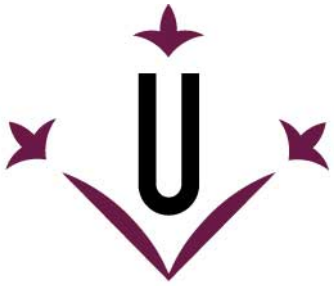
Effects of forest management, tree growth and climate on fungal communities

Eduardo Collado Coloma



Universitat de Lleida

PHD THESIS

Effects of forest management, tree growth and climate on fungal communities

Eduardo Collado Coloma

To obtain the degree of Doctor at the University of Lleida
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Supervised by
José Antonio Bonet Lledós
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Tutored by
José Antonio Bonet Lledós

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TESI DOCTORAL

Effects of forest management, tree growth and climate on fungal communities

Eduardo Collado Coloma

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“It is not the strongest of the species that survives, nor the most intelligent; it is the one most adaptable to change.”
- Charles Darwin

A mi padre

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RELATED WORKS AND MANUSCRIPTS

The following are the manuscript derived from this thesis:

i. Collado, E., Camarero, J. J., Martínez de Aragón, J., Pemán, J., Bonet, J. A., de-Miguel, S. 2018. Linking fungal dynamics, tree growth and forest management in a Mediterranean pine ecosystem. *Forest Ecology and Management* 422: 223–232.

ii. Collado, E., Bonet, J. A., Camarero, J. J., Egli, S., Peter, M., Salo, K., Martínez-Peña, F., Ohenoja, E., Martín-Pinto, P., Primicia, I., Büntgen, U., Kurttila, M., Oria-de-Rueda, J.A., Martínez de Aragón, J., Miina, J., de-Miguel, S. 2019. Mushroom productivity trends in relation to tree growth and climate across different European forest biomes. *Science of The Total Environment* 689: 602-615.

iii. Collado, E., Castaño, C., Bonet, J. A., Hagenbo, A., Martínez de Aragón, J., de-Miguel, S. 2020. Divergent above- and below-ground responses of fungal functional groups to forest thinning. *Soil Biology and Biochemistry*, 150, 108010. doi: https://doi.org/10.1016/j.soilbio.2020.108010

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Congress proceedings (oral presentations):

i. *Final Meeting, MC and WG meetings. COST Action FP1203: European non-wood forest products network (NWFPs), Slovenia.* Modeling on the height distribution of young cork oak plantation in Portugal. 09-03-2017.

ii. World Conference on Natural Resource Modeling, Spain. Modeling the relationship between forest management, tree growth and fungal dynamics. 09-06-2017.

iii. XXIXth International Biometric Conference, Spain. Modeling the linkages between mushroom yield and functional diversity, tree growth and climate across Europe. 13-07-2018.

iv. Regional Meeting on the Prades Forests, Spain. Vinculant dinàmica de fongs, creixement d'arbres i gestió forestal als boscos de pi pinastre del PNIN.16-11-2018.

v. National Meeting on "Forest modelling in the age of information", Spain. Análisis del efecto de distintas intensidades de clara sobre la biomasa de los hongos. 07-11-2019.

vi. National Meeting on "Forest modelling in the age of information", Spain. Modelización de las relaciones entre la productividad de las setas, el crecimiento de los árboles y el clima en diferentes biomas forestales europeos. 07-11-2019.

vii. 1st Research School on Forest Ecology and Management, Spain. Effect of thinning, tree growth and meteorological conditions on forest fungal biomass. 18-02-2020.

RESUM EN CATALÀ

Els fongs són importants tant per al benestar humà com per al funcionament de l'ecosistema forestal, gràcies als serveis ecosistèmics proporcionats per ells: aprovisionament (p.e., bolets comestibles), regulació (p.e., fixació de carboni), suport (p.e., formació de sòls) i cultural (p.e., recreació). La comprensió de les connexions entre les dinàmiques de les diferents estructures fúngiques (esporocarps i miceli), així com les dinàmiques fúngiques que es donen sota pertorbacions antropogèniques, son necessàries per avançar en el coneixement de les interaccions fong-sòl-planta en ecosistemes forestals. El principal objectiu d'aquesta tesi és entendre, descriure i quantificar els efectes de les aclarides forestals, del creixement dels arbres i del clima en la biomassa fúngica i en la productivitat i composició dels fongs.

La tesi doctoral va ser principalment desenvolupada en un conjunt de 28 parcel·les forestals permanents situades en el Paratge Natural d'Interès Nacional de Poblet (Catalunya, Espanya), les quals van ser aclarides l'any 2009 amb diferents intensitats de aclarida. El dispositiu experimental es va instal·lar en plantacions de *Pinus pinaster* Ait. amb edats entre 50 i 60 anys i amb diferents característiques de massa i estació (p.e., àrea basimètrica, pendent). Els bolets en aquestes parcel·les s'han anat recollint cada setmana des de setembre fins al desembre entre els anys 2008 i 2019. Tanmateix, al setembre de 2014 es van mostrejar testimonis de fusta en 10-15 arbres dominants de cada parcel·la per a descriure les relacions entre la producció de bolets i la composició de la vegetació. Similar metodologia es va seguir en diferents regions d'Europa i ecosistemes forestals per estudiar les relacions arbres-fong sota contrastades condicions climàtiques i de vegetació. Addicionalment, es van obtenir mostres de sòls (vuit testimonis de sòl per parcel·la) en les mateixes parcel·les de *P. Pinastre* durant 5 anys. Aquestes mostres es varen analitzar utilitzant vàries tècniques moleculars com la seqüenciació massiva d'ADN (PacBio RS II, Illumina MiSeq) i tècniques bioquímiques com l'extracció d'ergosterol. Les dades de les comunitats i biomassa de fongs obtingudes utilitzant aquestes tècniques juntament amb les dades d'esporocarps varen ser utilitzades per estudiar les dinàmiques de les comunitats fúngiques, tant en miceli com a esporocarps, sota els efectes de diferents intensitats d'aclarida.

Els resultats van mostrar que la fluctuació en la densitat de fusta tardana era el millor predictor de les produccions de bolets ectomicorrízics (ECM) en comparació amb l'amplada de la fusta primerenca i tardana (EW i LW, respectivament). L'anàlisi també va revelar que la precipitació durant el final de l'estiu i el principi de tardor, així com les aclarides forestals, desenvolupaven papers mediadors de la relació entre el creixement dels arbres i la producció de bolets. A diferència de les regions temperades i boreals, aquesta interacció entre els fongs ECM i el creixement dels arbres era més significativa en les regions mediterrànies, ja que és on es varen donar correlacions positives entre el creixement tardà i la producció de fongs ECM. Tanmateix, es va observar que els efectes de les aclarides en la biomassa de fongs total i en la biomassa de fongs ECM van tenir un efecte prolongat en les parcel·les amb clima mediterrani, tant al llarg dels anys com al llarg dels mesos en un mateix any. No obstant això, aquests efectes no es van observar en els fongs sapròfits. Tanmateix, la biomassa micel·liar tant de tots els fongs com dels fongs ECM estava correlacionada negativament amb la quantitat de bolets de tots els fongs i del ECM, respectivament. Les diferències entre la biomassa micel·liar i la d'esporocarps

incrementaven amb majors intensitats d'aclarida. Finalment, la composició de la comunitat d'esporocarps, a diferència de la diversitat d'esporocarps (p.e., riquesa, uniformitat), va mostrar canvis a curt termini (< 2 anys) en parcel·les aclarides amb diferents intensitats, en comparació amb les no aclarides. Els inesperats canvis composicionals degut a intensitat d'aclarida dèbils van ser exclusivament deguts a unes espècies d'interès comercial (*Lactarius* group *deliciosus*). Els factors climàtics, sobretot la temperatura mitjana dels mesos de setembre i octubre, influenciaven la resposta de la composicions de fongs a les aclarides.

Basant-me en aquests resultats, s'ha conclòs que: (i) només sota condicions limitades d'aigua, tant el creixement de l'arbre (sobretot el creixement de la fusta tardana) com la producció de bolets (sobretot ECM) són més sensibles a la precipitació, resultant en una major sincronia entre ambdós processos; (ii) els models es poden utilitzar per a reconstruir la producció de bolets a través de períodes històrics basant-nos en informació dendrocronològica, però també per a predir futures produccions de bolets segons les projeccions de creixements dels arbres sota diferents condicions climàtiques; (iii) les aclarides forestals poden causar canvis a curt termini en el moviment dels recursos des del miceli als esporocarps, prioritzant reproducció enfront de la colonització micel·liar; i (iv) les aclarides forestals amb l'eliminació acurada dels arbres (p.e., intensitat d'aclarida baixes) manté la diversitat de esporocarps, provocant només canvis de successió a curt termini en la composició dels fongs.

RESUMEN EN CASTELLANO

Los hongos son importantes tanto para el bienestar humano como para el funcionamiento del ecosistema forestal, gracias a los servicios ecosistémicos proporcionados por ellos: aprovisionamiento (p.ej., setas comestibles), regulación (p.ej., secuestro de carbono), soporte (p.ej., formación de suelo) y cultural (p.ej., uso recreacional). Para entender las interacciones existentes en el ecosistema forestal entre los hongos, el suelo y las plantas, es necesario investigar los vínculos entre las dinámicas de las distintas estructuras fúngicas (esporocarpos y micelio) así como las dinámicas de las masas forestales gestionadas. El objetivo principal de la tesis es entender, describir y cuantificar los efectos de las claras forestales, del crecimiento de los árboles y del clima sobre la biomasa fúngica y sobre la productividad y composición de los hongos.

La tesis doctoral se ha hecho principalmente en 28 parcelas forestales permanentes localizadas en el Paraje Natural de Interés Nacional de Poblet (Cataluña, España), las cuales fueron cortadas en el año 2009 con distintas intensidades de corta. El dispositivo experimental se instaló en plantaciones de *Pinus pinaster* Ait. con edades entre 50 y 60 años, abarcando diferentes características de estación y masa (p.ej., pendiente, área basimétrica). Desde el 2008 al 2019, se recolectó semanalmente de septiembre a diciembre todos los esporocarpos de cada parcela, y extrajimos en diciembre del 2014 testigos de madera proveniente de 10-15 árboles dominantes de cada parcela, con el fin de describir las relaciones entre la producción de setas y el crecimiento forestal. Esta metodología se realizó también en diferentes regiones de Europa y ecosistemas forestales para indagar en dichas relaciones árbol-hongo bajo otras condiciones climáticas y composiciones forestales. Además, se recogió muestras de suelo (ocho testigos de suelo por parcela) en las masas de *P. pinaster* durante 5 años. Estas muestras de suelo fueron analizadas mediante técnicas moleculares como la secuenciación de ADN de alto rendimiento (PacBio RS II, Illumina MiSeq), y técnicas bioquímicas como la extracción de ergosterol. Los datos de las comunidades y biomasa de hongos obtenidos mediante dichas técnicas se emplearon junto con los datos de esporocarpos para investigar las dinámicas de las comunidades fúngicas, tanto en micelio como en esporocarpos, bajo los efectos de distintas intensidades de clara.

Los resultados mostraron que las fluctuaciones de densidad intra-anual de la madera tardía fue el mejor predictor de la producción de setas ectomicorrícicas (ECM) en comparación con la anchura de la madera temprana y tardía (EW y LW, respectivamente). Los análisis también revelaron que la precipitación de finales de verano y principios de otoño, así como los efectos de la clara mediaron en la relación entre el crecimiento del árbol y la producción de setas ECM. A diferencia de las regiones templadas y boreales, esta interacción hongo-árbol fue más significativa en regiones mediterráneas, dando lugar a correlaciones positivas entre el crecimiento de LW y la biomasa de setas micorrícicas. También se observó en las parcelas mediterráneas que la clara produjo un efecto negativo, inter- e intra-anualmente, en la biomasa miceliar total y ECM, pero no en la biomasa miceliar de saprobios. Estas biomasas miceliares de los hongos totales y ECM fueron negativamente correlacionadas con las producciones de setas totales y ECM, respectivamente. Además, se incrementó las diferencias entre la biomasa miceliar y la de esporocarpos con intensidades más altas de clara. Finalmente, la composición de la comunidad de esporocarpos, a diferencia de la diversidad de esporocarpos (p.ej., riqueza, uniformidad), mostró cambios a corto plazo (< 2 años) en parcelas cortadas con diferentes intensidades de clara, en comparación con las no

gestionadas. Los inesperados cambios composicionales tras las claras de intensidad baja se debieron exclusivamente a unas especies de interés comercial (*Lactarius* group *deliciosus*). Los factores climáticos, sobre todo la temperatura media de los meses de septiembre y octubre, influenciaron la respuesta de la composición de hongos a las claras.

En base a estos resultados, se puede concluir que: (i) sólo bajo condiciones limitadas de agua, tanto el crecimiento del árbol (sobre todo LW) como la producción de setas (principalmente ECM) son más sensibles a la precipitación, resultando en una mayor sincronía entre ambos procesos; (ii) los modelos podrían ser usados para reconstruir las producciones de setas de periodos históricos mediante la información dendrocronológica, así como predecir producciones futuras de setas en base a proyecciones de crecimiento de árboles sensibles al clima y de masas forestales; (iii) la clara podría causar cambios potenciales a corto plazo en la distribución de los recursos desde el micelio a los esporocarpos, priorizando la reproducción frente a la colonización miceliar; y (iv) las claras con extracción cuidadosa de los árboles (p.ej., intensidad baja de clara) mantiene la diversidad de esporocarpos, provocando solo cambios de sucesión a corto plazo en la composición de los hongos.

ABSTRACT IN ENGLISH

Fungi are vital to both human well-being and forest ecosystem functioning due to the ecosystem services delivered by them: provisioning (e.g., edible mushrooms), regulating (e.g., carbon sequestration), supporting (e.g., soil formation) and cultural services (e.g., leisure). To provide further insights into fungi-soil-plant interactions in forest ecosystems, it is still necessary to understand the links between the dynamics of above- and below-ground fungal components together with stand dynamics under anthropogenic disturbances. The main objective of this thesis was to understand, describe and quantify the coupled effects of forest thinning, tree growth and climate on fungal biomass, productivity and community composition.

The doctoral thesis was mainly conducted in a long-term experimental set-up of 28 forest plots, located in the Natural Park of Poblet (Catalonia, Spain), which where thinned with different intensities in 2009. These plots were located in 52 – 57-year-old *Pinus pinaster* Ait. planted stands covering different sites and stand characteristics (e.g., slope, basal area). From 2008 to 2019, we collected sporocarps in each plot on a weekly basis from September to December, and extracted, in December 2014, wood cores from 10-15 dominant trees belonged to each plot. This fungal and dendrochronological information aimed to describe the relationships between mushroom production and forest growth. A similar methodology was conducted in different European regions and forest ecosystems to inspect such fungi-tree relations under other climatic conditions and vegetation composition. Additionally, soil samples (i.e., eight soil cores per plot) were collected in the *P. pinaster* stands, over 5 years. These soil samples were analysed by molecular techniques such as high-throughput DNA sequencing (PacBio RS II, Illumina MiSeq), and biochemical techniques such as ergosterol extraction. The belowground data obtained by the latter techniques together with the sporocarp data was used to inspect above- and below-ground fungal community dynamics under the effects of thinning intensity.

The results showed that the latewood intra-annual density fluctuations frequency was the best predictor of ectomycorrhizal (ECM) mushroom yield, i.e., better than early- or latewood width (EW and LW, respectively). The analysis also revealed that the precipitation of late summer and early autumn as well as forest thinning were mediating the relationship between tree growth and ECM mushroom production. Unlike in the boreal and temperate regions, this interaction between ECM fungi and the growth of host trees was more significant in Mediterranean regions, with positive correlations particularly between LW growth and mycorrhizal mushroom productivity. Thinning also showed in the Mediterranean plots a prolonged negative effect belowground, both inter- and intra-annually, on total fungal biomass and on the biomass of ECM fungi, but not on saprotrophic fungi. Moreover, belowground fungal biomass of total and ECM fungi were negatively correlated with total and ECM mushroom yields, respectively. Differences between the above- and below-ground biomass increased with higher thinning intensities. Finally, the total fungal sporocarp community composition, unlike the sporocarp diversity (i.e., richness, evenness), showed short-term (< 2 years) changes mainly under heavy and light thinning intensities compared to unthinned stands. The unexpected compositional change caused by light thinning intensities has been exclusively related to particular commercial ECM fungi (*Lactarius* group *deliciosus*). Climatic factors, mostly the mean temperature of September and October, modulated the compositional response to thinning.

Based on these results, it can be concluded that: (i) only under more water-limited conditions, both the tree growth (mostly LW) and the mushroom productivity (mainly ECM) are more sensitive to precipitation events, resulting in higher synchrony between both processes; (ii) models may be used to reconstruct mushroom production along historical periods based on dendrochronological information, but also to predict future mushroom yields based on climate-sensitive tree and stand growth predictions; (iii) forest thinning may cause potential short-term shifts in resource allocation of fungi from below- to above-ground structures, i.e., prioritizing increasing reproduction rather than colonizing the surrounding soil; and (iv) forest thinning practices with a careful removal of trees does not compromise the sporocarp diversity, but lead to short-term successional changes in fungal assemblages.

GENERAL INTRODUCTION

The role of fungi in forest ecosystems

The fungal kingdom, covering 1.5 – 6 million estimated species, is one of the most diverse of the eukaryotic kingdoms (Blackwell, 2011; Hawksworth and Lücking, 2017; Mueller and Schmit, 2007). In particular, forest fungi are a group of organisms that profit the energy stored in animal and plant biomass to support their own development, inasmuch as they are not able to fix energy and nutrients directly. Fungi are considered as 'ecosystem engineers', whose structure and life form simulate the plumbing of the ecosystem, being able to regulate temporal and spatial flows of energy and nutrient. These processes are conducted by the extensive and, largely, long-lived rhizomorphic and mycelial networks, reaching tens or hundreds of meters (Smith et al., 1992) (Fig. 1). Fungi can perpetuate themselves by growing as clonal organisms, reproducing based on asexual or sexual reproduction or both. The production of spores, that generates new offspring, are created and spread (from millimetres to kilometres) by a specialized fruiting structure that can be large and visible in the higher fungi (Basidiomycotina and Ascomycotina) (Fig. 1).

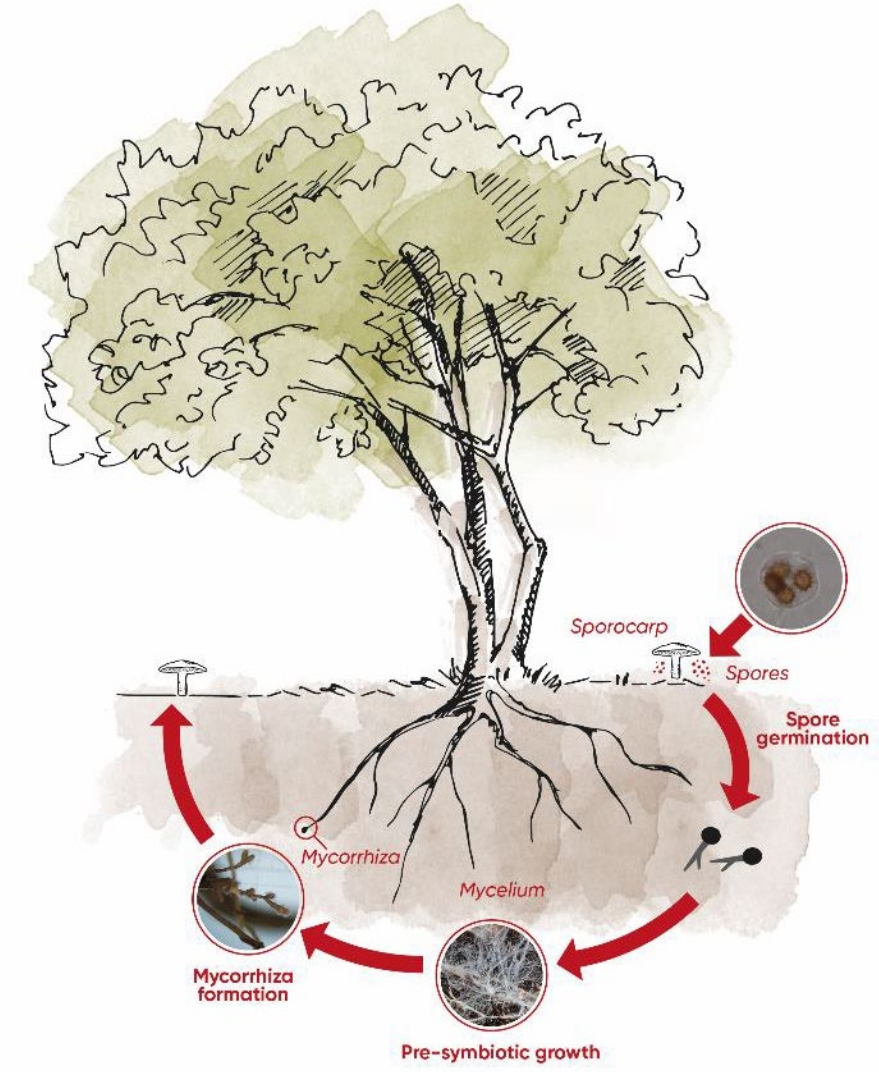

Figure 1: The life cycle of mycorrhizal fungi. Illustration: Samuel Garrido (design) and Francesc Bolaño. Adapted from *Mycorrhiza helper bacteria* [in *Molecular Mycorrhizal Symbiosis*], by A. Deveau and J. Labbé, 2016, F. Martin (Ed.).

These fruiting bodies (also called sporocarps, carpophores, mushrooms or macrofungi) represent a sink for internally translocated nutrients and carbon, since the production of spores entails additional energy and nutrients. Sporocarps have been traditionally used to study fungal ecology questions, although new methods (e.g., morphological analyses and molecular techniques) have allowed to dig deeper into such questions by analysing other fungal vegetative structures (e.g., mycorrhizae, mycelium, spores).

Fungi provide different ecosystem services, i.e., they are involved in key ecosystem processes leading to manifold benefits for humans (Fig. 2). Such ecosystem services include (Leemans and De Groot, 2003): (i) regulating services, like soil carbon sequestration and regulation of plant stress; (ii) provisioning services, such as a source of food (i.e., edible mushrooms); (iii) cultural services like recreational activity (e.g., mushroom picking); and (iv) supporting services, that are essential to maintain the other three services, like soil fertility and formation. The relevance of forest fungi in the ecosystem services will be further explained below.

