *Journal of Hydrology*, 347 (1-2): 79-89
- Stenlid, J., Penttilä, R. & Dahlberg, A. (2008) Wood-decay basidiomycetes in boreal forests: distribution and community development In Boddy, L., Frankland, J.C., van West, P. (eds), *Ecology of Saprotrophic Basidiomycetes*. British Mycological Society Symposia Series, 28. London: Elsevier.
- Tibbett, M., Sanders, F.E. & Cairney, J.W.G. (1998) The effect of temperature and inorganic phosphorus supply on growth and acid phosphatase production in arctic and temperate strains of ectomycorrhizal *Hebeloma* spp. in axenic culture. *Mycological Research*, 2: 129-135.
- Tuffen, F., Eason, W.R. & Scullion, J. (2002) The effect of earthworms and arbuscular mycorrhizal fungi on growth of and ³²P transfer between *Allium porrum* plants. *Soil Biology & Biochemistry*, 34: 1027-1036.
- van Schöll, L., Smits, M.M. & Hoffland, E. (2006) Ectomycorrhizal weathering of the soil minerals muscovite and hornblende. *New Phytologist*, 171: 805-814.
- Wallander, H., Nilsson, L.O., Hagerberg, D. & Baath, E. (2001) Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. *New Phytologist*, 151: 753-760.
- Wallander, H., Johansson, L. & Pallon, J. (2002). PIXE analysis to estimate the elemental composition of ectomycorrhizal rhizomorphs grown in contact with different minerals in forest soil. *FEMS Microbiology Ecology*, 39: 147-156.
- Wallander, H., Goransson, H. & Rosengren, U. (2004). Production, standing biomass and natural abundance of N and C in ectomycorrhizal mycelia collected at different soil depths in two forest types. *Oecologia*, 139: 89-97.
- Waring, R.H. & Running, S.W. (2007) Introduction in Forest Ecosystems: Analysis at multiple scales, 7nd ed. Academic Press, San Diego, California.
- Wilson, G.W.T., Harnett, D.C. & Rice, C.W. (2006) Mycorrhizal-mediated phosphorus transfer between tallgrass prairie plants *Sorghastrum nutans* and *Artemisia ludoviciana*. *Functional Ecology*, 20 (3): 427-435.