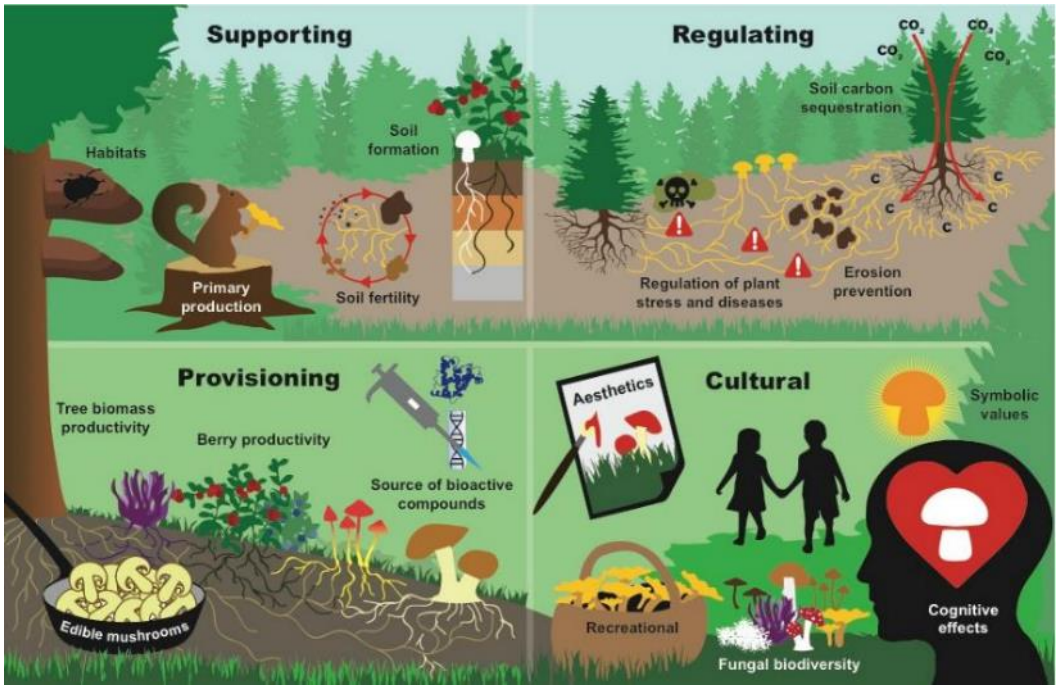

Figure 2: Ecosystem services provided by forest fungi. Reprinted from *Interactions between fungi, forest management, and ecosystem services* (p. 17), by K. Varenius, 2017.

Fungi play essential roles in forest ecosystems by interacting with other organisms and with the abiotic environment to mediate ecosystem processes. Indeed, the role of fungi becomes even more relevant in Mediterranean ecosystems, characterized both by harbouring a large number of endemic species (i.e., a hot spot of fungal biodiversity; Brooks et al., 2002) and by being highly faced with the climate change (Ágreda et al., 2016; Tedersoo et al., 2014). Fungi are also able to occupy multiple niches within a forest ecosystem, and even to alter their niche extent by changing environment and resources within the niche (Swift et al., 1979). According to the strategy to obtain energy, fungi may behave as (Fig. 3): (i) mycorrhizal symbionts, expanding the plant root system and sustaining primary production in forests; (ii) saprotrophs, driving the global carbon cycle; and (iii) parasites, regulating the population dynamics of their hosts.

Figure 3: Ectomycorrhizal (left), saprotrophic (centre) and parasitic (right) fungal species: *Boletus pinicola*, *Macrolepiota procera* and *Fomitopsis* sp., respectively.

The mycorrhizal species, specially ectomycorrhizal (ECM) and arbuscular species, are particularly crucial in forest ecosystems because they provide nitrogen and phosphorus to the host trees and, in exchange, mycorrhizal fungi acquire organic carbon compounds photosynthetically fixed by trees (Read and Perez-Moreno, 2003; Smith and Read, 2008) (Fig. 4). In forest ecosystems, about half of the photosynthetic carbon supply is allocated belowground to roots and ECM fungi (Gill and Finzi, 2016). Additionally, ECM fungi are also essential in both alleviation of drought stress for trees (Mohan et al., 2014), either by increasing access to soil water (Allen, 2007) or by improving soil structure and porosity (Querejeta, 2017), and facilitation of nutrient uptake by trees under nutrient- and water-limited conditions (Read and Perez-Moreno, 2003). The extramatrical mycelium (EMM) is the main belowground fungal structure aiming both at acquiring nutrients in soils and supplying them to their plant host, and at encountering new root tips to colonize (Cairney, 2012). Furthermore, saprotrophic, or saprobic, species obtain carbon by degrading the soil organic material (e.g., coarse woody debris and leaf litter), precipitating in turn massive CO_2 release (Boddy et al., 2007; Rayner and Boddy, 1988) (Fig. 4). Different saprotrophic species, as specialist of organic substrate, may decompose different types of wood (Kubartová et al., 2012) and litter (Prescott and Grayston, 2013), allowing them to colonize diverse habitats. Likewise, wood-inhabiting fungi, apart from regulating the carbon cycle and releasing nutrients from wood, may provide different niches for other organisms (e.g., other fungi, insects and hole-nesting birds) (Stokland et al., 2012).

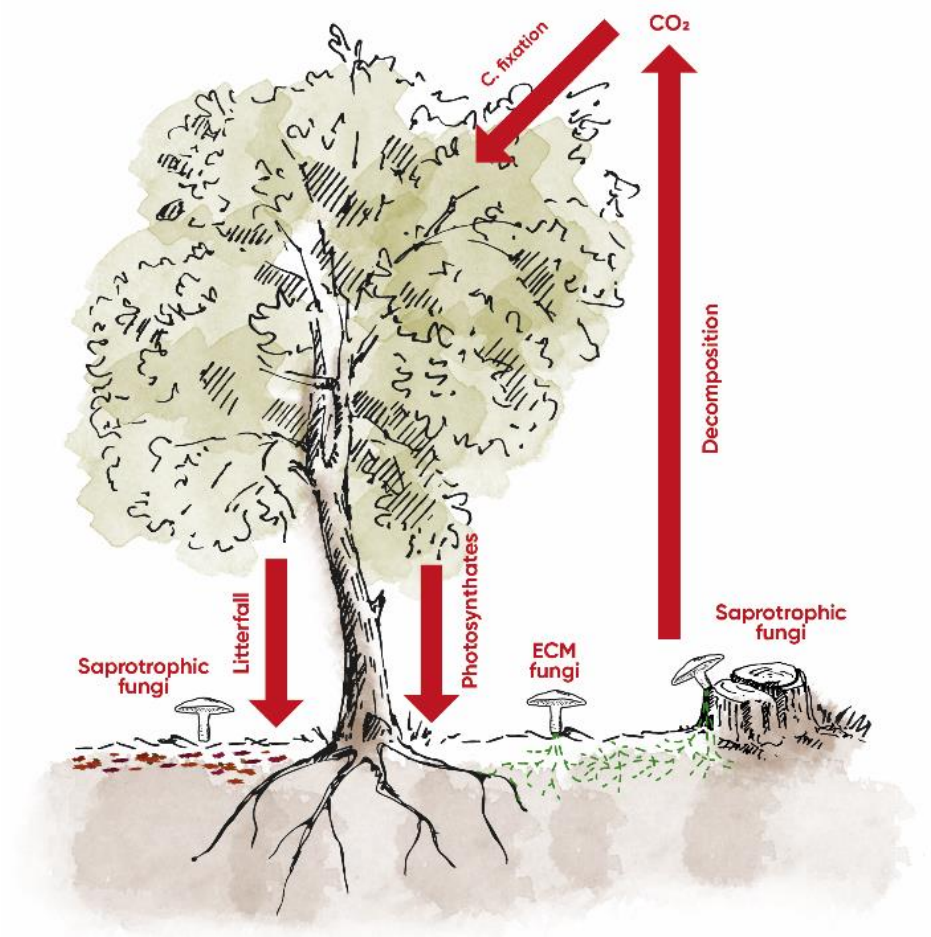

Figure 4: The strategies of ectomycorrhizal (ECM) and saprotrophic fungi to obtain carbon. ECM fungi obtain carbon compounds derived from the photosynthates of their host trees. Saprotrophic fungi obtain carbon by decomposition of organic matter (e.g., litter, stump), whose activity is limited by ECM fungi due to the competition for nitrogen. Illustration: Samuel Garrido. Adapted from "Microbial activity and the dynamics of ecosystem processes in forest soils", by P. Baldrian, 2017, *Current Opinion in Microbiology*, 37, 128–134.

ECM and saprotrophic guilds interact each other in the same habitat, resulting in a growth inhibition for both as a consequence of the competition for limited soil resources (Leake et al., 2002). In this sense, ECM fungi may diminish the saprotrophic fungal growth and activity with cascading effect on a decrease of decomposition rates and, therefore, an increase of carbon storage in the forest soil (Fernandez and Kennedy, 2016; Gadgil and Gadgil, 1975; Koide and Wu, 2003; Rasanayagam and Jeffries, 1992). Carbon availability is the key element in the belowground inter-guild interactions: ECM fungi is less competitive for nutrient uptake than saprotrophic fungi when there is no carbon limitation (Bödeker et al., 2016; Lindahl et al., 2001). Additionally, the nutrient availability in soils is the main factor on the allocated quantity of carbon-input into the soil, either by ECM fungi (i.e., recently assimilated carbon; Högberg et al., 2003) or by leaf litter. For instance, saprotrophic fungi are benefited under non-limited nutrient availability, since trees provide them an abundant carbon source via the high amount of nutrient-rich litter supplied by trees (Högberg et al., 2010, 2003).

In addition to the supporting and regulating ecosystem services of forest fungi, saprotrophic and ECM species are of socio-economic importance worldwide by providing provisioning and cultural resources with their mushrooms (Boa, 2004) (Fig. 2). In Mediterranean regions, i.e., drought-prone areas with low profitability of timber, the value of wild mushrooms may be even higher than that of the timber (Palahí et al., 2009; Pettenella and Secco, 2006). Indeed, the economic value of marketable and edible mushrooms in Catalonia are estimated at 32 and 48 million €, respectively (Bonet et al., 2014). This value is increased whether mushroom picking is included, being this leisure activity very important in many parts of Europe (Martínez de Aragón et al., 2011). For instance, in a rural area of Northern Spain, it has been estimated that a family of four people can derive profits of 5600-8400€ from picking *Lactarius deliciosus s.l.* (Fig. 5) over one season (De Román and Boa, 2004). Actually, the latter species group represents one of the most important edible ECM species in Spain, reaching its economic impact 5.3 million € $year^{-1}$ during 2002-2008, with on average ca. 500 tons of *L. deliciosus* sold every year (Voces et al., 2012). In addition to the genus *Lactarius*, the most representative saleable species in the Mediterranean region are (Martínez-Ibarra et al., 2019): *Boletus edulis*, *B. aereus*, *Cantharellus cibarius*, *Craterellus* group and *Tuber melanosporum*. Furthermore, there are also multiple cultural services provided by forest fungi, such as education, recreation, social and aesthetic pleasure (e.g., photographing sporocarps). However, this NWFPs in Spain may be threated due to doomsday scenarios of climate change (Andrew et al., 2016; Boddy et al., 2014; Kauserud et al., 2008), the high interannual variability of the Mediterranean climate and its limited regulation of the use or exploitation.

Figure 5: Sporocarp of *Lactarius deliciosus*.

Despite the high ecological and socioeconomic values of forest fungi in Mediterranean areas, their hidden life remains quite unknown. This is due to the difficulty to monitor and analyse belowground fungal processes, most of the studies focusing on fungal fruiting patterns (Tomao et al., 2020, 2017; Tóth and Barta, 2010). Moreover, only few studies have conducted long-term experimental designs on fungal fruiting patterns, being complex to elucidate actual fungal community dynamics because of the large amount of factors and stochasticity involved in the fungal fructification. In this sense, molecular techniques have become more relevant to overcome issues related to sampling of sporocarps, being capable to quantify fungal biomass and characterize the fungal community. Some techniques, such as high-throughput sequencing methods, have aimed at analysing mycelia (e.g., from soil samples) and airborne spores by spore trapping.

Key factors affecting fungal dynamics

Fungal community dynamics are largely determined by the combination of three main factor groups (Fig. 6): climate variability (e.g., temperature, precipitation), forest stand structure (e.g., canopy cover, tree species, stand age) and site characteristics (e.g., slope, aspect, altitude, soil properties).

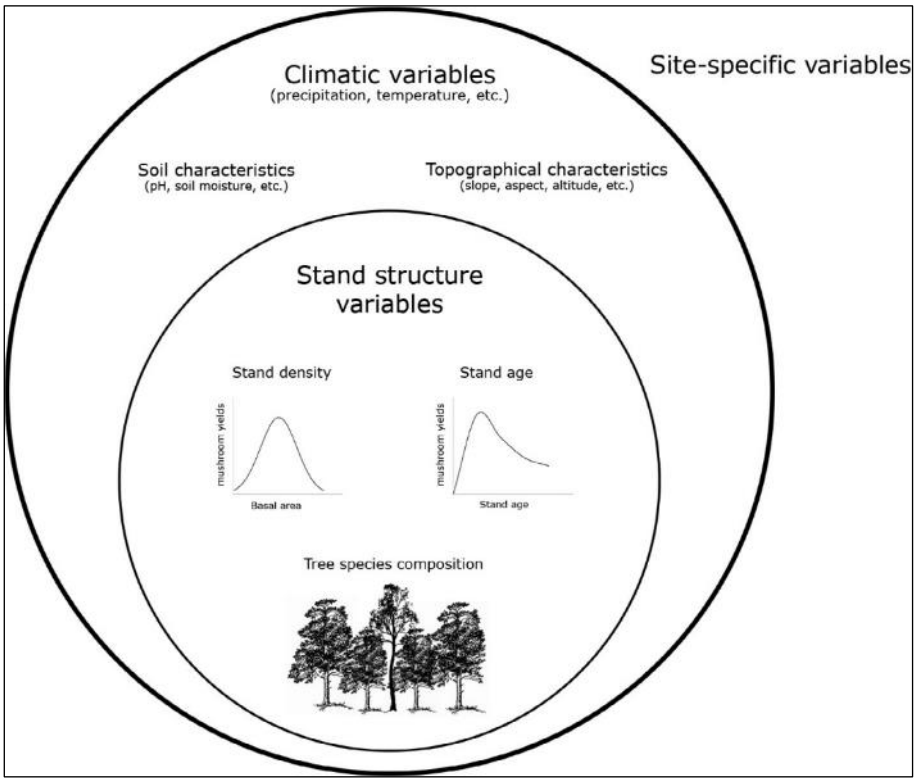

Figure 6: Factors involved in the fungal community dynamics. Reprinted from Tomao et al. (2017).

Effects of site characteristics

Site characteristics, including soil properties (e.g., pH, C/N, texture) and topographical characteristics (e.g., slope, aspect, altitude), are considered long-term conditioning factors in fungal community dynamics. Anthropological disturbances may alter soil properties, and thus also forest fungal communities, but topographic characteristics generally remain unchanged over time.

Alterations in soil properties, either by inter-guilds interactions or by disturbances (e.g., fire, fertilization) (e.g., Awad et al., 2018; Rincón et al., 2014), may contribute to variation of belowground fungal biomass. For instance, forest liming (i.e., direct input of Mg and Ca in forest soil) has demonstrated, apart from being efficient to restore tree mineral nutrient, a negative effect on both the abundance of ECM sporocarps and ECM root tip communities of acidophilic fungi (Rineau et al., 2010). Likewise, elevated nitrogen levels in forest soil have generally caused negative effects on both above- and belowground ECM communities, the sporocarp ECM production varying highly in both extent and response time (Gillet et al., 2010). Indeed, saprotrophic fungi, unlike most of the ECM species (e.g., Nilsson and Wallander, 2003), are much less affected by the increase of NO_3^- and NH_4^+ (e.g., Peter et

al., 2001; Wiklund et al., 1995). This shift in fungal community composition lies in the fact that higher nitrogen availability in forest ecosystems triggers a reduction of carbon allocation to roots and, therefore, to mycorrhizal fungi (Demoling et al., 2008; Högberg et al., 2007). Although nitrogen and pH are among the most important soil properties influencing on the distribution of fungi (e.g., Tedersoo et al., 2020), there are other relevant factors such as litter depth and soil texture (Dowson et al., 1988; Martínez-Peña et al., 2012). These factors impact on water holding capacity and soil-moisture content, being of importance in particular ecosystems such as drought-prone forests. For instance, Taye et al. (2016) observed in Mediterranean stands higher *L.* group *deliciosus* productions on sandy-loam texture, since loam soils are capable to retain more water than, for example, loamy sands (Moore et al., 1998).

Additionally, topographic factors play a relevant role in the fungal fruiting patterns, likely as a consequence of the microclimate conditions shaped by such factors. For instance, de-Miguel et al. (2014) found, under different forest ecosystems and along an altitudinal gradient, significant effects of aspect and altitude on the probability of sporocarp occurrence and the sporocarp production, respectively. The latter authors pointed out that the effect of altitude is relative to the climate of the region: higher sporocarp productions are found at higher altitudes in coastal pine forests, unlike in mountain pine stands. Bonet et al. (2010) also observed in the Spanish pre-Pyrenees that at higher altitudes (up to 1500 m) and on north aspects the number of species increased significantly. Likewise, negative effects on the sporocarp yield have been linked to steeper slope, this factor leading to higher water runoff and thinner soils (Bonet et al., 2008).

Effects of climate

In the soil, both mycorrhizal and saprotrophic fungal communities demand different climate conditions. Higher relative abundances of soil ECM fungi have been found during summer or autumn under temperate and boreal conditions (Jumpponen et al., 2010; Santalahti et al., 2016; Voříšková et al., 2014; Wallander et al., 2001), likely linked to an increased carbon allocation from host trees in the growth season (Högberg et al., 2010; Žifčáková et al., 2017). Belowground ECM fungal biomass oscillates intra-annually in Mediterranean ecosystems, observing the minimum mycelium production during summer and winter (Castaño et al., 2017; Iotti et al., 2014; Queralt et al., 2017). In such drought-prone ecosystems, changes in belowground fungal community composition were partly determined by inter-annual fluctuations in precipitation and temperature: the relative abundance of mycorrhizal species were promoted under drier and colder conditions, while the abundance of saprotrophic species was increased in wetter conditions (Castaño et al., 2018). Non-mycorrhizal fungal species (e.g., litter saprotrophs and moulds) have shown seasonal shifts in community composition, the relative abundance usually peaking under colder conditions (Andreetta et al., 2012; Jumpponen et al., 2010; Santalahti et al., 2016; Voříšková et al., 2014).

Climate also arises as the foremost driver of sporocarp emergence and yield, acting as a limiting or mediating factor according to local conditions (Büntgen et al., 2012). Overall, fungal fruiting is mainly boosted by humid and warm conditions (Alday et al., 2017; Hernández-Rodríguez et al., 2015). In temperate and mostly in boreal forest ecosystems,

mushroom production is greatly driven by temperature (Büntgen et al., 2013; Ohenoja, 1993; Sato et al., 2012; Tahvanainen et al., 2016). In temperate regions, mushroom production has been enhanced and ahead due to the recent trends of temperature increase triggered by climate warming, while delayed and decreasing productivity has been found under Mediterranean conditions (Boddy et al., 2014). In particular, the forecasted climate in Mediterranean regions will entail: (i) a temperature rise (1.4 - 5.1 °C by 2055; Bravo et al., 2008), (ii) a possible reduction in total annual precipitation (Evans, 2009; Giorgi and Lionello, 2008), (iii) more extreme rainfall events (García-Ruiz et al., 2011), and (iv) a decreased soil moisture (Dai, 2013). For instance, in particular Mediterranean forest stands, higher estimated mushroom productions were caused by the elongation of the fruiting season due to climate change (i.e. an increased precipitation at the beginning of the season and warmer temperatures at the end) (Karavani et al., 2018). In such drought-prone conditions, precipitation-temperature interactions may be the main limiting factor for forest growth and mushroom yield since high evapotranspiration rates may reduce soil water availability (Büntgen et al., 2015; Karavani et al., 2018; Martínez de Aragón et al., 2007; Primicia et al., 2016; Salerni et al., 2002). In the light of the predicted climate change in drought-prone regions, new approaches must be developed to increase our knowledge on how the interaction between fungal community and forest responses to disturbances. In this sense, only a few studies have used dendrochronological techniques to disentangle complex fungi-tree interactions that may be further mediated by climatic conditions (Primicia et al., 2016). For example, Egli et al. (2010) found, after thinning, positive relationships between radial tree growth and the production of ECM and, to a lesser extent, saprotrophic fungi. Likewise, particular seasonal wood formation (earlywood –EW– and latewood –LW– production) has been also linked to fungal yields in certain Mediterranean pine forests: LW production and ECM yield from the most xeric sites were positively correlated (Primicia et al., 2016). However, further research must be devoted to the linkages between mushroom yield and tree radial growth in drought-prone ecosystems, as well as inspecting such relationships in different bioclimatic regions and forest ecosystems to better support the existent literature. Models based on dendrochronological information could be also valuable to reconstruct past mushroom production, as well as to predict future mushroom yield based on climate-sensitive tree and stand growth projections. Moreover, the use of dendrochronological methods have additionally shown lagged-effects between tree growth of previous years and current sporocarps production (Egli et al., 2010). Likewise, lagged-effects have also found between climate variables and mushroom fruiting (Krebs et al., 2008; Yang et al., 2012), given by a hierarchy of resource allocations in the trade-off between mycelia growth and sporocarp production (Deacon and Fleming, 1992; Gardes and Bruns, 1996). For instance, Karavani et al. (2018) observed that the effect of precipitation on mushroom yield exhibited a one-month delay. In this sense, Ágreda et al. (2015) reported that temperature and water availability affected similarly to both mycorrhizal and saprotrophic mushroom yields, but with differences between both guilds in the exact timings of these climatic factors.

Effects of forest stand structure

Overall, the stand structure attributes that drive fungal dynamics include among others: forest stand age, canopy cover and stand density, or tree species composition (Tomao et al., 2020, 2017). Alterations in these variables by natural or anthropogenic disturbances may result in changes in fungal diversity and community composition as well as in fungal fructification, leading eventually to shifts in the forest ecosystem services provided by fungi. In particular, such changes in fungi due to disturbances may largely be caused either indirectly, by modifying the microclimate conditions (Karavani et al., 2018; Pilz and Molina, 2002) or directly, by interfering in the carbon flux (Högberg et al., 2001). Forest management have also shown indirect shifts in fungal community by soil scarification and compaction that result, for instance, in a reduction of water retention capacity (Hartmann et al., 2012).

Forest anthropogenic disturbances have so far shown contrasting effects on fungal fruiting (Tomao et al., 2017) (Fig. 7A). For instance, several studies have observed the highest mushroom production with low to moderate thinning intensities (e.g., Ayer et al., 2006; Bonet et al., 2012; Kropp and Albee, 1996; Salerni and Perini, 2004). However, clear-cutting (e.g., Durall et al., 2006; Ohenoja, 1988) or heavy thinning (e.g., Salerni and Perini, 2004) severely diminished the mushroom yield. Moreover, forest management have generally shown, by monitoring sporocarps, changes in the fungal community composition (Tomao et al., 2020) (Fig. 7B). However, forest thinning practices have shown, in different ecosystems, contrasting effects on sporocarp species richness. For instance, Egli et al. (2010) detected an increase in ECM and saprotrophic sporocarp richness four years after the thinning of a mixed temperate forest, whereas Lin et al. (2015) observed a decline in saprotrophic sporocarp richness in the first year of post-thinning in a tropical plantation. The latter study also found less impact on the sporocarp community under 25% thinning treatment than 50%-thinning. Conversely, Shaw et al. (2003) did not observe, in temperate coniferous stands, any community-level response of ECM sporocarps to thinning in the five years after the removal of 50% of pines. Therefore, both the intensity of the disturbance and forest ecosystem characteristics may differently shape the aboveground macrofungal sporocarp composition and diversity over time. Yet, the existent literature on aboveground community composition is even more scant and mainly focused on rather short-term disturbance impacts (< 5 years). In this sense and considering the predicted climate change, further research must be conducted in drought-prone regions to inspect how the sporocarps community composition and diversity behaves under both water-limited conditions and different treatment intensities. However, this is only possible with long-term monitoring (> 10 years) to cope with the stochastic fruiting dynamics, typical from Mediterranean ecosystems.

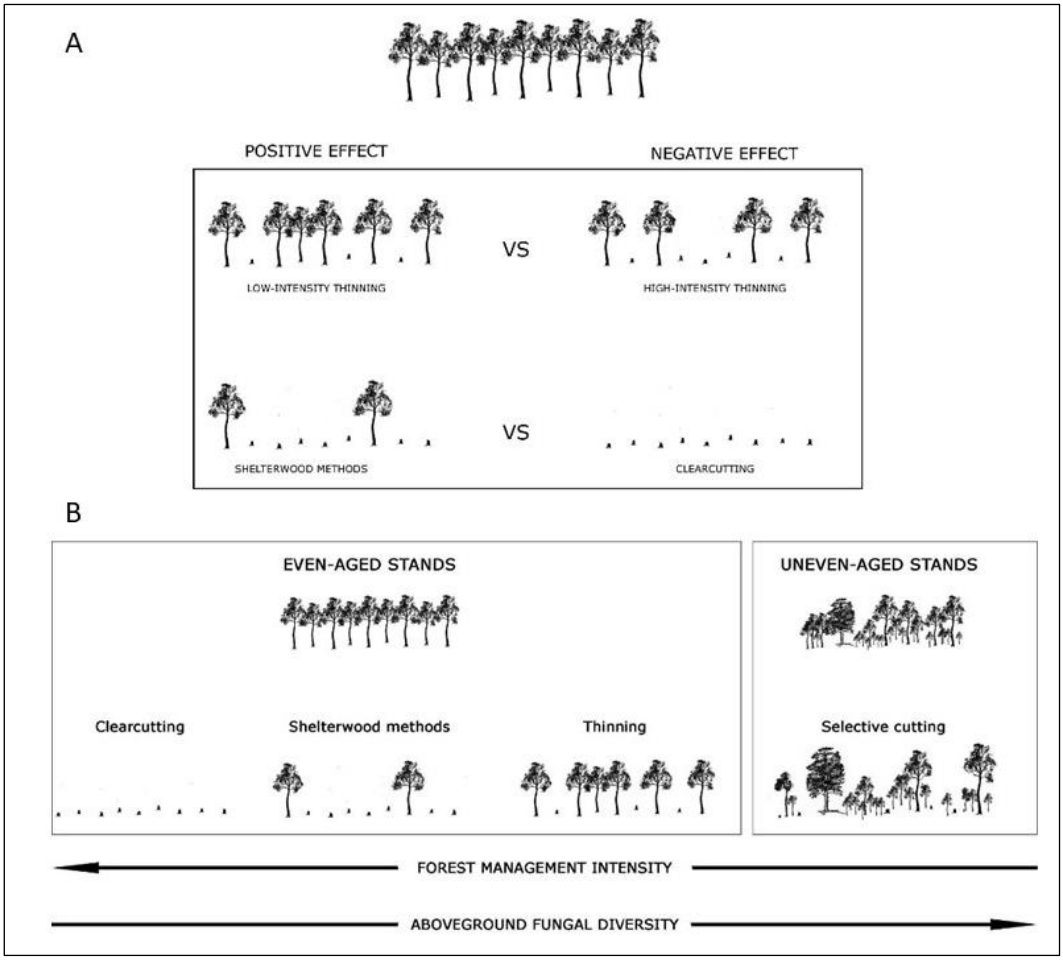

Figure 7: Effects of different intensities of anthropogenic disturbances on production (A) and fungal diversity (B) of sporocarps. Reprinted from Tomao et al. (2020, 2017).

Forest management has a strong effect on fungal community composition, forest carbon allocation and belowground processes (Jones et al., 2003). Nevertheless, only few studies have aimed at how soil fungal community dynamics cope with anthropogenic disturbances, showing contrasting results (Tomao et al., 2020). In short, heavy disturbances (e.g., clear-cutting) usually result in drastic alterations of the belowground fungal community composition, while less intensive disturbances (e.g., thinning, foliage defoliation) cause limited changes in fungal biomass (e.g. Hendricks et al., 2016; Parladé et al., 2019) or in soil fungal communities (e.g., Castaño et al., 2018a; Sterkenburg et al., 2018). After heavy disturbances, opportunistic non-ECM fungi (e.g., saprotrophs) are capable of benefiting from the removal of ECM fungal guild, as a result of the interruption of carbon allocation (Kyaschenko et al., 2017; Parladé et al., 2019). However, the belowground fungal biomass may remain unchanged after disturbances whether some host trees stay intact in the stand, leading to a preserving of fungal network (cf. Mediavilla et al., 2017; Parladé et al., 2017; Sterkenburg et al., 2019).

Studies devoted to inspect the influence of disturbances on aboveground and belowground fungal biomass components are extremely important to have a whole picture of the fungal dynamics. However, such studies are scant and only focused on specific species, with still non-conclusive results. For instance, some of these findings on the relationship between the biomass of sporocarps and mycelium found either no significant correlations (De la

Varga et al., 2013; Parladé et al., 2017) or positive relationships (Mediavilla et al., 2017; Suz et al., 2008). These studies may shed light on how fungi reallocate resources under environmental stressors, prioritizing either colonizing the surrounding soil or reproducing.

Gaps in knowledge

Even today, the state of the art on aboveground (sporocarps) and belowground fungal dynamics and on the complex fungi – tree interactions have many gaps in knowledge and open questions for further research. In the light of the predicted climate change, addressing these issues to maintain the ecosystem services provided by fungi in drought-prone regions is becoming increasingly important. In this sense, the following gaps in knowledge were identified and, partly, addressed in this thesis (see Objectives section):

- There is a need for disentangling the relationships between sporocarp production and tree growth, distinguishing among different fungal functional guilds, by means of new approaches such as dendrochronological techniques. Understanding such relationships may shed light on how trees allocate carbon to fungi.
- Such fungi-tree interactions, highly influenced by climate and vegetation composition, have to be further inspected in different biomes and forest ecosystems.
- At belowground level, how both ectomycorrhizal and saprotrophic fungal dynamics deal with anthropogenic disturbances is still quite unknown, due partly to the high demanding effort arisen from monitoring and analysing of soil samples.
- How different fungal functional guilds reallocate carbon into different fungal structures (e.g., mycelia, sporocarps) under environmental stressors is also a great mystery. To inspect such carbon reallocation requires, not only monitoring and analysing of soil samples, but also an intensive fungal sporocarp sampling and analysis.
- At aboveground level, there are still weak evidences about the long-term responses to anthropogenic disturbances of the sporocarps community composition and fungal diversity. Today, there is a need of addressing such responses by conducting long-term experiments to cope with the stochastic fruiting dynamics typical from Mediterranean regions.

OBJECTIVES

On the basis of the gaps identified in the literature, the objectives of this thesis are:

1. To analyze the relationships between the productivity of both saprotrophic and ectomycorrhizal fungi with climate and tree growth dynamics under different thinning intensities in Mediterranean pine stands.

2. To study the effects of climate conditions on both mushroom productivity and sporocarp density (i.e., number of sporocarps per unit area) as related to tree radial growth across different European bioclimatic regions and forest types based on long-term data series.

3. To investigate the response of belowground fungal biomass to different thinning intensities over time, both inter- and intra-annually, in order to contribute to further understanding the aboveground-belowground fungal dynamics.

4. To investigate the response of the aboveground fungal community composition and diversity to different thinning intensities, disentangling in turn how climate conditions modulate such fungal response.

THESIS STRUCTURE

This thesis has been organized in chapters, written in the format of scientific articles, with the aim of publishing them in international, peer-reviewed, scientific journals. The first objective was to integrate dendrochronological techniques to investigate the links between mushroom productivity and tree growth under different thinning intensities conducted in a Mediterranean pine forest (Chapter I). Second, I aimed at deepening the first objective by investigating the relationship between mushroom productivity and tree growth throughout different biomes and European forest ecosystems (Chapter II). Third, I studied the effects of thinning intensity on the belowground fungal biomass over time, both inter- and intra-annually (Chapter III). I also compared the previous belowground effects with the effect of thinning on aboveground fungal biomass (sporocarps), to elucidate how fungi reallocate carbon fluxes into different fungal structures under disturbances (Chapter III). Finally, I further inspected the short- to long-term response of the aboveground macrofungal sporocarp community composition and diversity to forest thinning intensity as well as how climate conditions modulate such fungal response to thinning (Chapter IV).

i. CHAPTER I: Linking fungal dynamics, tree growth and forest management in a Mediterranean pine ecosystem.

ii. CHAPTER II: Mushroom productivity trends in relation to tree growth and climate across different European forest biomes.

iii. CHAPTER III: Divergent above- and below-ground responses of fungal functional groups to forest thinning.

iv. CHAPTER IV: Impact of forest thinning on aboveground macrofungal community composition and diversity in Mediterranean pine stands.

GENERAL METHODOLOGY

Site selection

All chapters are based on samplings conducted in the Natural Protected Area of Poblet (Prades, Catalonia, Spain), whereas Chapter II also included samplings from (Fig. 8): Kitsi (Lieksa, Finland), Kalimeenoja (Oulu, Finland), La Chanéaz (Payerne, Switzerland), Pre-Pyrenees (Catalonia, Spain), Pyrenees (Catalonia, Spain), Solsonés (Catalonia, Spain), Pinar Grande (Soria, Spain), Almazán (Soria, Spain), Villaluenga de la Vega (Palencia, Spain) and Tudela del Duero (Valladolid, Spain).

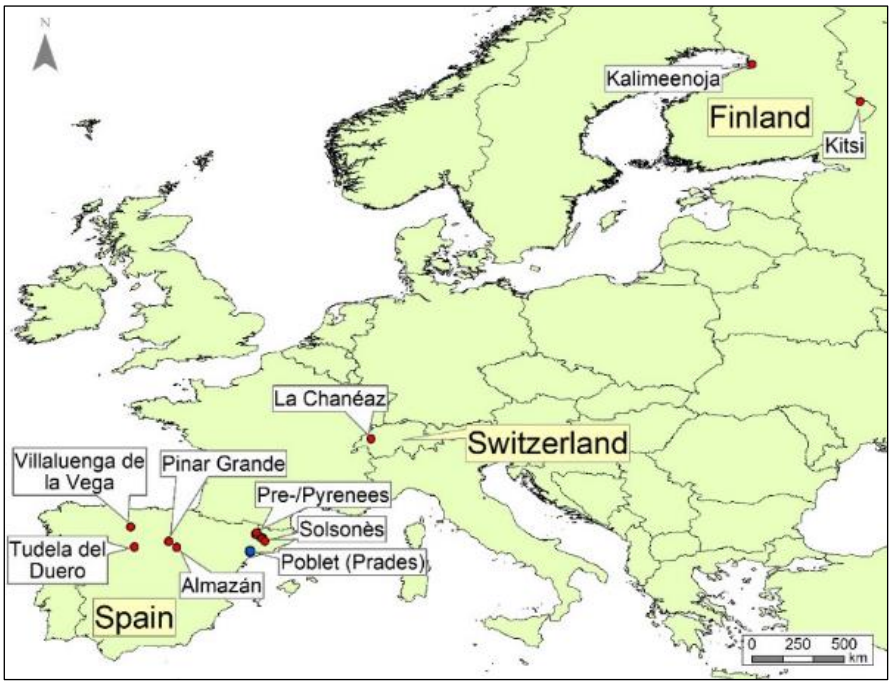

Figure 8: Location of all study sites.

In 2008, it was established a long-term experimental setup in Prades with 28 inventory plots of 52 – 57-year-old *Pinus pinaster* Ait. planted stands (15 plots set up in 2008 and 13 plots in 2009, Fig. 9), with isolated *Quercus ilex* L. trees or shrubs. The climate is characterised by a drought-prone summer season, typical from Mediterranean areas, with an average annual temperature of 11.8 ºC and an average annual rainfall of 659 mm (data obtained from L'Espluga de Francolí station, 41° 23′ 47″ N, 1° 06′ 10″ E, 446 m a.s.l.). The natural vegetation is dominated by *Q. ilex* coppice stands with understorey shrubs such as *Phillyrea latifolia* L., *Arbutus unedo* L. and *Calluna vulgaris* (L.) Hull. The soils are classified as a calcic cambisol (FAO, 1998), and are characterized by siliceous minerals with sandy loam textures, pHs ranging from 6.1 to 6.6 and organic matter contents ranging from 2.95 to 10.51% (Castaño et al., 2017).

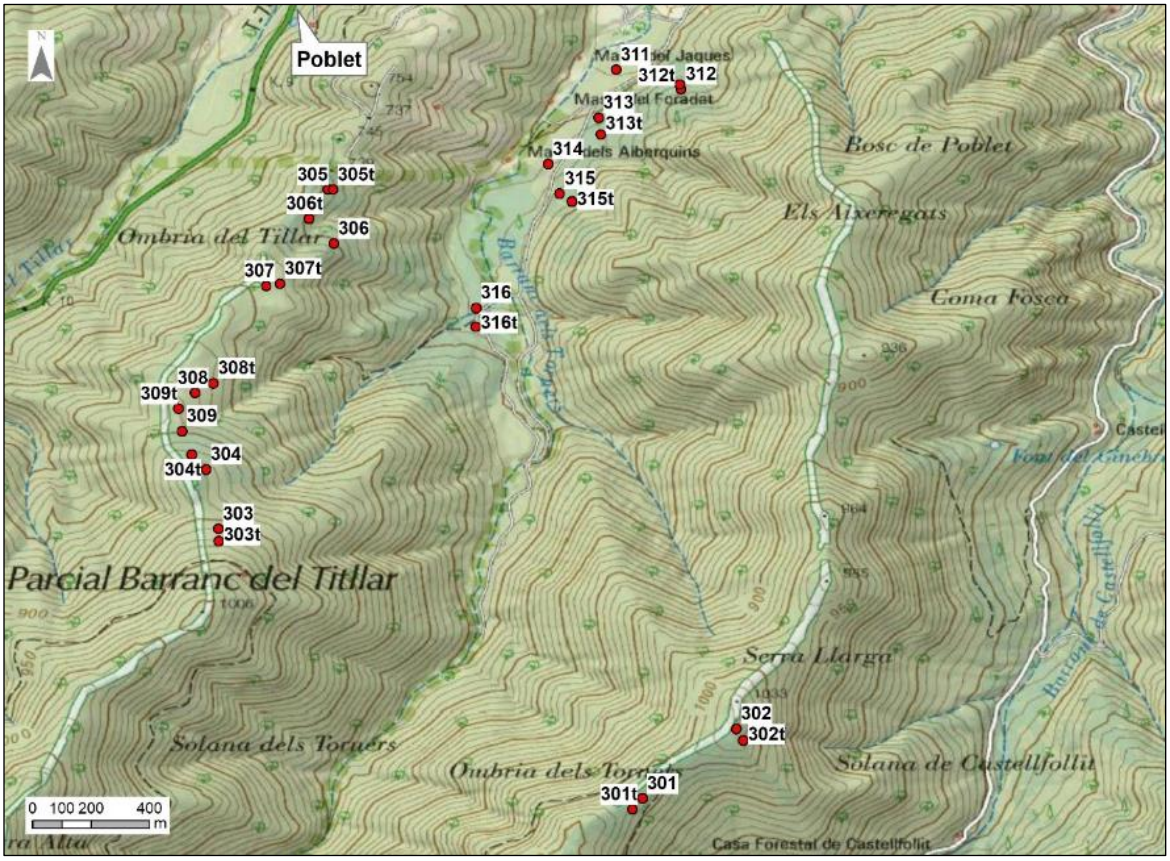

Figure 9: Location of the mushroom inventory plots in the Natural Protected Area of Poblet (Prades, Catalonia, Spain). The number of the plot with 't' denotes plots that were thinned in 2009. Image source: The Spanish National Mapping Agency (Instituto Geográfico Nacional; https://www.ign.es/web/ign/portal/inicio).

The experimental design carried out in the even-aged *P. pinaster* stands of Prades (Spain) consisted of 28 permanent sporocarp inventory plots of 100 m^2 (10 m x 10 m) (Fig. 9 and 10). 15 plots without any thinning treatment were established in 2008, whereas the other 13 plots were established in the summer of 2009 representing different thinning intensities (from 20% to 71% in stand basal area). Such thinned plots were located in the centre of larger thinning plots (40 m x 40 m) in order to prevent edge effects. Plots differ from each other in their altitudes (594 – 1013 m a.s.l.), aspects (north, west, east), slopes (3 – 23%), remaining stand basal area (control plots: 21 – 82 m^2 ha^{-1}, thinned plots: 17 – 47 m^2 ha^{-1}) and remaining stand densities (control plots: 446 – 2657 trees ha^{-1}, thinned plots: 350 – 1528 trees ha^{-1}). All felled trees were cut by a chainsaw and removed them carefully, avoiding soil disturbance. Further information about the thinning procedure and the stand variables are available in Bonet et al. (2012).

Figure 10: A control (unthinned) plot (above) and a thinned plot (below) after tree removal in 2009.

In Chapter II, I used a database of 111 permanent stands, both pure and mixed stands, dominated by European beech (*Fagus sylvatica* L.) or pine species (Scots pine, *Pinus sylvestris* L.; Black pine, *Pinus nigra* Arn.; Maritime pine. *Pinus pinaster* Ait.; Aleppo pine, *Pinus halepensis* Mill.) across different latitudes from Finland through Switzerland to Spain (Fig. 8). Permanent stands were classified into eleven study sites and, in turn, these were clustered into seven macrosites based on spatial proximity and similarity of climatic conditions. The main sampling units, hereafter called "plots" (only in Chapter II), were established by the combination of each site and the different tree species in such site.

Climate data

In Chapter I and IV, climate data was obtained, following the DAYMET methodology, by interpolating plot-specific daily weather variables from meteorological stations. In Chapter II, seasonal climatic variables were calculated from monthly data obtained from the gridded E-OBS climate dataset by selecting the 0.25º grid.

Sampling

Aboveground fungal (sporocarps) sampling

In all chapters, all epigeous sporocarps (except parasitic fungi) were collected in each plot of Prades (Spain) on a weekly basis from early September to late December. In Chapter II, mushroom production was inventoried weekly or biweekly during summer and/or autumn (depending on mushroom season on the site). All sporocarps were taken to the laboratory for identification, classification and weight (fresh and dry) (Fig. 11).

Figure 11: Processing of sporocarps in the laboratory.

Belowground fungal (mycelium) sampling

In Chapter III, soil samples were systematically taken, on the one hand, once every year at the month of November and, on the other hand, once every month during a particular year. Eight soil cores (5 cm in diameter and 12 cm deep), two cores from each side of the plot, and at least 10 m apart to avoid spatial autocorrelation, were extracted from each plot (Fig. 12). We discarded the litter but included humus and mineral soil to obtain soil profiles with a depth of 12 cm and a composite sample of approximately 500 g for each plot. Soil samples were stored at 4 ^{o}C for < 24 h and then sieved using a 3-mm mesh. Sieved soils were freeze-dried and pooled to obtain a composite sample representing each plot for each of the sampling time-points. Each composite soil sample was homogenized using a pestle and mortar, resulting in a fine powder, and stored at -20 ^{o}C before DNA extraction and molecular analyses. In total, 416 composite soil samples were used in Chapter III. The belowground fungal community composition of each composite soil sample was obtained by PacBio sequencing platform, whereas the belowground fungal biomass of the samples was estimated by quantifying ergosterol.

Figure 12: Extraction of soil cores by a soil sampler.

Dendrochronological sampling

In Chapter I and Chapter II, we randomly selected 10 to 15 dominant trees representative of each mushroom inventory plot for tree-ring measurements. We extracted two radial wood cores per tree at 1.3 m above ground level using a Pressler increment borer. These cores were air-dried, mounted on wood boards and carefully polished (Fig. 13).

Figure 13: Extraction of one radial wood core by a Pressler increment borer (left) and polishing of the core (right).

The wood samples were visually cross-dated (Fig. 14). Tree ring width (TRW), EW and LW widths were separately measured by using Lintab-TSAP sliding-stage measuring device (Fig. 14). In Chapter II, TRW, EW and LW width series were additionally standardized and detrended by fitting 32-year long splines with a 50% cut-off frequency. In Chapter I, latewood intra-annual density fluctuations (IADFs) were also visually identified in all cross-dated cores under a binocular microscope (Fig. 14).

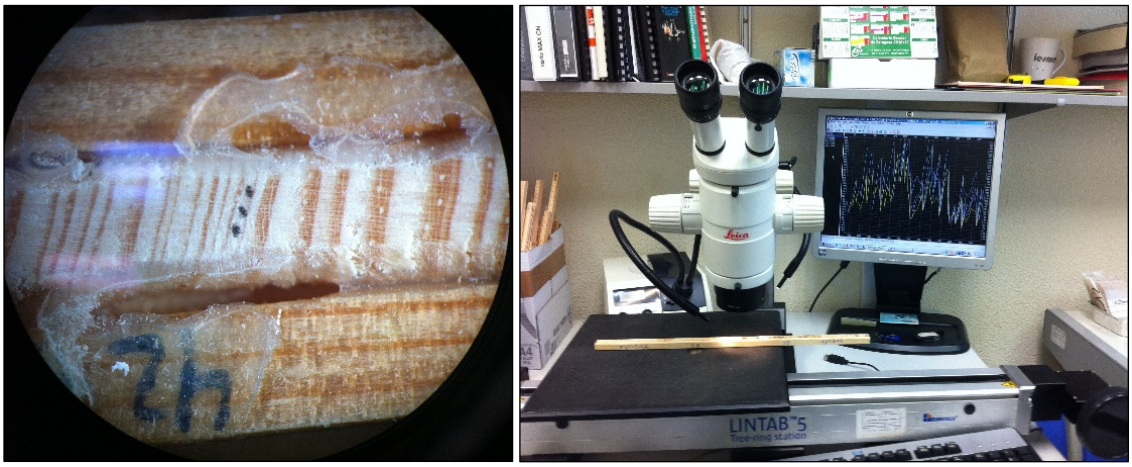

Figure 14: Visual cross-dating of wood samples and identification of latewood IADFs (left) and measuring of raw EW and LW widths by using Lintab-TSAP sliding-stage measuring device (right).

CHAPTER

1

LINKING FUNGAL DYNAMICS, TREE GROWTH AND FOREST MANAGEMENT IN A MEDITERRANEAN PINE ECOSYSTEM

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Linking fungal dynamics, tree growth and forest management in a Mediterranean pine ecosystem

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Abstract

Fungal dynamics are a key component of forest ecosystem functioning. Understanding the links between stand dynamics and mushroom productivity together with the impact of anthropogenic disturbance (i.e., forest management) is necessary to provide further insight into plant-soil interactions in forest ecosystems. The aim of this research was to shed light on the relationship between tree growth and mushroom yield of ectomycorrhizal (ECM) and saprobic fungi in a Mediterranean forest ecosystem. We hypothesized that: i) increased tree growth is linked to higher ECM mushroom yield arising from increased carbohydrate allocation to ECM fungi; ii) saprobic mushroom yield is less dependent on tree growth patterns; and iii) mushroom yields can be predicted based on certain wood-anatomical features. The study area was a Mediterranean *Pinus pinaster* forest located in northeastern Spain. Mushroom yield data were measured from 2008 to 2014 in 27 permanent plots within a thinning experiment. Dendrochronological analyses were conducted in each plot to characterize and quantify seasonal radial growth (earlywood and latewood width) and the frequency of latewood intra-annual density fluctuations (IADFs). Spearman correlation and "Gleichläufigkeit" (GLK) analyses were conducted to detect significant correlations and to quantify the synchrony between tree-ring features and ECM and saprobic mushroom yield patterns, the latter being used as a benchmark to better assess the relationships between tree growth and ECM fungi. To further inspect tree growth-mushroom yield relationships, mixed-effects models using dendrochronological variables as predictors were fitted to annual ECM and saprobic mushroom occurrence and yield data. We observed that the latewood IADFs frequency was the best predictor of ECM mushroom yield, i.e., better than early- or latewood width. The analysis also revealed that not only the precipitation of late summer and early autumn, but also forest thinning effects, were mediating the relationship between tree growth and ECM mushroom production. We found 2-year lagged effects between the current saprobic mushroom production and latewood width, whereas ECM mushroom yield was more correlated with current latewood production. The models presented in this study may be used to reconstruct mushroom production along historical periods based on dendrochronological information, but also to predict future mushroom yield based on climate-sensitive tree and stand growth predictions.

Keywords: forest dynamics; dendroecology; mixed models; non-wood forest products; mushroom; fungi

1. Introduction

Fungi play an important role in forest ecosystem functioning and, in turn, may be also affected by changes in forest growth and productivity (Egli et al., 2010). Ectomycorrhizal (ECM) fungi are crucial for nutrient and water uptake by trees and, therefore, they might mediate forest responses to environmental changes (Mohan et al., 2014; Orwin et al., 2011). In exchange for providing nitrogen and phosphorus to the host trees, ECM fungi get organic carbon compounds photosynthetically fixed by trees (Brundrett, 1991; Högberg et al., 2001; Tedersoo et al., 2010). On the other hand, saprobic fungi are crucial for soil nutrient cycling in forests, as they decompose carbon from coarse woody debris and leaf litter (Ferris et al., 2000; Rayner and Boddy, 1988).

In addition to these regulating and supporting ecosystem services, edible forest mushrooms (from both ECM and saprobic fungi) are important provisioning and cultural resources due to their socio-economic importance worldwide (Boa, 2004). Indeed, forest mushrooms are of significant importance for both recreation and trade (Gorriz-Mifsud et al., 2017; Martínez de Aragón et al., 2011), so that edible fungi are often more valuable than timber in low-productivity and drought-prone biomes such as Mediterranean forests (Palahí et al., 2009). Being mushrooms such valuable resources in Mediterranean forests, there is increasing interest to understanding what drives fungal dynamics (Tomao et al., 2017).

Forest stand structure and management, in addition to climate and site characteristics, can affect mushroom productivity and diversity (e.g., Bonet et al., 2008, 2010; Taye et al., 2016; Tomao et al., 2017). Therefore, it is important to know the relationships between the dynamics and management of fungi guilds. Previous studies have shown that forest thinning can increase the yield of certain ECM species (Bonet et al., 2012). Furthermore, a range of optimal stand characteristics (e.g., basal area, stand age) enhancing the productivity of some ECM species has been observed for some Mediterranean forest ecosystems (Bonet et al., 2010; Martínez-Peña et al., 2012; de-Miguel et al., 2014; Taye et al., 2016). All these previous findings reflect complex fungi-tree interactions that may be further mediated by climatic conditions (Primicia et al., 2016).

Although dendrochronology has been used to understand long-term interactions between forest growth and fungal production (Büntgen and Egli, 2014), research on the relationship between dendrochronological variables and mushroom yield is still scarce. Egli et al. (2010) found positive relationships between increased radial growth after thinning and both subsequent production of ECM and, to a lesser extent, saprobic fungi. Primicia et al. (2016) analyzed the relationship between seasonal wood formation (earlywood –EW hereafter– and latewood –LW hereafter– production) and fungal yields in different Mediterranean pine forests growing in xeric and mesic sites. The authors found some positive association between LW production and ECM yield in the most xeric sites, characterized by severe summer droughts followed by autumn rainfall episodes. Therefore, the aim of this research is to shed more light on the relationships between mushroom yield and tree radial growth by focusing on maritime pine (*Pinus pinaster* Ait.) plantations growing under Mediterranean climatic conditions. To achieve this, the following specific objectives were defined: (1) to analyse the interactions of both mushroom guilds with climate and dendrochronological variables under different thinning intensities, (2) to study lag-effects between current mushroom production and previous radial growth, and (3) to develop models capable of predicting saprobic and ECM mushroom yields based on

dendrochronological variables. We hypothesize that increased tree growth, mainly LW formation, is linked to higher ECM productivity as a result of higher carbohydrate allocation from the host trees to mycorrhizal fungi, whereas saprobic mushroom yield is less, and indirectly, dependent on tree growth. We also hypothesize that ECM and saprobic yields can be predicted considering particular wood-anatomical features reflecting rainfall variability in late summer and autumn. To this end, we quantify novel tree-ring information not considered in previous research, namely, the frequency of intra-annual density fluctuations (IADFs) observed in the latewood. These IADFs are characterized by the presence of earlywood-like tracheids (i.e. wide lumen and thin cell walls) within the latewood, and they are formed in response to humid conditions in late summer and early autumn (Vieira et al., 2009), being these weather conditions also a key driver of mushroom yield. Lastly, we also compare thinned and unthinned plots to disentangle the interactions between forest management, tree growth and fungal yield, by comparing the fruiting patterns between saprobic and ECM guilds.

2. Material and methods

2.1. Study area

The study was conducted in the Natural Protected Area of Poblet, Catalonia, Northeastern Spain (41° 21' 06.5" N and 1° 02' 25.8" E), at an altitude of 400-1201 m a.s.l. The average annual rainfall is 659 mm and the average annual temperature is 11.8 °C (data from L'Espluga de Francolí station, 41° 23' 47" N, 1° 06' 10" E, 412 m) with a summer drought lasting three months, typical of coastal Mediterranean climate (Ogaya et al., 2015). The natural vegetation is a *Quercus ilex* L. coppice forest with other woody species as *Arbutus unedo* L. and *Phillyrea latifolia* L. in the understory. The study area also contains many even-aged *P. pinaster* stands planted between 1963 and 1968.

2.2. Data collection

2.2.1. Mushroom productivity sampling

The sampling design consisted of 27 permanent mushroom inventory plots of 100 m^2 (10 m x 10 m), 14 of which were established in 2008 and did not undergo any thinning treatment, whereas the other 13 plots were established in the summer of 2009 representing different thinning intensities (from 28% to 71%). All plots were located in 50 - 55-year-old *P. pinaster* planted stands covering different aspects, altitudes, slopes, stand densities and basal areas (see their characteristics in Table 1). In order to avoid edge effects, these thinned plots were centred on larger thinning plots (40 m x 40 m). All trees within both control (unthinned) and thinned plots were inventoried and measured. Further details regarding the setting up of the plots and associated treatments can be obtained from Bonet et al. (2012).

From 2008 to 2014 in control plots and from 2009 to 2014 in thinned plots, all mushrooms (except parasitic fungi) were collected in each plot on a weekly basis throughout the autumn fruiting season, namely, from September to December. The fruit bodies were taken to the laboratory for identification at species level (otherwise, at genus level) and fresh weight measurements (see Martínez de Aragón et al. (2007) for further details about this procedure). Mushrooms were then classified into two functional groups according to their strategy to obtain carbon, based on expert knowledge and the existing literature (e.g.,

Agerer, 2006; Tedersoo et al., 2014): ectomycorrhizal (ECM) and saprobic fungi (including both wood and soil saprotrophs) (Table 1). Saprobic mushroom yield patterns were analyzed as a benchmark to better assess the hypothesized relationships between tree growth and ECM fungi, i.e., assuming that, opposite to ECM, saprobic mushroom yield is not related to tree growth as saprobes do not depend on the carbon allocation from host trees.

Table 1. Summary of the main data used concerning site characteristics, mushroom yield and dendrochronological variables. Values between brackets denote standard deviation. Data were obtained from 2008 to 2014 for control (unthinned) plots and from 2009 to 2014 for thinned plots.

				Basal area (m^2 ha^{-1})			Yield (kg ha^{-1})*		Width (mm)*		
Plot	Alt	Asp	Slo	Initial	After	Thinning	ECM	Saprobic	Earlywood	Latewood	IADFs (%)*
301	1010	110	19	77.84	77.84 (0.12)	–	70.23 (106.99)	18.51 (14.87)	0.74 (0.13)	0.22 (0.04)	16.54 (18.59)
303	903	20	19	49.68	49.68 (0.12)	–	86.90 (102.34)	15.68 (14.52)	0.60 (0.13)	0.24 (0.05)	24.06 (27.99)
304	879	360	22	35.30	35.30 (0.32)	–	14.59 (21.70)	6.41 (6.27)	0.83 (0.19)	0.19 (0.06)	6.25 (8.84)
305	744	90	18	61.91	61.91 (2.11)	–	71.20 (92.93)	19.24 (15.93)	0.81 (0.23)	0.27 (0.05)	24.06 (27.43)
306	759	40	23	59.78	59.78 (0.35)	–	105.15 (111.28)	25.90 (19.92)	0.66 (0.19)	0.27 (0.08)	27.93 (28.72)
307	796	60	18	36.07	36.07 (0.22)	–	56.79 (75.66)	39.85 (32.27)	1.00 (0.27)	0.24 (0.08)	20.71 (25.40)
308	835	65	15	32.30	32.30 (0.06)	–	91.47 (116.67)	38.23 (32.24)	0.91 (0.23)	0.27 (0.07)	27.14 (33.65)
309	852	20	13	31.53	31.53 (0.34)	–	27.55 (47.01)	9.96 (9.63)	0.69 (0.18)	0.28 (0.06)	26.94 (31.73)
311	594	360	3	21.01	21.01 (0.02)	–	124.81 (156.10)	14.93 (15.06)	1.99 (0.39)	0.43 (0.16)	42.86 (43.22)
312	633	10	23	30.97	30.97 (0.07)	–	170.49 (159.05)	20.21 (18.80)	0.91 (0.20)	0.35 (0.06)	26.81 (34.13)
313	609	340	5	42.53	42.53 (0.14)	–	23.48 (28.71)	16.34 (11.72)	0.81 (0.17)	0.28 (0.10)	22.22 (26.25)
314	612	10	8	30.10	30.10 (0.42)	–	81.77 (91.28)	14.22 (11.33)	1.64 (0.19)	0.39 (0.11)	37.50 (33.85)
315	626	260	23	40.66	40.66 (2.14)	–	0.56 (1.40)	46.21 (51.38)	1.22 (0.37)	0.29 (0.12)	27.24 (33.86)
316	644	30	3	34.02	34.02 (0.36)	–	22.80 (41.42)	12.60 (12.04)	1.05 (0.22)	0.33 (0.12)	30.78 (38.76)
301t	1010	110	19	60.11	29.23 (1.57)	54.86	21.21 (31.59)	11.22 (15.61)	1.03 (0.25)	0.44 (0.07)	46.83 (38.26)
302t	1013	135	22	53.65	41.37 (2.10)	28.12	69.53 (58.59)	14.68 (8.77)	1.10 (0.29)	0.32 (0.10)	35.76 (37.81)
303t	903	20	19	58.29	34.32 (2.39)	46.60	103.70 (199.99)	17.48 (22.07)	1.27 (0.43)	0.40 (0.12)	26.10 (31.76)
304t	879	360	22	47.15	28.68 (2.64)	46.68	52.05 (87.93)	16.35 (17.45)	1.72 (0.53)	0.43 (0.10)	32.50 (31.90)
305t	744	90	18	58.20	44.96 (4.25)	32.52	219.96 (170.16)	30.92 (32.20)	1.03 (0.26)	0.33 (0.08)	19.17 (17.15)
306t	759	40	23	54.09	24.83 (1.74)	58.39	61.84 (87.93)	12.22 (16.38)	1.45 (0.49)	0.40 (0.17)	42.50 (35.46)
307t	796	60	18	29.21	22.82 (2.05)	31.23	125.17 (170.16)	23.36 (18.42)	1.30 (0.35)	0.38 (0.13)	41.12 (38.10)
308t	835	65	15	32.30	22.54 (1.44)	36.18	52.58 (69.02)	24.26 (22.27)	1.25 (0.32)	0.36 (0.09)	35.00 (34.93)
309t	852	20	13	53.04	18.16 (2.12)	71.08	63.55 (90.22)	7.92 (5.77)	1.72 (0.42)	0.67 (0.14)	45.00 (36.47)
312t	633	10	23	47.54	41.29 (6.65)	31.82	174.01 (133.67)	16.57 (9.39)	0.81 (0.16)	0.32 (0.07)	37.62 (37.24)
313t	609	340	5	73.65	31.75 (3.12)	62.54	41.88 (44.95)	16.57 (13.56)	1.36 (0.43)	0.38 (0.10)	29.82 (29.48)
315t	626	260	23	61.22	49.76 (3.37)	26.07	19.33 (28.42)	18.67 (14.44)	1.26 (0.24)	0.37 (0.11)	33.33 (32.22)
316t	644	30	3	76.33	33.74 (3.05)	61.14	46.15 (42.62)	19.03 (14.64)	2.02 (0.41)	0.66 (0.26)	50.11 (43.05)

*Values are averaged by years (n=7 years in control plots, and n=6 years in thinned plots).

Note: Plots with letter 't' denotes thinned plot, otherwise control plot. 'Alt' is the altitude above the sea level, 'Asp' is the aspect, 'Slo' is the slope, 'BA' is stand basal area, 'ECM' stands for ectomycorrhizal fungi, and 'IADFs (%)' shows the frequency of latewood intra-annual density fluctuations.

2.2.2. Dendrochronological methods

In December 2014, 10 - 15 dominant trees representative of each plot were randomly selected for tree-ring measurements. Two radial cores per tree were extracted at 1.3 m above ground level using a Pressler increment borer. These cores were air-dried, mounted on wood boards, carefully polished and visually cross-dated. Afterwards, earlywood (EW) and latewood (LW) widths were measured with a precision of 0.01 mm by using Lintab-TSAP sliding-stage measuring device (F. Rinn, Heidelberg, Germany). In addition, the COFECHA software (Holmes, 1983) was used to verify the visual cross-dating by calculating correlations between tree-ring width series and the mean plot ring-width series. We used raw EW and LW data instead of detrended indices because: (1) no significant trends appeared during the study period (2008-2014), and (2) the raw data preserve the annual EW and LW year-to-year autocorrelation and variability (Primicia et al., 2016). Mean series of EW and LW widths were achieved by averaging annual values of all trees sampled within each plot (Table 1). Latewood IADFs were visually identified in all cross-dated cores under a binocular microscope, and then we computed their percent annual frequency by plot. This was calculated as the ratio of the number of cores showing IADF in a given year and the number of cores considered in that year (Campelo et al., 2013), and it was presented as a percentage.

2.2.3. Climate data

The DAYMET methodology (Thornton et al., 2000; Thornton and Running, 1999), implemented in the R package "meteoland" (De Cáceres et al., 2017) was used to interpolate plot-specific daily weather variables from Spanish meteorological stations [1990–2011], and from both stations of both the Spanish and Catalan Meteorological Services [1990–2015]. For each permanent plot, the daily precipitation, temperature and relative humidity values (min, max and mean) were estimated by averaging the values of several meteorological stations. The estimates were weighted according to the geographic proximity to a given plot, and were further corrected for the elevation differences between the meteorological stations and the plots. Further details concerning the method are described by Karavani et al. (2018).

2.3. Statistical analysis

First, Spearman correlations were computed among growth variables (EW, LW and IADFs), meteorological conditions (precipitation and temperature), site (altitude, aspect and slope) and stand characteristics (basal area), thinning intensity and mushroom productivity (i.e., mycorrhizal and saprobic fungal yields) to detect significant relationships between the variables of interest. Spearman partial correlations were also computed between LW and mushroom production controlling for meteorological conditions such as, for instance, the precipitation of September, because climate may be mediating the actual fungi – tree growth relationships. In addition to current-year tree growth patterns, lagged effects (ranging from 1 to 3 years) of previous EW or LW formation on current-year mushroom production were also considered in the analysis.

Furthermore, a "Gleichläufigkeit" (GLK) analysis between fungal yield and mean EW and LW series was conducted to further inspect their associations. GLK measures the trend

pattern of two compared curves and it represents the percentage of parallel agreement or accordance over the analyzed intervals. The GLK ranges from 1 (100% agreement) to 0 (no agreement) (Egli et al., 2010; Schweingruber, 1983). As in the partial correlation analysis, lagged effects ranging from 1 to 3 years were also tested in the GLK analysis in addition to current-year seasonal wood formation.

Since there were differences between plots (e.g. site, soil and forest variability) and, moreover, there were repeated measurements of the same plots over the years, a mixed-effects modeling approach (Pinheiro and Bates, 2000) was used to further inspect the relationships between tree growth patterns and mushroom yield. Plot identity was considered as a grouping factor, allowing the intercept to fluctuate randomly between plots. An autoregressive correlation structure of first order was evaluated to account for the repeated measures on the same plot. We did not include meteorological variables into the mushroom yield models because weather conditions are by far the main drivers of mushroom yield and, therefore, they may hide the relationships between tree growth data and mushroom yield. For the same reason, the effect of thinning (i.e., forest management) on mushroom yield – tree growth relationships was also inspected inasmuch as thinning changes the stand structure and affects the growth patterns of the trees associated to the fungi.

Due to the small size of inventoried plots and the intrinsic stochastic nature of sporocarp emergence, zero inflation due to zero annual mushroom yield values for ECM fungi was high in several plots. To deal with this issue, a two-stage modeling approach was applied for estimating annual ECM production, accounting for two different states (Hamilton & Brickell, 1983; de-Miguel et al., 2014). The first stage focused on estimating the probability of sporocarp emergence using logistic regression (Eq. 1) by means of a logit link function (Eq. 2) based on binomially distributed data with regard to the absence or presence of mycorrhizal mushrooms in a given year and plot (saprobic mushrooms were always present in all plots and years). The second stage aimed at estimating mushroom (ECM and saprobic) yield in log scale, conditional on the probability of occurrence, using linear mixed-effects models (Eq. 3). Snowdon' s bias correction factor (Snowdon, 1991) was used to correct the predictions for the back-transformation bias to the original scale.

Thus, mushroom yield predictions were obtained by multiplying the probability of occurrence by the yield conditional on the probability of occurrence (Eq. 4).

$$p(y=1\,|\,x)_{ij} = \pi(x) = \frac{1}{1+e^{-\left[(\alpha_0+a_{0i})+\alpha x_1\right]}} \qquad \text{Eq. 1}$$

$$g(x) = \log\left[\frac{\pi(x)}{1-\pi(x)}\right] = \left(\alpha_0 + a_{0i}\right) + \alpha x_1 \qquad \text{Eq. 2}$$

$$\ln\left(yield_c\right)_{ij} = \left(\beta_0 + b_{0i}\right) + \beta \ln\left(x_2\right) + \varepsilon \qquad \text{Eq. 3}$$

$$yield_{ij} = \pi(x) \times e^{\ln(yield_c)} \times CF \qquad \text{Eq. 4}$$

where $p(y=1/x)_{ij}$ is probability of mushroom occurrence in plot i and year j, $(yield_c)_{ij}$ is the yield (kg ha^{-1} yr^{-1}) conditional on occurrence of mushrooms (saprobic and ECM), $yield_{ij}$ is the predicted yield of both mushroom guilds (kg ha^{-1} yr^{-1}), α and β denote fixed-effects model parameters, a_0 and b_0 denote random effects, X_1 and X_2 are vectors of predictor variables, ε

is residual following a normal distribution with mean equal to zero and variance equal to σ^2, and *CF* is Snowdon's correction factor of the back-transformation bias.

2.4. Model evaluation

The following criteria were considered when evaluating the suitability of the models: consistency with current ecological knowledge, parsimony and robustness, statistical significance of parameters ($p \leqslant 0.05$ or $t \geqslant 2$), absence of bias, precision, homoscedasticity, normal distribution of residuals and absence of multicollinearity among independent variables. The root-mean-square deviation (RMSD) was calculated to quantify the differences between observed and predicted values. In addition, the receiver operating characteristics (ROC) curve and the corresponding area under the curve (AUC) were also computed to evaluate the predictive ability of the logistic model. All the analyses and models were conducted using R software 3.3.3 (R Core Team, 2014). Models were fitted using "glmer" functions belonging to "lme4" package (Bates et al., 2014).

3. Results

3.1. Relationships between mushroom yield, dendrochronological, climatic and management-related variables

The strongest positive significant relationship was observed between IADFs frequency and ECM mushroom yield and occurrence. Moreover, LW showed a significant positive correlation with the annual yield of ECM fungi, whereas EW showed a significant negative (but small) correlation with the annual yield of saprobic fungi (Fig. 1).

Only August and September precipitation showed a significant positive relationship with the yield of ECM fungi. Similarly, the occurrence of ECM mushrooms was significantly and positively correlated with the precipitation of August, September and October. On the contrary, the production of saprobic fungi did not show any significant correlation with any monthly precipitation variable.

Both EW and LW showed a significant negative relationship with stand basal area and slope, and a significant positive correlation with thinning intensity. Moreover, IADFs frequency and LW were both mainly correlated (positively) with the precipitation of August and September. However, only the mean temperature of October was negatively related to the frequency of IADFs, unlike the LW width.

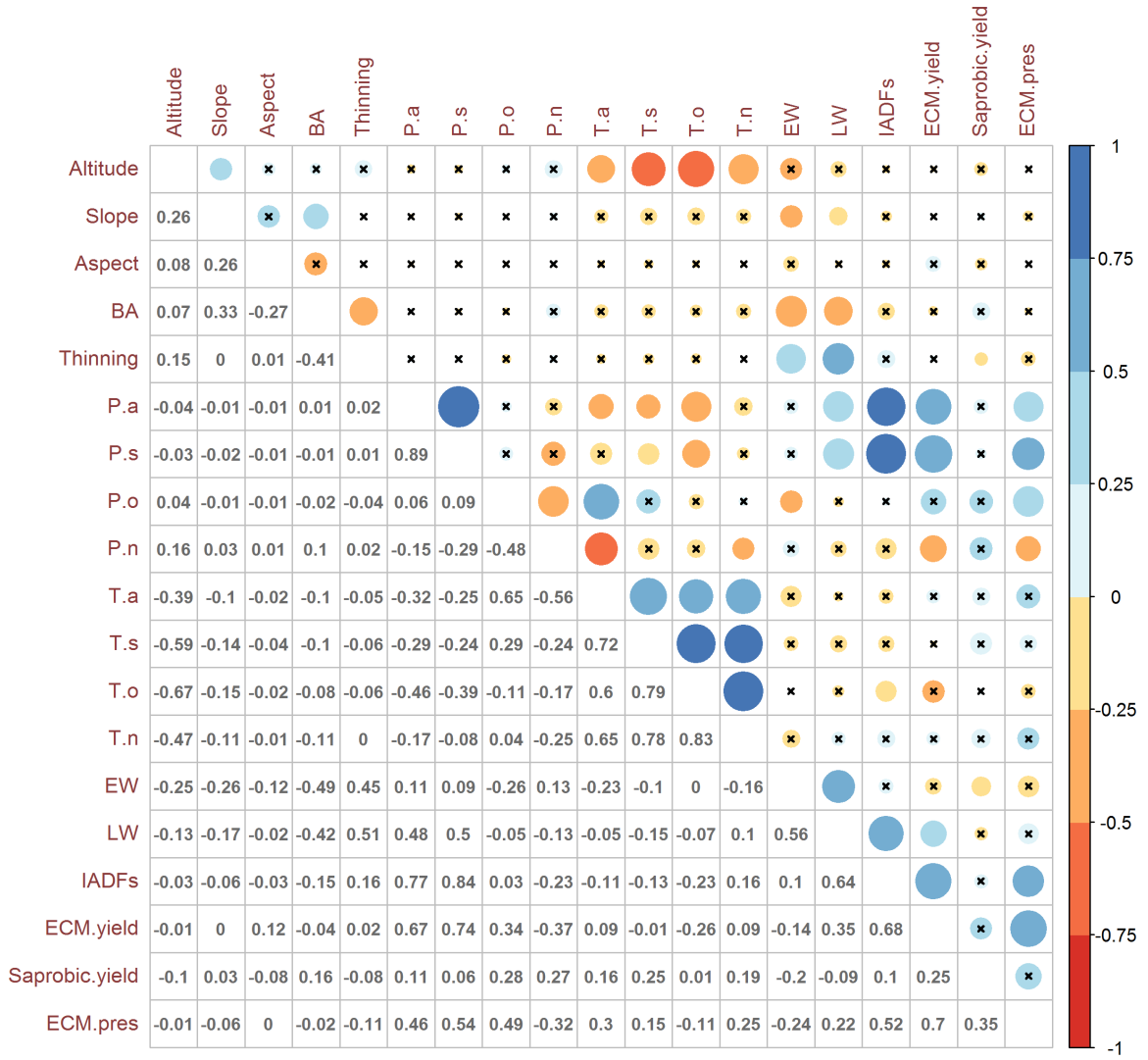

Figure 1: Spearman correlation matrix among the main variables involved in this study. At the top-right diagonal, correlations (range between 1 and -1) are shown by the circle size, whereas colours denote the correlation sign. At the bottom-left diagonal, correlation coefficients are shown. In the mushroom variables, the term 'yield' after Saprobic and ECM means mushroom yield, and 'pres' denotes a presence-absence of mushrooms. Concerning the climatic variables, 'P' denotes precipitation, 'T' is the mean temperature, 'a', 's', 'o', and 'n' denote August, September, October and November, respectively. 'Aspect' is the combination between the cosine aspect and the slope, 'BA' is stand basal area, 'Thinning' is the thinning intensity. Regarding growth variables, EW denotes the earlywood width, LW is the latewood width, and IADFs is the frequency of intra-annual densitity fluctuations. Crosses denote non-significant correlations (p value > 0.05).

Thinning had a strong, positive and immediate effect on ECM production (see years 2009 and 2010 in Fig. 2). The thinned plots whose treatment intensity was around 35%, reached the highest ECM mushroom productions. However, saprobic mushroom yield did not react to the thinning treatment and showed a more erratic pattern along time. Likewise, since thinning was conducted, both EW and LW production increased in the thinned plots as compared to the control (unthinned) plots (Fig. 3C and 3D). In addition, the thinned plots with low thinning intensity (equal to or lower than 30%) showed wider rings from 2009 to

2010 than those plots that were moderately thinned (i.e., thinning intensity between 31% - 50%), though they changed from 2011 (Fig. 2).

A positive relationship between LW width and ECM yield was observed for the interval 2008-2009 in control plots (Fig. 2). The same pattern was detected from 2011 to 2014 for both thinned and control plots. However, the thinned plots with high thinning intensity (i.e., equal or higher than 51%) showed better synchronies in this relation (even in the interval 2009-2010), i.e., when the ECM mushroom yield was high the LW width was also elevated. On the other hand, saprobic fungal yields were low in years when EW was high.

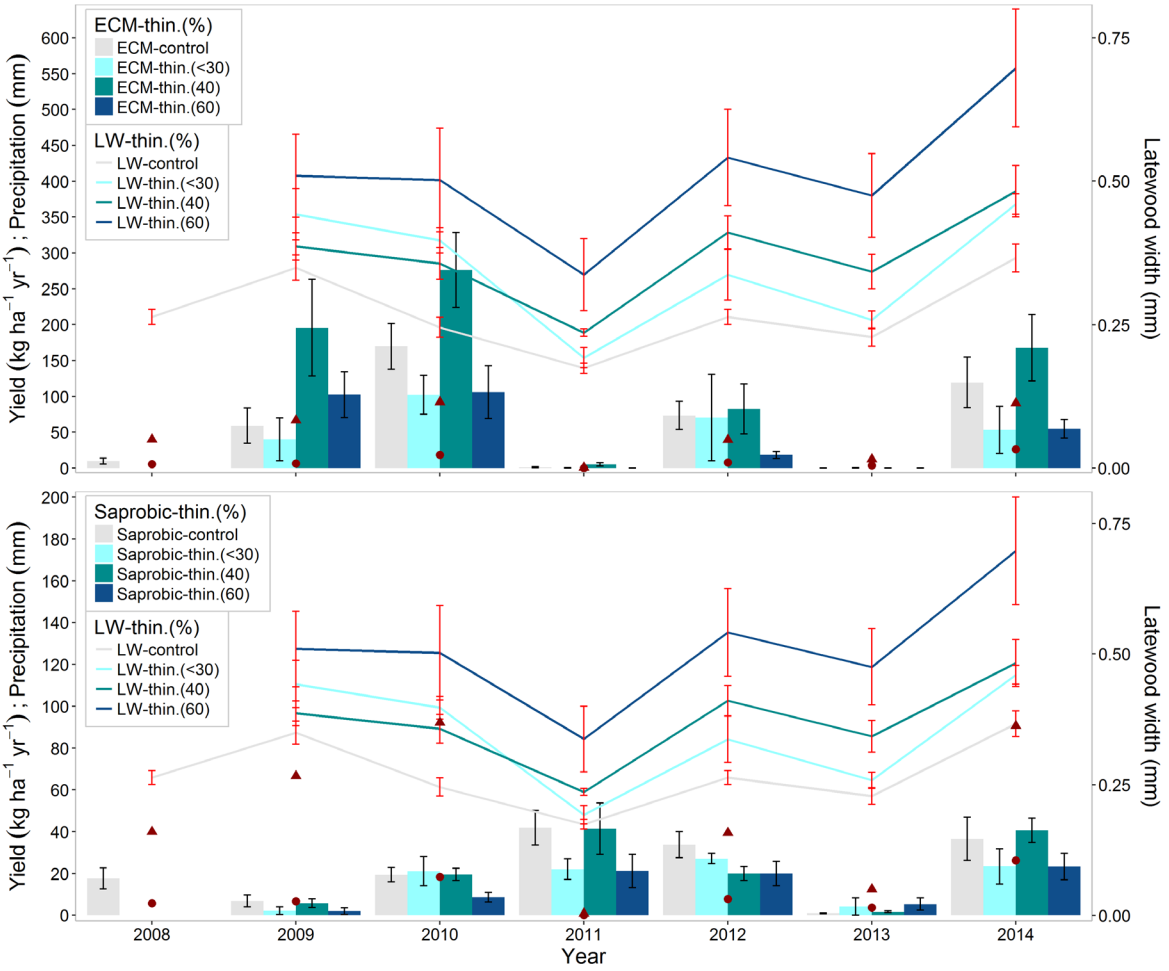

Figure 2: Ectomycorrhizal (ECM) and saprobic mushroom yield (bars, left y axes), and latewood (LW) production (lines, right y axes) of P. pinaster trees in control (unthinned) and thinned plots from 2008 to 2014. Thinned plots are classified into three thinning intensity ranges: "<30" covers thinned plots equal or lower than 30%, "40" covers thinned plots between 31% and 50% (both inclusive), and "60" covers thinned plots equal or higher than 51%. Brown dots denote precipitation of August and brown triangles indicate precipitation of September. Error lines denote the standard error of mean.

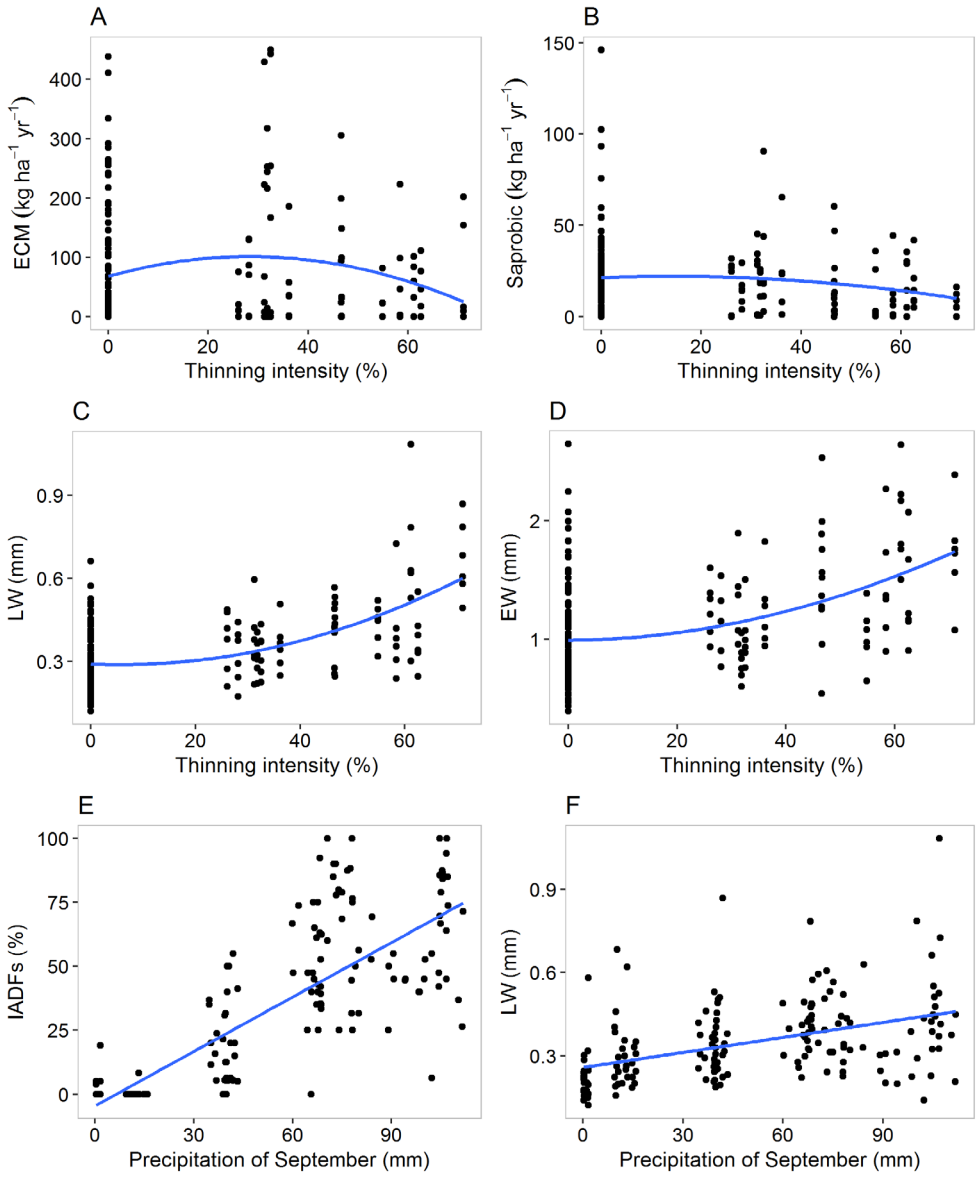

Figure 3: Effect of: (1) thinning intensity on the yield of both mushroom guilds (saprobic and ectomycorrhizal 'ECM') (A, B), as well as on the seasonal wood formation (earlywood –EW– and latewood –LW– widths) (C, D); and (2) precipitations of September on the frequency of IADFs and LW (E, F). Blue lines denote best fit regression lines.

ECM production showed a closer relationship with the frequency of IADFs (Figure. 4) than with LW width (Figure 2). For instance, for the interval 2009-2010, the frequency of IADFs was high in the control plots when ECM production was also elevated, while LW width was low. On the other hand, the influence of thinning on the frequency of IADFs showed a changing pattern over time (Figure 4). Thus, prior to thinning, similar IADFs frequencies were observed in all plots, being slightly higher in the control plots. However, from the thinning treatment conducted from year 2009 onwards, thinned plots showed higher frequency of IADFs than the control plots.

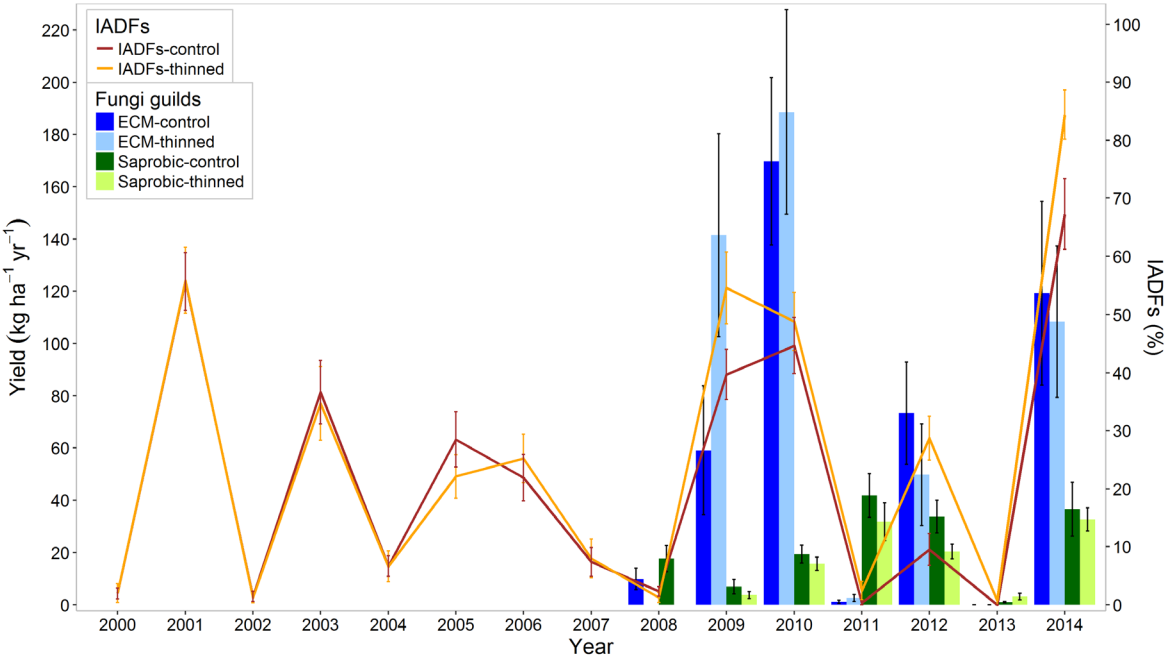

Figure 4: Ectomycorrhizal (ECM) and saprobic mushroom yields (bars) from 2008 to 2014, and frequency of latewood intra-annual density fluctuations (IADFs, lines) formed from 2000 to 2014 in *P. pinaster* trees sampled in control (unthinned) and thinned plots. Error lines denote the standard error of mean.

3.2. Time lags between tree growth and mushroom yield

Lagged effects concerning the relationship between LW and mushroom production were found with contrasting trends between the two functional fungal guilds (Figure 5). Spearman correlations revealed that the strongest relationship between current ECM mushroom yield and LW width was a positive correlation at time lag 0 (i.e., current year growth), while the highest correlation (positive) with saprobic fungi occurred at a time lag of 2 years (Fig. 5A). Similar results were obtained from GLK analysis (Fig. 5C). Interestingly, differences with these results were found when computing Spearman partial correlations, i.e. controlling for the correlation with a third variable (Fig. 5B). Namely, when controlling for the precipitation of September, the correlation between ECM mushroom yield and LW width showed different patterns depending on the time lag, whereas partial correlations between saprobic fungi and seasonal wood formation remained almost unchanged compared to the standard Spearman correlations. Both saprobic and ECM mushroom yield showed the strongest partial correlation with LW width at time lag 2, i.e. two years prior to the current mushroom production (Fig. 5B).

Notwithstanding, some discrepancies regarding both Spearman correlation types ("standard" and partial) were observed when the relationship between mushroom production and LW width was evaluated by including the effect of forest management treatment (i.e. thinning *versus* control plots), while GLK results remained almost the same. For instance, the strongest Spearman correlation observed between ECM fungi and LW production in thinned plots was negative and at time lag 3. On the other hand, when the precipitation of September was introduced as a mediating variable, the strongest correlation between ECM fungi and LW in thinned plots occurred at time lag 1, also with negative sign.

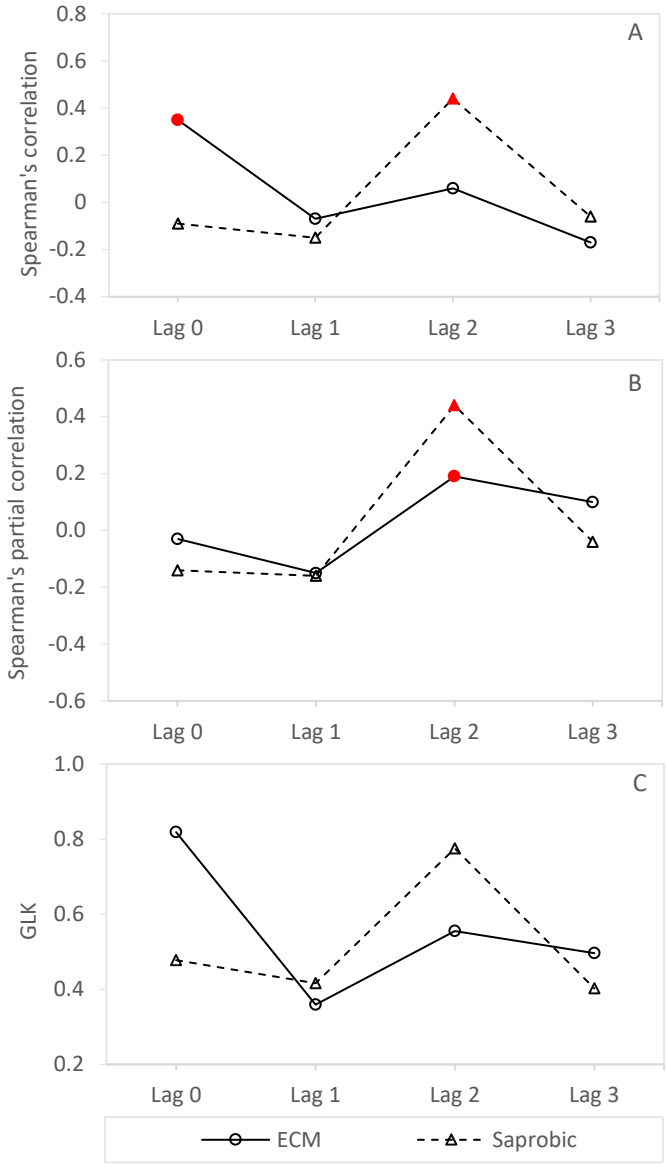

Figure 5: (A) Spearman correlations calculated by relating latewood width (LW) and ectomycorrhizal (ECM) and saprobic mushroom yield. (B) Spearman partial correlation between LW and mushroom yield controlling for the effect of the precipitation of September. (C) "Gleichläufigkeit" (GLK) analysis between LW and mushroom yield. Correlations and GLK were computed for both fungi guilds (saprobic and ectomycorrhizal fungi) with time lags up to 3 years (Lag 0 to Lag 3 years). For Spearman correlations figures, red markers denote the highest significant correlation (p value $\leqslant 0.05$) for each fungi guild.

3.3. Mushroom yield – tree growth models

The fitted models for ECM and saprobic fungi yields were as follows:

$$p(y_{ij}=1)=\frac{1}{1+e^{-\left(\alpha_0+a_{0i}+\alpha_1\ln\left(IADFs_{ij}+0.01\right)\right)}} \quad \text{Eq. 5}$$

$$\ln\left(ECM_{ij}\right)=\beta_0+b_{0i}+\beta_1\sqrt{LW_{ij}}+\beta_2\sqrt{IADFs_{ij}}+\beta_3\sqrt{LW_{ij}IADFs_{ij}}+\varepsilon_{ij} \quad \text{Eq. 6}$$

$$\ln\left(sapro_{ij}\right)=\beta_4+b_{1i}+\beta_5 LW_{2ij}+\beta_6\sqrt{LW_{2ij}}+\beta_7\ln\left(IADFs_{ij}+0.01\right)+\beta_8\ln\left(EW_{ij}\right)+\varepsilon_{ij} \quad \text{Eq. 7}$$

where $p(y=1/x)$ is probability of mushroom occurrence in plot i and year j, ECM and $sapro$ are, respectively, ectomycorrhizal and saprobic mushroom yield conditional on mushroom occurrence (kg ha^{-1} yr^{-1}), α_0 and α_1 and β_0 to β_8 are fixed effects, a_{0i} and b_{0i} denote random plot effects, $IADFs_{ij}$ is the frequency of intra-annual density fluctuations (%), LW_{ij} is the current latewood width, LW_{2ij} is latewood two years before current mushroom yield (Lag 2) (mm), EW_{ij} is current earlywood width (mm), and ε_{ij} is residual.

The probability of occurrence in the ECM model (AUC = 0.93) was positively correlated with the frequency of IADFs (Eq. 5). The ECM yield conditional on occurrence model (residual variance 2.250, plot random effects variance 1.676) includes the positive influences of IADFs and LW variables that are interacting with each other (Eq. 6). The RMSD of ECM yield estimates was 96.15 kg ha^{-1} yr^{-1}.

The model for saprobic mushroom yield (residual variance 1.746, random effects variance 0.473) showed significant increasing-decreasing trend for LW_2, indicating that extreme LW widths of 2 years of lag might cause a reduction in the saprobic yield (Fig. 6). In addition, the frequency of IADFs was positively correlated to saprobic yields, whereas EW had a negative influence on the saprobic yield. The RMSD of the saprobic yield model after correcting for the back-transformation bias was 22.2 kg ha^{-1} yr^{-1}.

The information concerning the mushroom yield models (kg ha^{-1} yr^{-1}) of both ECM and saprobic fungal guilds based on dendrochronological predictors and the uncertainty of their estimates, is presented in Table 2 together with the information regarding the model for the probability of occurrence of ECM mushrooms. The effect of each predictor on the production of both ECM and saprobic mushroom yield is shown in Fig. 6.

Table 2: Fixed parameter estimates (α and β) of the models describing the relationship between mushroom yield and tree growth predictors, and the Snowdon's bias correction factors (CF).

Model	Eq.	Parameters	Estimate	Std. error	t-value	p-value
Probability of occurrence of ECM	5	α_0	1.833	0.337	-	0.000
		α_1	0.434	0.088	-	0.000
ECM yield	6	β_0	-3.380	1.629	-2.076	-
		β_1	8.363	3.139	2.665	-
		β_2	1.169	0.214	5.468	-
		β_3	-1.348	0.383	-3.524	
		CF	1.358	-	-	-
Saprobic yield	7	β_4	-9.651	2.608	-3.700	-
		β_5	-18.375	7.413	-2.479	-
		β_6	31.860	8.887	3.585	-
		β_7	0.078	0.036	2.166	-
		β_8	-1.248	0.335	-3.730	
		CF	1.467	-	-	-

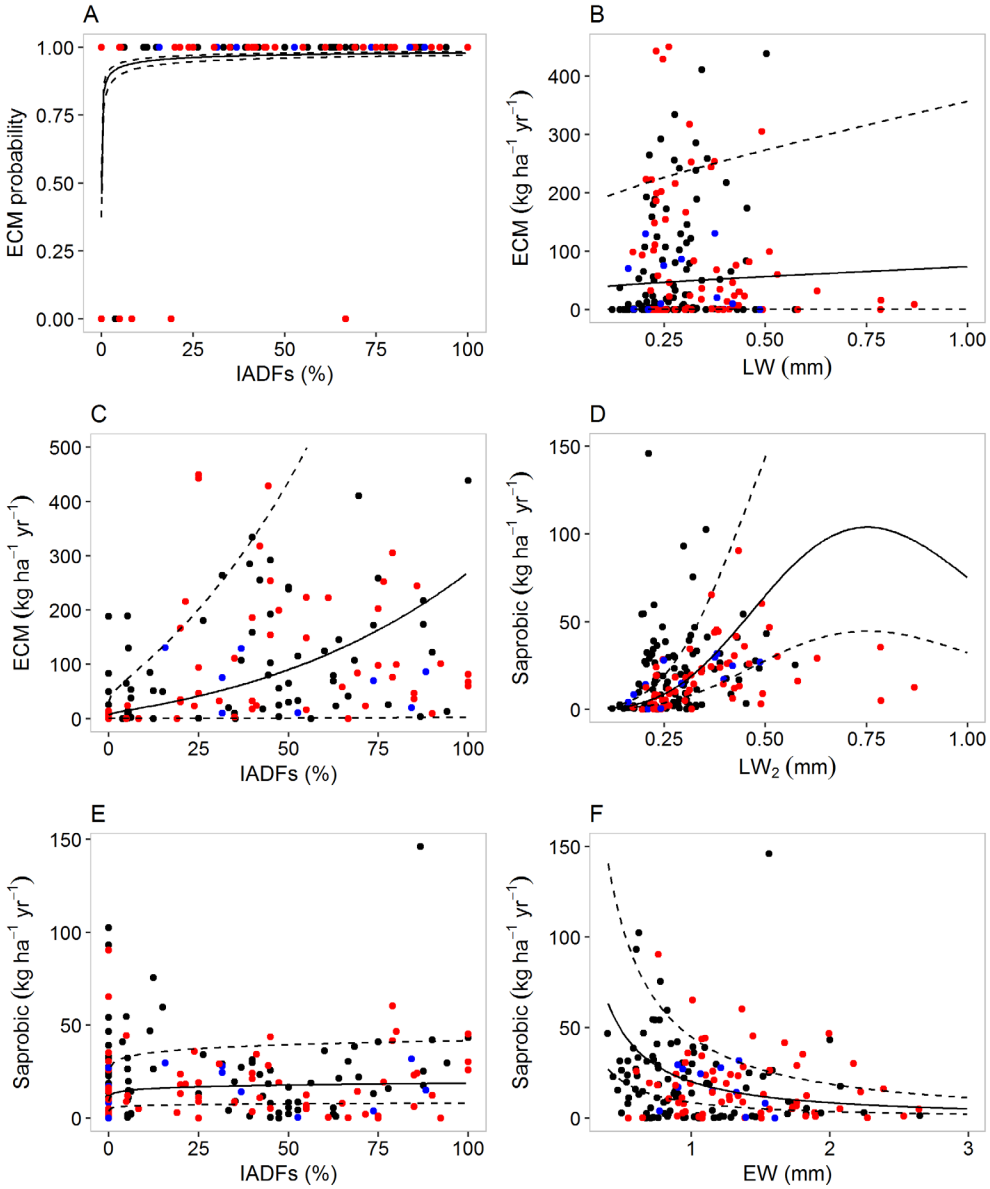

Figure 6: Effect of dendrochronological predictors on mushroom yield of saprobic and ectomycorrhizal fungi. *ECM probability* is the probability of occurrence of ectomycorrhizal mushrooms, *ECM* is ectomycorrhizal fungi yield, *LW* is the current latewood width, *IADFs* is the frequency of latewood intra-annual density fluctuations, *EW* is the current earlywood width, and LW_2 is the latewood width with a 2-year lag. Black dots denote control (unthinned) plots, blue dots denote thinned plots with intensity equal or lower than 30%, and red dots denote thinned plots with intensity higher than 30%. The values assigned to the predictors in the simulation correspond to the mean values in the modeled data. The solid line is simulated with random effects equal to zero and the dashed lines represent the plots with the highest and lowest random parameters.

4. Discussion

4.1. Relationship between dendrochronological variables and ECM mushrooms

Our findings point out the suitability of using latewood IADFs frequency to predict mushroom (saprobic and ECM) production in drought-prone Mediterranean environments, as well as a significant relationship between ECM and LW production, being IADFs frequency a better predictor of ECM production than LW. Actually, tree growth (in particular EW formation) under such Mediterranean climate is improved by mild and wet meteorological conditions in spring and summer, whereas mushrooms yield is enhanced by wet late-summer and autumn conditions, which favor IADF formation in the latewood during the late growing season (Primicia et al., 2016). Namely, the starting point of the mushroom fruiting season in late summer is associated to the maximum LW growth rates and the occasional formation of latewood IADFs as a response to summer/autumn storms. In this sense, Pasho et al. (2012), Mazza et al. (2014) and also Primicia et al. (2016) observed the positive response of LW to precipitation from late summer to early autumn in Mediterranean pine forests. Likewise, it has been demonstrated that *P. pinaster* is a very sensitive pine species to precipitation, and that this climate variable plays a major role in driving IADF formation (Rozas et al., 2009; Zalloni et al., 2016).

The proportion of IADFs was the most significant variable when predicting both the probability of ECM occurrence model and the yield of ECM fungi, due to its close relationship with the precipitation of September (Figure 3E), which also enhances mushroom fruiting. This agrees with previous findings, such as Bonet et al. (2012) also found that the most significant factors predicting the annual yield of *Lactarius deliciosus* group mushrooms in *P. pinaster* forests was the precipitation during August and September, apart from thinning intensity. Since September precipitation is partly mediating the mushroom–LW relationship, only Spearman partial correlations were able to show the underlying relationship between mushroom production and tree radial growth, unlike the GLK function used here and also by Egli et al. (2010). It is therefore not surprising that the GLK function showed the same results as those obtained by the standard Spearman correlations without controlling for a third climatic variable. In contrast to previous research conducted by Egli et al. (2010) and Büntgen et al. (2013) in more mesic forests from Switzerland, tree growth in our study area is limited by water availability (typical of Mediterranean ecosystems). In this regard, Büntgen et al. (2015) mentioned that a positive relationship between tree growth and mushroom yield may indicate reduced carbon allocation to the fungi under such xeric, water-limited growing conditions, whereas this relationship may turn vaguer under mesic conditions. This may explain the different results obtained between our standard and partial correlation analysis for the ECM mushroom yield-LW relationship when controlling for the precipitation of September, the latter being the main driver of mushroom yield in the study area (Karavani et al., 2018). Moreover, although previous research found temperature to be also a driver of fungal fruiting (Martínez-Peña et al., 2012; Martínez de Aragón et al., 2007; Primicia et al., 2016), we did not find any significant correlation with that climate variable. This may be due to the fact that mushroom emergence may be more sensitive to daily extreme temperatures than to mean monthly values (Karavani et al., 2018), and also because the effect of temperature may be more limiting in colder environments, as mentioned by Taye et al. (2016). Forest

management (i.e. thinning intensity) also acted as a mediating factor in the tree growth-mushroom yield relationship, in such a way that the LW – ECM mushroom yield relationship was positive in those plots under low to moderate thinning intensities (i.e. around 30% in stand basal area). This thinning intensity caused a considerable immediate increase on ECM production (at least in some species) (Bonet et al., 2012), whereas saprobic fungi did not react to tree removal (Figure 3B). However, this relationship was negative in plots more heavily thinned (Fig. 3A and 3C), and consequently, LW formation was negatively correlated with ECM mushroom production, which may be explained by the effect of strong thinning on the trade-off between ECM fungi production and LW formation. Namely, the remaining trees of the plots that were strongly thinned increased their radial growth because of the reduced competition for water and nutrients, while the ECM fungi may be strongly affected by a drastic decrease in the number of host trees, resulting in reduced mushroom yield. Indeed, the remaining trees from the thinned plots could have allocated more carbohydrates to the associated fungi, as a result of colonization and trophic strategies of a few species.

The relationship between ECM mushroom production and LW width may not be completely obvious due to several factors: (i) some ECM fungi may be able to behave as saprobic fungi and obtain carbon not only from carbohydrates derived from the photosynthesis of the host trees, but also from the decomposition of organic matter (Talbot et al., 2008), (ii) the carbon allocated from the host tree to ECM may not necessarily be invested to promote mushroom fruiting but to mycelium growth belowground (Diez et al., 2013), and (iii) other covariables such as the host tree physiology (e.g. shifts in the priority of carbon sinks), the competition among host trees and the influence of the understory may also intervene. Even though it is complex to distinguish the different effects interacting on fungal fructification, our results contribute to shedding light on these relationships based on the thinning treatment carried out in 2009.

4.2. Relationship between dendrochronological variables and saprobic mushrooms

The saprobic mushroom yield model resulted in an unexpected effect of LW_2 formation on saprobic mushroom yield, that could reflect the effect of changing micro-climatic conditions as a consequence of high-intensity thinning (Figure 3C), such as the difference in temperature between control and thinned plots, and the potential increased litter supply resulting from increased biomass production in trees experiencing higher growth, as Egli et al. (2010) noted. The lagged effect of two years may lie in the fact that the litter follows a decomposition process that may take some time until the saprobic fungi can use it for sexual reproduction (Straatsma et al., 2001). Surprisingly, EW was another predictor variable involved in the saprobic mushroom yield model, negatively related to mushroom production (Figure 6F). The explanation could lie in climatic drivers since EW is positively linked to high spring precipitation, which is negatively correlated with autumn precipitation in the study area, as Karavani et al. (2018) and Primicia et al. (2016) previously observed. In addition, this is in agreement with the fact that the precipitation of September is associated to latewood IADFs frequency as well as to the saprobic mushroom production (Fig. 3E). Furthermore, our results do not show clear relationships between saprobic mushroom production and any monthly precipitation, in contrast to Primicia et al. (2016),

who found higher sensitivity of saprobic fungi to weather conditions compared to ECM in Mediterranean pine forests. The reason behind this might be that saprobic fungi were more sensitive to occasional weather events along the fruiting season, as long as the temperature and moisture conditions suitable to decomposition processes carried out in the top layers of the soil are met. Besides, in this study we used a dataset of meteorological conditions much more accurate than in the aforesaid previous research (i.e., interpolated data from a grid of local meteorological stations).

5. Conclusions

This study provides further insights into the linkages between tree growth and mushroom production. In spite of the strong effects of weather factors mediating these relationships, we have observed the appropriateness of using the information from latewood formation and, in particular, IADFs frequency to glimpse the responses of ECM mushroom production in relation to changes in forest growth and to forest management practice. The observed association between ECM production and latewood IADFs becomes more evident in drought-prone environments where tree growth and mushroom yield are driven by late-summer and early autumn water availability. In addition to shedding more light on the relationship between forest tree and fungal dynamics, the models presented in this study may be also used to reconstruct past mushroom production based on dendrochronological information, but also to predict future mushroom yield based on climate-sensitive tree and stand growth projections.

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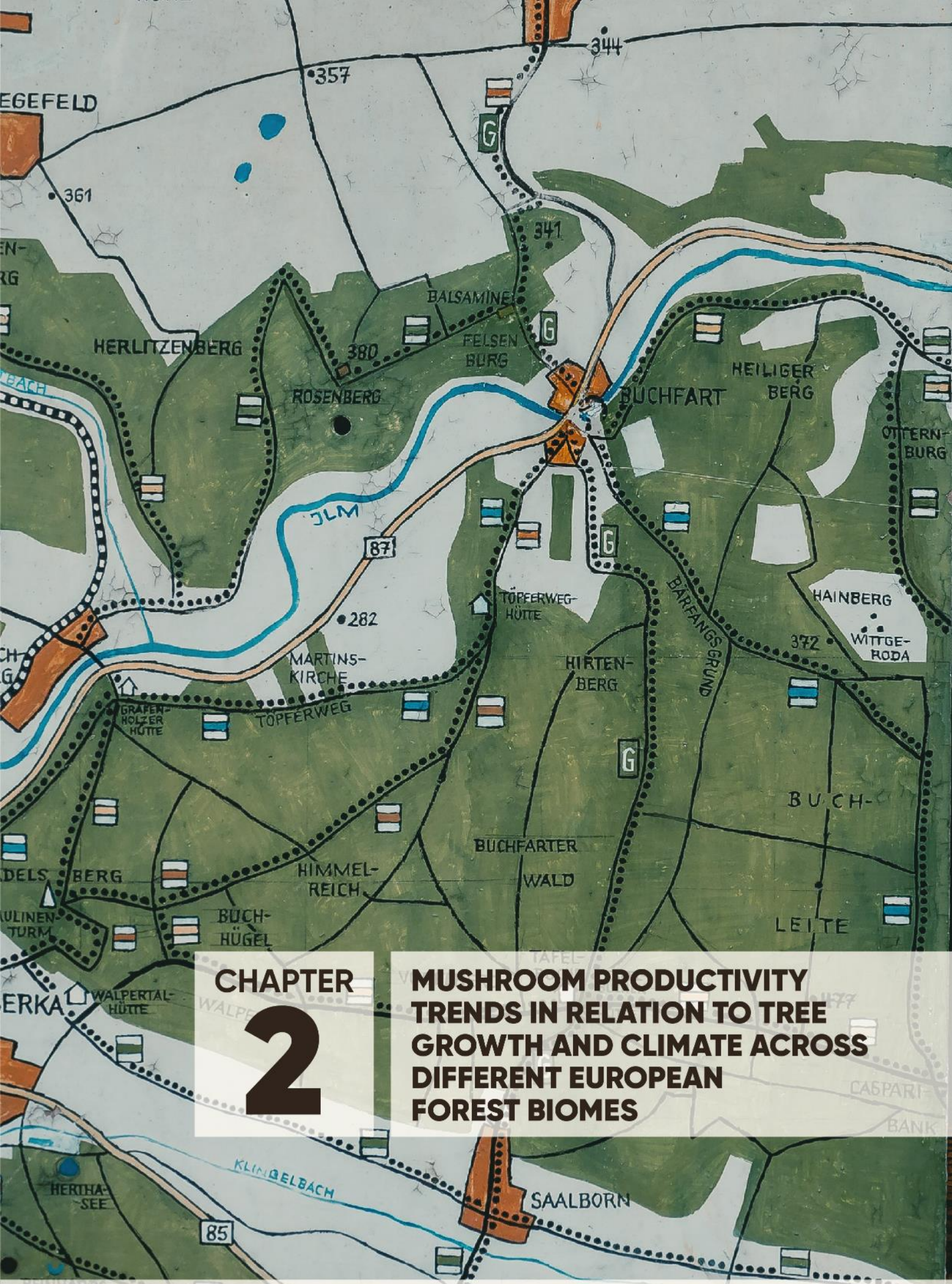

CHAPTER 2

MUSHROOM PRODUCTIVITY TRENDS IN RELATION TO TREE GROWTH AND CLIMATE ACROSS DIFFERENT EUROPEAN FOREST BIOMES

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Mushroom productivity trends in relation to tree growth and climate across different European forest biomes

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Abstract

Although it is logical to think that mycorrhizal mushroom production should be somehow related to the growth of the trees from which the fungi obtain carbohydrates, little is known about how mushroom yield patterns are related to tree performance. In this study, we delved into the understanding of the relationships between aboveground fungal productivity, tree radial growth patterns and climatic conditions across three latitudinally different bioclimatic regions encompassing Mediterranean, temperate and boreal forest ecosystems in Europe. For this purpose, we used a large assemblage of long-term data of weekly or biweekly mushroom yield monitoring in Spain, Switzerland and Finland. We analyzed the relationships between annual mushroom yield (considering both biomass and number of sporocarps per unit area), tree ring features (tree ring, earlywood and latewood widths), and meteorological conditions (i.e. precipitation and temperature of summer and autumn) from different study sites and forest ecosystems, using both standard and partial correlations. Moreover, we fitted predictive models to estimate mushroom yield from mycorrhizal and saprotrophic fungal guilds based on climatic and dendrochronological variables. Significant synchronies between mushroom yield and climatic and dendrochronological variables were mostly found in drier Mediterranean sites, while few or no significant correlations were found in the boreal and temperate regions. We observed positive correlations between latewood growth and mycorrhizal mushroom biomass only in some Mediterranean sites, this relationship being mainly mediated by summer and autumn precipitation. Under more water-limited conditions, both the seasonal wood production and the mushroom yield are more sensitive to precipitation events, resulting in higher synchrony between both variables. This comparative study across diverse European

forest biomes and types provides new insights into the relationship between mushroom productivity, tree growth and weather conditions.

Keywords: fungi, long-term data, mixed models, functional guilds, dendroecology, biomes

1. Introduction

Fungi represent a key component in forest ecosystem functioning (Hawksworth and Lücking, 2017). The ecological functions of fungal communities include among others decomposition and nutrient cycling, symbiosis with plants and pathogenic interactions with animals and plants (Stokland et al., 2012; Van Der Heijden et al., 2015). In addition, fungi are increasingly recognized for their contribution to economic, social and cultural values (Boa, 2004; Gorriz-Mifsud et al., 2017; Martínez de Aragón et al., 2011). Fungi are classified into different functional guilds according to their strategy to obtain carbon. While saprotrophs decompose dead organic matter (Rayner and Boddy, 1988), mycorrhizal fungi acquire carbon from host plants in exchange for nutrients and water (Högberg et al., 2001; Smith and Read, 2008). Therefore, the interaction between forest and fungal functional diversity and productivity depends on the fungal guild, as well as on the quality and quantity of carbon resources (Gao et al., 2013; Peay et al., 2013). This varies among biomes, i.e., regions characterized by different major types of natural vegetation driven by a particular set of climatic and soil conditions (Lomolino et al., 2010).

Many factors can influence the mushroom diversity and productivity, such as forest stand structure, site characteristics and management. Indeed, thinning and burning have widely shown a positive effect mostly on specific ectomycorrhizal mushroom productivity under different biomes (e.g. Mediterranean and temperate) and ecosystem types (e.g. pine woodlands and scrublands) (Bonet et al., 2010, 2012; Egli et al., 2010; de-Miguel et al., 2014; Hernández-Rodríguez et al., 2015a), while the effect of management on saprotrophic productivity has proved to be more erratic across forest biomes (Collado et al., 2018; Kim et al., 2010). However, climate is the main key driver of fungal fruit body emergence and yield, acting as a limiting or mediating factor depending on local conditions (Büntgen et al., 2012). Hence, in temperate forest ecosystems, mushroom production is greatly driven by temperature (Büntgen et al. 2013; Sato et al., 2012). The same has been found in boreal ecosystems, where the mushroom productivity season is narrower than in temperate or Mediterranean forests (Ohenoja, 1993; Tahvanainen et al., 2016). However, in drought-prone Mediterranean biomes, precipitation-temperature interactions may be the main limiting factor for tree growth and fungi yield since high evapotranspiration rates may reduce soil water availability (Büntgen et al., 2015; Karavani et al., 2018; Martínez de Aragón et al., 2007; Primicia et al., 2016; Salerni et al., 2002). There are also lagged-effects between climate variables and mushroom fruiting (Krebs et al., 2008; Yang et al., 2012), given by a hierarchy of resource allocations in the trade-off between mycelia growth and sporocarp production (Deacon and Fleming, 1992; Gardes and Bruns, 1996).

In this framework, dendroecology has been proved to be a powerful tool for inferring long-term carbon allocation process from the host tree to the associated mycorrhizal mushroom (Büntgen and Egli, 2014), and the coupling between climate conditions, radial growth and mushroom production (Büntgen et al., 2015; Büntgen and Egli, 2014). In this sense, a

pioneer study, conducted in a Swiss beech forest, revealed a clear relationship between annual tree growth (i.e. tree-ring width) and fruit body numbers, particularly of mycorrhizal fungi, after forest thinning intervention (Egli et al., 2010). Other works carried out in different Mediterranean pine forests of Catalonia (Collado et al., 2018; Primicia et al., 2016) deepened this knowledge by inspecting the intra-annual growth variability in trees considering earlywood (EW) formation that arises from carbohydrates synthesized from the previous year and current spring, and latewood (LW) that is mostly formed by current-year photoassimilates (Kagawa et al., 2006). The current-year photosynthates formed by trees seem to have a strong influence on the production of mycorrhizal mushroom fruit bodies (Högberg et al., 2008) and, therefore, LW formation and mushroom yield might be synchronized. However, this synchrony is also highly influenced by the climatic conditions (e.g. the autumn precipitation in drought-prone regions) that affect both LW and mushroom productions. Previous research carried out along different woodlands in Spain (Collado et al., 2018; Primicia et al., 2016) have suggested that LW formation and mycorrhizal fungi yields are linked in Mediterranean pine forests, whereas correlations between seasonal wood formation and saprotrophic mushroom production were weaker, reflecting the absence of a direct symbiotic relationship between trees and saprotrophic fungi. Notwithstanding, all previous research on this topic has been conducted in isolation at local to regional scales in Mediterranean and temperate forest ecosystems, and omitting some other relevant biomes such as the boreal forests.

While previous research has been devoted to studying fungal communities throughout Europe (e.g., Andrew et al., 2017; Heegaard et al., 2016; Kauserud et al., 2010, 2008; Shi et al., 2014; Tedersoo et al., 2012), little is known about the influence of different latitudes and biomes on mushroom productivity in relation to tree growth, largely due to the lack of large, long-term datasets of multiple spatio-temporal observations of tree growth and sporocarp production.

Here, we studied the effects of climate conditions on both mushroom biomass and sporocarp density (i.e. number of sporocarps per unit area) as related to tree radial growth across different European bioclimatic regions based on long-term data. The time overlap between both mushroom and dendrochronological dataset ranged from 6 to 32 years. We hypothesize that: (1) climate has different effects on the relationship between mushroom production and tree growth (particularly LW width) in different bioclimatic regions, expecting to find stronger linkages in water-limited forest ecosystems; and that (2) this relationship also varies between functional guilds, i.e. mycorrhizal and saprotrophic fungi. We expect stronger correlations between tree growth and the yield of mycorrhizal species than with saprotrophic species which are hypothesized to be less coupled to tree growth.

For this purpose, we studied the relationships among tree ring features (tree-ring width, EW and LW widths), climate conditions and mushroom production across different European forest biomes including boreal (Finland), temperate (Switzerland) and inland and coastal Mediterranean forests (Spain). The mushroom production data considered both mushroom biomass and sporocarp density in boreal and Mediterranean regions, whilst we only measured sporocarp density in temperate biome. The inventory plots (or "permanent stands" in this study) of Spain included different pine species as dominant tree, while the Finnish stands were composed of one dominant tree (*Pinus sylvestris*). In contrast, the permanent stands of Switzerland included a mixed forest of deciduous and coniferous trees

(mostly *Fagus sylvatica*). Lastly, we used statistical models to predict mycorrhizal and saprotrophic mushroom biomass, as well as sporocarp density, based on dendrochronological tree-growth variables.

2. Material and methods

2.1. Mycological data collection

We used a database of 111 permanent stands, both pure and mixed stands, dominated by European beech (*Fagus sylvatica* L.) or pine species (Scots pine, *Pinus sylvestris* L.; Black pine, *Pinus nigra* Arn.; Maritime pine. *Pinus pinaster* Ait.; Aleppo pine, *Pinus halepensis* Mill.) across different latitudes from Finland through Switzerland to Spain (Fig. 1). This database has been used in previous studies (references in Table 1). Permanent stands were classified into eleven study sites and, in turn, these were clustered into seven macrosites based on spatial proximity and similarity of climatic conditions (Table 1). The main sampling units, hereafter called "plots", were established by the combination of each site and the different tree species in such site (Table 1).

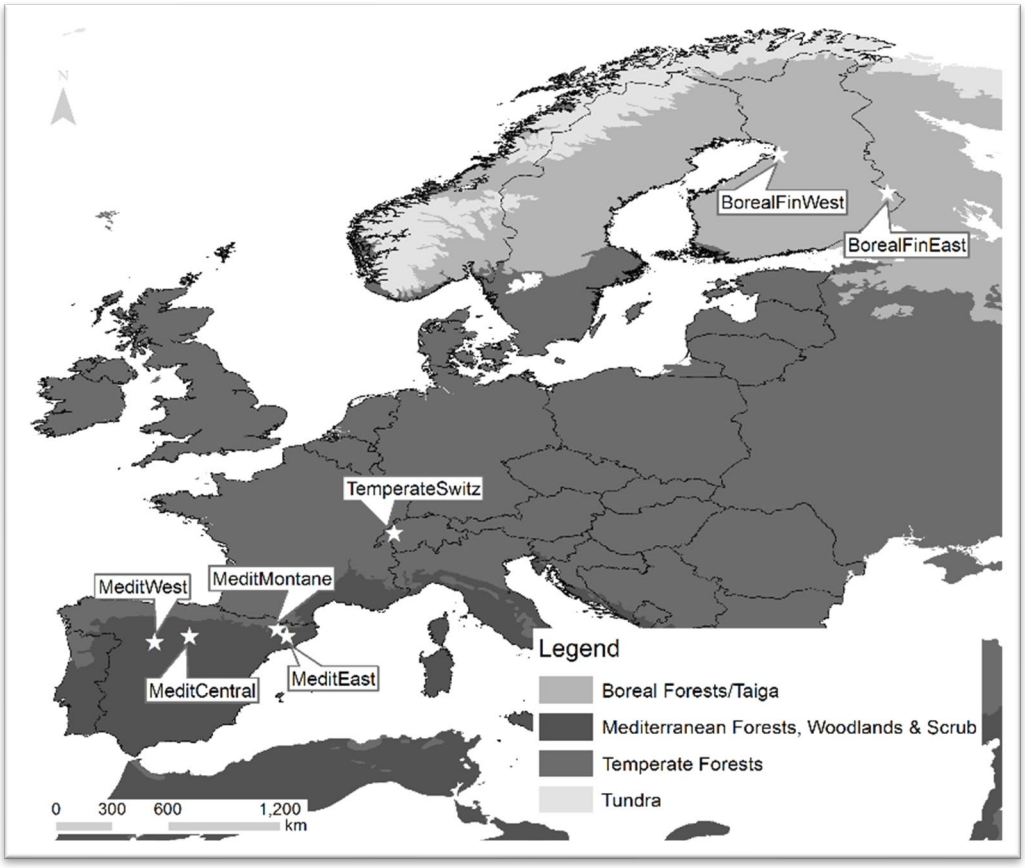

Figure 1: Macrosites across different biomes in Europe, distributed between Spain, Switzerland and Finland, representing Mediterranean, temperate and boreal bioclimatic conditions, respectively. BorealFinEast and BorealFinWest denote, respectively, the sites located in eastern and western Finland (Kitsi and Kalimeenoja), TemperateSwitz is the study site in Switzerland (La Chanéaz), MeditMontane denotes the sites situated in the pre-Pyrenees and Pyrenees of Catalonia, MeditEast covers the sites located in the central and pre-coastal Catalan region (Solsonès and Prades), MeditCentral and MeditWest include the sites from central and western Spain (Villaluenga de la Vega and Tudela de Duero sites).

Table 1. Classification of the permanent stands into plots (site – species ID), sites and macrosites, as well as the main available characteristics of the plots on climate, vegetation composition and forest management. The database and main characteristic sources concerning forest stand, mushroom productivity and tree growth are also provided.

Macrosite	Site (region, country)	Plots	No. stands (total area, m^2)	T (ºC)	P (mm)	Dominant tree	Other vegetation	Observations	Mycological and site references	Dendrochronological references
BorealFinEast	Kitsi (Lieksa, Finland)	BorealFinEast-PS	6 (600)	2.1	601	*P. sylvestris*	*Picea abies* L., *Betula pendula* Roth, *Betula pubescens* Ehrh.	Forest fire area located within the boreal vegetation zone	Salo & Kouki (2018)	-
BorealFinWest	Kalimeenoja (Oulu, Finland)	BorealFinWest-PS	7 (700)	1.3	500	*P. sylvestris*	*P. abies, Betula pubescens*	Forests in natural state or under moderate forestry measures	Ohenoja (1993)	-
TemperateSwitz	La Chanéaz (Payerne, Switzerland)	TemperateSwitz-FS	5 (1500)	8.5	845	*F. sylvatica*	Coniferous species	Mixed old forest, multi-storied management	Straatsma et al. (2001), Egli et al. (2010), Büntgen et al. (2012), Büntgen et al. (2013), Andrew et al. (2016)	Egli et al. (2010), Büntgen et al. (2012), Büntgen et al. (2013)
MeditMontane	Pre-Pyrenees (Catalonia, Spain)	MeditMontane1-PN	2 (200)	6.2 - 9	595 (south) - 1051 (north) (summer drought)	*P. nigra*	-	-	de-Miguel et al. (2014), Alday et al. (2017)	-
		MeditMontane1-PSPN	2 (200)			*P. sylvestris, P. nigra*	-	-		-
	Pyrenees (Catalonia, Spain)	MeditMontane2-PS	4 (400)	6.2 - 9	595 (south) - 1051 (north) (summer drought)	*P. sylvestris*	-	Mono-specific naturalized forests	de-Miguel et al. (2014), Alday et al. (2017)	-
MeditEast	Prades (Catalonia, Spain)[6]	MeditEast1-PS	2 (200)	11.8	659 (summer drought period)	*P. sylvestris*	-	In a natural park	Bonet et al. (2012), de-Miguel et al. (2014)	Primicia et al. (2016)
		MeditEast1-PP	15 (1500)			*P. pinaster*	-	In a natural park, 50-55 years old, planted stands,		Primicia et al. (2016), Collado et al. (2018)
		MeditEast1-PH	1 (100)			*P. halepensis*	-	Outside but near the natural park		-
	Solsonés (Catalonia, Spain)	MeditEast2-PS	5 (500)	11.1	600 (south) - 1000 (north) (summer drought)	*P. sylvestris*	-	Managed for lumber production	Martínez de Aragón et al. (2007), Bonet et al. (2010), de-Miguel et al. (2014)	Primicia et al. (2016)
		MeditEast2-PN	7 (700)*			*P. nigra*	-			
		MeditEast2-PH	4 (400)			*P. halepensis*	-			
		MeditEast2-PNPH	3 (300)			*P. nigra, P. halepensis*	-			-
MeditCentral	Pinar Grande (Soria, Spain)	MeditCentral-PS	18 (2700)	8.8	865	*P. sylvestris*	-	Managed by a periodic block method, rotation of 100 years (clear-cutting)	Martínez-Peña et al. (2012), Martínez-Peña et al. (2012), Büntgen et al. (2015) Andrew et al. (2016)	Büntgen et al. (2015)
	Almazán (Soria, Spain)	MeditCentral-PP	18 (2700)	10.1	500 - 700	*P. pinaster*	-	Harvesting interval of 80 years, regeneration period of 10 years	Fernández-Toirán et al. (2006), De la Varga et al. (2013)	-
MeditWest	Villaluenga de la Vega (Palencia, Spain)	MeditWest1-PS	3 (300)	10	622	*P. sylvestris*	-	Even-aged, 50–60-year-old reforested stands	Oria-de-Rueda et al. (2010), Gassibe et al. (2015)	-
		MeditWest1-PP	3 (300)			*P. pinaster*	-			-
	Tudela del Duero (Valladolid, Spain)	MeditWest2-PP	6 (600)	12.5	430	*P. pinaster*	-	Natural 50–60-year-old, homogeneous even-aged stands	Gassibe et al. (2015)	-

Abbreviations: *FS: Fagus sylvatica, PS: Pinus sylvestris, PN: Pinus* nigra, PH: *Pinus halepensis*, PP: *Pinus pinaster*, PSPN: *P. sylvestris* and *P.nigra*, PNPH: *P. nigra* and *P. halepensis*, T: mean annual temperature, P: mean annual total precipitation, Plots: codification of sites by their bioclimate region and dominant tree species.
* New collected dendrochronological data in 3 out of 7 permanent stands for this study.

Mushroom production was inventoried weekly or biweekly during summer and/or autumn (depending on mushroom season on the site) and the sampling focused on macrofungi that produce sporocarps visible to the naked eye and larger than 1 mm in size (Arnolds, 1981). All collected sporocarps were identified at the species level whenever possible. We based on the expert knowledge and the existing literature (e.g., Agerer, 2006; Gadd et al., 2007; Hobbie and Agerer, 2010; Taylor et al., 2003; Tedersoo et al., 2014, 2010; Trudell et al., 2004) to classify the species, according to their strategy to obtain carbon, into the mycorrhizal and saprotrophic functional guilds. The period of mushroom monitoring of the permanent stands ranged from 6 to 32 years. Sporocarp density was collected in all permanent stands as an indicator of mushroom yield, whereas biomass-based mushroom yield data (fresh weight of fungi sporocarps in kg ha^{-1}) were collected in all permanent stand with the exception of those located in Switzerland. Table 1 provides further information on the source of mushroom sampling sites and productivity, and Table A1 shows additional information about the study sites. Table 2 summarizes the mushroom productivity data.

Table 2. Summary of the available plot data on seasonal climatic conditions (precipitation and temperature of both summer and autumn), mushroom productivity (both mycorrhizal and saprotrophic guilds) and tree growth (tree ring, earlywood and latewood widths).

		Meteorological data[a]				Mycological data[b]				Dendrochronological data[b]		
Plots	Time overlap (years)	Tsum (°C)	Taut (°C)	Psum (mm)	Paut (mm)	Biomass myco. (kg ha^{-1} yr^{-1})	Biomass sap. (kg ha^{-1} yr^{-1})	No. myco. (No. ha^{-1} yr^{-1})	No. sap. (No. ha^{-1} yr^{-1})	TRW (mm)	EW (mm)	LW (mm)
BorealFinEast-PS	12 (1993-2004)	14.51 ± 1.02	2.14 ± 1.76	225.78 ± 64.48	174.68 ± 49.32	62.91 ± 42.18	18.94 ± 7.13	5688 ± 3764	15102 ± 17442	0.60 ± 0.20	0.42 ± 0.14	0.21 ± 0.08
BorealFinWest-PS	13 (1976-1988)	13.45 ± 1.12	1.93 ± 1.13	170.38 ± 61.81	142.93 ± 43.93	98.85 ± 101.36	4.11 ± 3.82	8300 ± 7513	22957 ± 20988	2.49 ± 0.78	1.74 ± 0.61	0.68 ± 0.19
TemperateSwitz-FS	32 (1975-2006)	16.36 ± 1.06	8.51 ± 0.78	344.62 ± 78.32	296.03 ± 85.81	-	-	13182 ± 9289	9442 ± 7984	1.51 ± 0.61	-	-
MeditMontane1-PN	8 (2007-2014)	19.97 ± 1.06	12.18 ± 1.25	161.36 ± 60.34	175.20 ± 61.46	115.85 ± 189.37	8.57 ± 8.70	34225 ± 55430	5863 ± 3842	0.88 ± 0.22	0.51 ± 0.08	0.37 ± 0.16
MeditMontane1-PSPN						54.37 ± 93.90	3.97 ± 3.39	29700 ± 47629	2156 ± 1665	1.06 ± 0.21	0.73 ± 0.10	0.33 ± 0.13
MeditMontane2-PS	8 (2007-2014)	15.76 ± 0.92	8.88 ± 1.19	161.36 ± 60.34	175.20 ± 61.46	98.69 ± 108.41	11.86 ± 7.14	14191 ± 21692	8738 ± 5087	0.94 ± 0.10	0.66 ± 0.07	0.28 ± 0.05
MeditEast1-PS	7 (2008-2014)	22.05 ± 0.82	14.34 ± 1.14	50.26 ± 14.32	157.08 ± 49.03	225.31 ± 184.13	24.59 ± 32.56	11743 ± 10139	24850 ± 27933	0.93 ± 0.17	0.65 ± 0.11	0.33 ± 0.09
MeditEast1-PP						67.16 ± 70.05	23.14 ± 16.25	6519 ± 7500	15841 ± 14501	1.20 ± 0.20	0.92 ± 0.17	0.29 ± 0.07
MeditEast1-PH						21.07 ± 46.66	15.41 ± 21.09	1586 ± 2308	12942 ± 13082	1.14 ± 0.30	0.90 ± 0.20	0.25 ± 0.10
MeditEast2-PS	13 (1997-2001, 2007-2014)	20.90 ± 0.93	13.17 ± 1.03	126.94 ± 47.76	154.51 ± 45.61	77.44 ± 45.68	4.10 ± 3.26	10322 ± 7681	4751 ± 5347	1.09 ± 0.20	0.78 ± 0.14	0.29 ± 0.09
MeditEast2-PN						67.62 ± 62.15	5.59 ± 6.25	9080 ± 15447	8227 ± 11937	0.78 ± 0.19	0.52 ± 0.10	0.26 ± 0.11
MeditEast2-PH						36.87 ± 47.08	5.34 ± 8.78	5214 ± 9438	11046 ± 20527	0.77 ± 0.29	0.54 ± 0.16	0.21 ± 0.14
MeditEast2-PNPH	8 (2007-2014)					63.49 ± 63.56	3.28 ± 3.11	6513 ± 7526	9067 ± 8887	1.28 ± 0.29	0.89 ± 0.20	0.40 ± 0.14
MeditCentral-PS	17 (1995-2011)	20.24 ± 0.92	12.21 ± 0.95	63.45 ± 39.08	132.90 ± 53.82	105.64 ± 90.34	7.97 ± 8.24	6013 ± 7144	2811 ± 2713	1.56 ± 0.27	1.14 ± 0.18	0.37 ± 0.10
MeditCentral-PP	6 (2007-2012)	19.95 ± 0.92	11.87 ± 1.07	71.47 ± 39.19	145.18 ± 56.16	91.41 ± 108.04	10.49 ± 11.29	6863 ± 8139	5266 ± 6230	1.64 ± 0.37	-	-
MeditWest1-PS	8 (2008-2015)	18.99 ± 0.79	12.16 ± 1.1	54.50 ± 21.48	147.34 ± 36.33	181.12 ± 143.63	47.51 ± 44.50	26863 ± 19009	46525 ± 29805	1.33 ± 0.31	0.97 ± 0.25	0.36 ± 0.12
MeditWest1-PP	12 (2003-2006, 2008-2015)					157.29 ± 174.89	29.26 ± 26.62	15692 ± 17355	36214 ± 35645	1.30 ± 0.29	1.00 ± 0.21	0.31 ± 0.09
MeditWest2-PP	7 (2006-2009, 2011-2013)	21.36 ± 0.91	13.81 ± 1.33	45.26 ± 27.69	111.40 ± 34.53	162.68 ± 90.11	25.83 ± 4.80	12361 ± 6792	31180 ± 14141	1.21 ± 0.47	0.91 ± 0.36	0.30 ± 0.08

Abbreviations: Time overlap: years of available data that match between sporocarps harvests and tree rings, Tsum: mean temperature of summer (June, July and August), Taut: mean temperature of autumn (September, October and November), Psum: total precipitation of summer (June, July and August), Paut: total precipitation of autumn (September, October and November), Biomass myco.: mycorrhizal mushroom biomass, Biomass sap.: saprotrophic mushroom biomass, No. myco.: density of mycorrhizal sporocarps, No. sap.: density of saprotrophic sporocarps, TRW: tree ring width, EW: earlywood width, LW: latewood width. a Data from the gridded E-OBS climate dataset (version 17.0) (Cornes et al., 2018).

[a] Values are averaged by years (time overlap) of each plot.

[b] Values are averaged by years (time overlap) and permanent stands of each plot.

2.2. Dendrochronological methods

In this study, we obtained data on annual tree growth from the permanent stands where dendrochronological data were not previously collected, i.e. BorealFinEast-PS, BorealFinWest-PS, MeditMontane1-PN, MeditMontane1-PSPN, MeditMontane2-PS, MeditCentral-PP, MeditWest1-PS, MeditWest1-PP, MeditWest2-PP, MeditEast1-PH and MeditEast2-PNPH (see the dendrochronological data sources in Table 1). Likewise, we collected and added new data from 3 permanent stands in MeditEast2-PN to improve the common signal of the mean series of the plot. Between 10 and 15 dominant trees were randomly selected for sampling in each permanent stand. They were selected during different periods, ranging from 2012 to 2016 according to the plot: TemperateSwitz and MeditCentral-PS in 2012; MeditCentral-PP in 2013; MeditWest2-PP in 2014; MediMontane and MeditEast in 2015; and MeditWest1 and BorealFinEast/West in 2016. Two cores per tree were extracted at 1.3 m using Pressler increment borers. Details of trees selected for the analyses of the relationship between production at different fungal guilds and tree growth can be found in Table 2 and A1. Cores were air-dried, mounted on wood boards and polished with sandpaper grits until rings were clearly visible. The wood samples were visually cross-dated. Tree ring width (TRW) and earlywood (EW) and latewood widths (LW) were separately measured to the nearest 0.001 mm using a stereomicroscope and a Lintab sliding-stage measuring device with the TSAP-WinTM software (F. Rinn, Heidelberg, Germany). EW and LW were obtained for all permanent stands excepting two pine forests and the Swiss beech forest since these two wood types cannot be distinguished in the later tree species. Earlywood and latewood were visually distinguished based on the different lumen area and cell-wall thickness of the tracheids forming each type of wood. Cross-dating was verified using the COFECHA software (Holmes, 1983). The time series ranged from 59 to 216 years. TRW, EW and LW width series were standardized and detrended by fitting 32-year long splines with a 50% cut-off frequency to remove age- and size-related trends (Cook and Peters, 1981). This allowed obtaining dimensionless TRW, EW and LW width indices (TRWi, EWi and LWi, respectively). The individual indices were averaged for each plot. The detrending and chronologies construction were done using the Dendrochronology Program Library (*dplR*) package (Bunn, 2010) in the R software (R Core Team, 2014).

2.3. Climate data

Seasonal climatic variables, i.e. mean temperature and total precipitation, were calculated from monthly data obtained from 1950 to 2015 from the gridded E-OBS climate dataset (version 17.0) (Cornes et al., 2018) by selecting the 0.25° grid including the plot. The selected seasons for this study were summer (from June to August) and autumn (from September to November), because they represent the most relevant periods for mushroom productivity in most sites (cf. Primicia et al., 2016). Table 2 summarizes the seasonal climatic conditions.

2.4. Statistical analysis

Spearman correlation analysis was used to analyse the response of mean annual mushroom yield, for both mycorrhizal and saprotrophic guilds, quantified as sporocarp density (in No. ha^{-1} $year^{-1}$) and biomass (in kg ha^{-1} $year^{-1}$) to the seasonal climate variables, as well as to dendrochronological variables. Spearman partial correlations were also used to assess the

relationships between the yield of both mushroom guilds and dendrochronological information (i.e. TRWi and LWi) controlling for the main climatic variables affecting mushroom production. Both analyses were represented as a percentage of plots in which the correlations were significant (i.e, p-value $\leqslant 0.1$) over all plots and separately per each macrosite.

The relationships between mushroom yield, climate and dendrochronological variables were analysed by fitting linear mixed-effects models using the *nlme* package (Pinheiro and Bates, 2000) in the R statistical software (R Core Team, 2014), including either all plots or only those plots dominated by Scots pine which was the most intensively sampled tree species (in 7 out of 18 plots). Therefore, six models with different number of observations, according to the plots, were formulated for both mushroom biomass (kg ha^{-1} $year^{-1}$) and sporocarp density (No. ha^{-1} $year^{-1}$), and per each fungi guild (mycorrhizal and saprotrophic). Biomass was predicted encompassing all and only Scots pine plots for which mushroom biomass and LWi width data were available (i.e. all plots except TemperateSwitz-FS and MeditCentral-PP), resulting in n=16 and 7 observations, respectively. Furthermore, the sporocarp density was fitted taking into account all plots (n=18). Mushroom biomass or the sporocarp density was regressed against those predictors showing the strongest correlations with mushroom production, namely, seasonal climate variables (i.e. mean temperature and precipitation in summer and autumn), and ring widths indices (i.e., TRWi and LWi). The response variable was square-root transformed in order to meet the assumptions on the error structure. When analysing all plots, we considered the id of each plot as a grouping random factor, allowing the intercept to fluctuate randomly between plots. An autoregressive correlation structure of first order was included to account for the repeated measures on the same plot (Pinheiro and Bates, 2000), while a variance function was included to account for non-homogeneous variances between plot. The models used for Scots pine differed in the sense that, for the random effects, the autoregressive correlation structure and the variance structure were related to the plot id only, instead of the permanent stand. The appropriateness of the random effects and the autoregressive correlation and variance structures was analysed by comparing nested models with and without considering the different variance structures based on likelihood ratio tests using the restricted maximum likelihood (REML) estimation procedure. Models ranged from the null model (only with an intercept) to models with all variables. Snowdon's bias correction factor (Snowdon, 1991) was used to correct the predictions for the back-transformation bias to the original scale.

2.5. Model evaluation

The best-fit (most parsimonious) models, considered as those showing the lowest Akaike Information Criterion (AIC) values (Burnham and Anderson, 2003), were identified using the Multi-Model Inference (*MuMIn*) package (Bartoń, 2013). We estimated a pseudo-R^2 of the selected models following Nakagawa & Schielzeth (2013), which comprises both marginal (R^2m, accounting for the proportion of variance explained by the fixed factors) and conditional (R^2c, accounting for the proportion of variance explained by the whole model) R^2 values. Furthermore, the following criteria were taken into account in model evaluation: parsimony and robustness, consistency with current ecological knowledge, statistical significance of parameters (*t-value* $\geqslant 2$), mean bias (from both marginal and

conditional predictions), homoscedasticity, precision, absence of multicollinearity among predictor variables (assessed by Variance Inflation Factor – VIF), normal distribution of residuals and root-mean-square error (RMSE). All statistical analyses were conducted using R statistical software (R Core Team, 2014).

3. Results

3.1. Mushroom yield – tree growth relationship

Some synchrony (i.e. positive correlation) was observed between dendrochronological variables and the annual mushroom yield, taking into account that data on LW width was not available in Switzerland nor Almazán (Spain), as well as only the sporocarp density (No. ha^{-1}, yr^{-1}) was measured in Switzerland. These synchronies were observed for both mycorrhizal and saprotrophic biomass and sporocarp density in particular, in Mediterranean plots (Figs. 2, 3, A2 and A3). This synchrony was the highest for the relationship between mushroom biomass and LWi (Fig. 3), while the mushroom biomass – EWi relationship showed a lower degree of synchrony. Indeed, we found positive correlations between LWi and mycorrhizal mushroom biomass only in some plots of the montane and eastern Mediterranean regions with 67% and 43% of plots, respectively, with significant correlations (Table 3 and Table A2). However, these correlations were mediated by climatic variables (Table 4 and Table A3) with both the summer and autumn precipitations being the most important mediators (unlike, for instance, summer temperature). Actually, LWi and mycorrhizal mushroom biomass were significantly correlated throughout all mountain plots of northeastern Spain (MeditMontane1 and MeditMontane2 sites), when controlling for both climatic variables of autumn (total precipitation and mean temperature) (Table A3). For instance, we detected clearer synchronies between LWi width and mycorrhizal biomass and, to a lesser extent, saprotrophic biomass in the mixed *P. sylvestris* - *P. nigra* forests of northeastern Spain (MeditMontane1-PSPN) (Fig. A3). In contrast to LWi – mycorrhizal mushroom biomass relationship, the significant correlations between TRWi and density of mycorrhizal sporocarps were less frequent (11%) (Table 3), and the main mediating variable in that case was summer precipitation (Table 4). In addition, this relationship also denoted a poorer synchrony (Fig. 2) than the relationship between mushroom biomass and the indices of seasonal wood formation (Fig. 3). Furthermore, despite both mycorrhizal biomass – ring-widths relationships and saprotrophic biomass – ring-widths relationships showed visually quite similar degree of synchrony (Fig. 3), LWi was poorly related with saprotrophic mushroom biomass with a 19% of plots with significant correlations (Table 3). The summer precipitation was mediating in the latter relationship by decreasing the frequency of significant plots (6%) (Table 4). Likewise, only one significant and negative correlation appeared between TRWi and the density of saprotrophic sporocarps (BorealFinWest) (Table 3), and this relationship was only slightly controlled by the mean summer temperature (Table 4).

Table 3. Spearman correlation between fungal productivity, tree growth and seasonal climate. Namely, percentage of plots in which mushroom yield of mycorrhizal and saprotrophic fungi were significantly correlated with the seasonal climate and dendrochronological variables over all plots and separately per each macrosite. The statistical method was the Spearman correlation (significant p-value $\leqslant 0.1$). The mushroom yield variables were both biomass in kg ha^{-1} yr^{-1} and sporocarp density in No. ha^{-1} yr^{-1}.

	No. plots	Biomass mycorrhizal					Biomass saprotrophic					Density mycorrhizal					Density saprotrophic				
		Psum	Paut	Tsum	Taut	LWi	Psum	Paut	Tsum	Taut	LWi	Psum	Paut	Tsum	Taut	TRWi	Psum	Paut	Tsum	Taut	TRWi
All plots	**18**	**47%**	**24%**	**6% neg**	**6%**	**31%**	**12%**	**18% 6% neg**	**6% neg**	**ns**	**19%**	**39%**	**11%**	**6%**	**11%**	**11%**	**6%**	**33% 11% neg**	**6%**	**ns**	**6%**
BorealFinEast	1	100%	ns	100% neg	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
BorealFinWest	1	100%	ns	ns	ns	ns	ns	ns	ns	ns	ns	100%	ns	ns	ns	ns	ns	ns	ns	ns	100% neg
TemperateSwitz	1	-	-	-	-	-	-	-	-	-	-	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
MeditMontane	3	100%	ns	ns	ns	67%	33%	ns	ns	ns	33%	67%	ns	ns	ns	33%	ns	33%	ns	ns	ns
MeditEast	7	ns	29%	ns	ns	43%	ns	29%	ns	ns	14%	29%	14%	14%	ns	14%	ns	57%	ns	ns	ns
MeditCentral	2*	100%	ns	ns	ns	ns	50%	50%	ns	ns	ns	50%	50%	ns	ns	ns	50%	ns	ns	ns	ns
MeditWest	3	33%	67%	ns	33%	ns	ns	33% neg	33% neg	ns	33%	33%	ns	ns	67%	ns	ns	33% 67% neg	33% neg	ns	ns

Abbreviations: The macrosites are given in Table 1. Climate variables: Psum – precipitation of summer (June – August), Paut – precipitation of autumn (September – November), Tsum – temperature of summer (June – August), Taut – temperature of autumn (September – November). Dendrochronological variables: LWi – the latewood width index, TRWi – the tree-ring width index. *ns* means non-significant and *neg* negative (otherwise, positive).

* MeditCentral is composed only of 1 plot for the correlations in Biomass mycorrhizal and Biomass saprotrophic due to LW width was measured only in 1 out of 2 plots (i.e., MeditEast-PS).

Table 4. Spearman correlation between fungal productivity and tree growth controlling for climate effect. Namely, percentage of plots in which mushroom yield of mycorrhizal and saprotrophic fungi were significantly correlated with LWi and TRWi, under the controlling effect of climate variables, over all the plots and separately per each macrosite. The statistical method was the Spearman partial correlation (significant p-value $\leqslant 0.1$). The mushroom yield variables were biomass in kg ha^{-1} yr^{-1} and sporocarp density in No. ha^{-1} yr^{-1}, and the climate variables were precipitation and temperature of autumn and summer.

	No. plots	Biomass myco. - LWi				Biomass sap. - LWi				Density myco. - TRWi				Density sap. - TRWi			
		Psum	Paut	Tsum	Taut	Psum	Paut	Tsum	Taut	Psum	Paut	Tsum	Taut	Psum	Paut	Tsum	Taut
All plots	**18**	**13%**	**38%**	**25%**	**31%**	**6%**	**13%**	**19%**	**13%**	**ns**	**17%**	**6%**	**11%**	**6% neg**	**6% neg**	**6% 6% neg**	**6% neg**
BorealFinEast	1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	100%	ns	ns	ns	ns
BorealFinWest	1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	100% neg	100% neg	100% neg	100% neg
TemperateSwitz	1	-	-	-	-	-	-	-	-	ns	ns	ns	ns	ns	ns	ns	ns
MeditMontane	3	33%	100%	67%	100%	ns	33%	33%	33%	ns	33%	33%	33%	ns	ns	ns	ns
MeditEast	7	14%	29%	29%	29%	ns	14%	29%	ns	ns	29%	ns	ns	ns	ns	14%	ns
MeditCentral	2*	ns	33%	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
MeditWest	3	ns	ns	ns	ns	33%	ns	ns	33%	ns	ns	ns	ns	ns	ns	ns	ns

Abbreviations: The macrosites abbreviations are given in Table 1. Fungi variables: Biomass myco. – mycorrhizal biomass, Biomass sap. – saprotrophic biomass, Density myco. – density of mycorrhizal sporocarps, Density sap. – density of saprotrophic sporocarps. Climate variables: Psum – precipitation of summer (June – August), Paut – precipitation of autumn (September – November), Tsum – temperature of summer (June – August), Taut – temperature of autumn (September – November). Dendrochronological variables: LWi – the latewood width index, TRWi – the tree-ring width index. *ns* means non-significant, and *neg* stands out for negative (otherwise, positive).

*MeditCentral is composed only of 1 plot for the correlations in Biomass mycorrhizal and Biomass saprotrophic due to LW width was measured only in 1 out of 2 plots (i.e., MeditEast-PS).

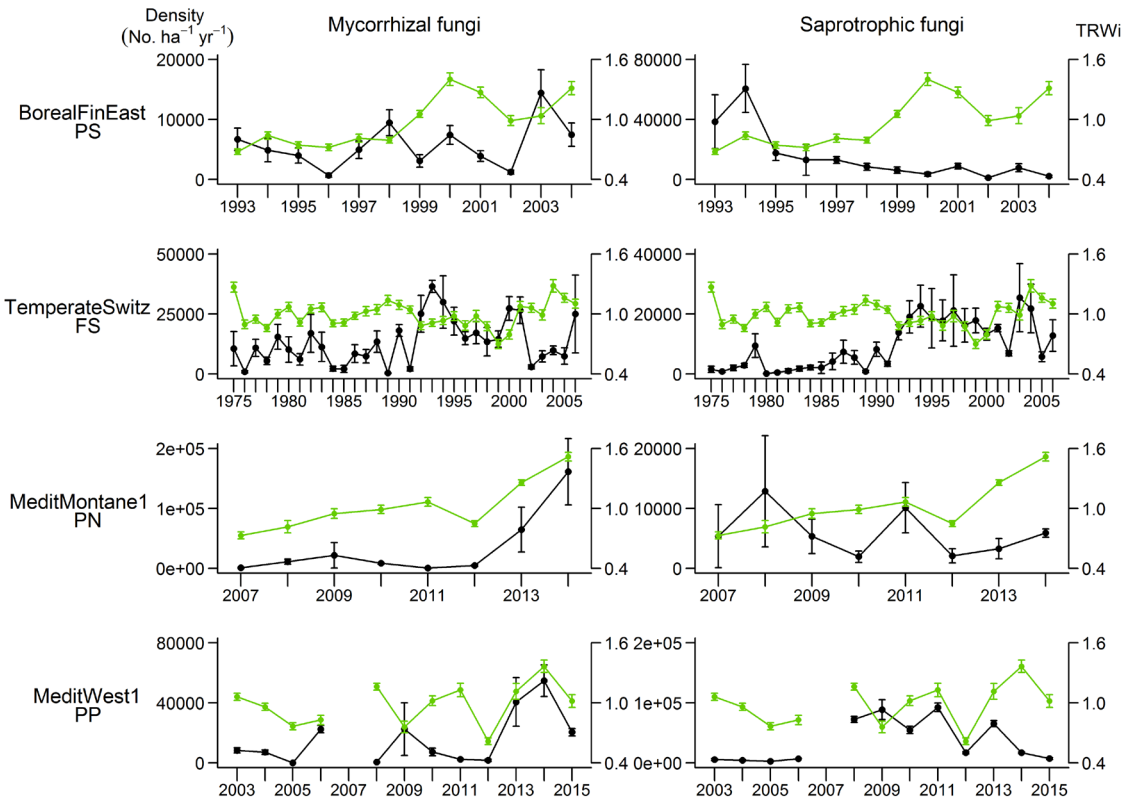

Figure 2: Temporal trends of mean (± SD) annual mycorrhizal and saprotrophic fungi sporocarps (No. ha^{-1} year^{-1}) in black line and tree-ring width indices (TRWi, green line) in selected plots. These plots were chosen to show the key trends of different ecosystems in different bioclimatic regions. Plots and species abbreviations are given in Table 1.

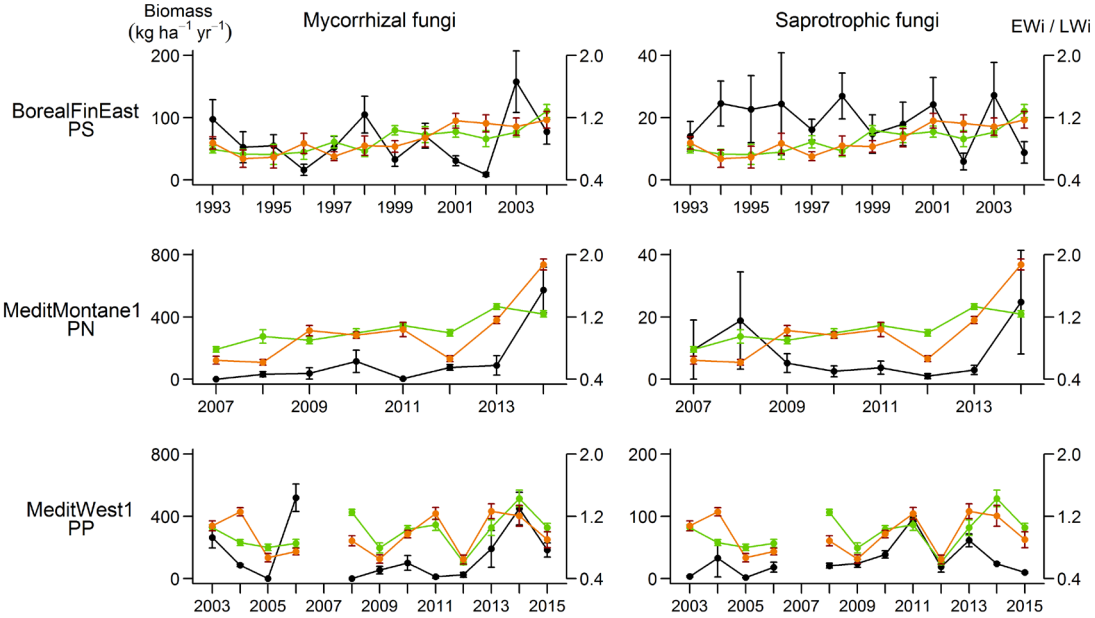

Figure 3: Temporal trends of mean (± SD) annual mycorrhizal and saprotrophic fungi biomass (kg ha^{-1} year^{-1}) in black line, and earlywood (EWi) and latewood (LWi) width indices (green and brown lines, respectively) in selected plots. These plots were chosen to show the key trends of different ecosystems in different bioclimatic regions. Plots and species abbreviations are given in Table 1.

3.2. Relationship between mushroom yield and seasonal climate variables

Summer precipitation was significantly positively correlated with mycorrhizal biomass in those plots located largely either at high latitude or high altitude, such as the Finland macrosites (BorealFinEast and BorealFinWest) and the mountain areas of northeastern Spain (MeditMontane), respectively (Table 3). In addition, other positive correlations were found in the central and western Mediterranean Spanish continental macrosites (MeditCentral and MeditWest1-PP plots; Table A2). Total autumn precipitation showed less significant correlations with mycorrhizal biomass than the precipitation of summer along the plots. For example, apart from the positive correlations of mycorrhizal biomass with autumn precipitation in both forests of the western Mediterranean Basin (MediWest1-PS and MediWest1-PP plots), we only found significant correlations in the Scots and Aleppo pine forests of the eastern Mediterranean (MeditEast2-PS and MeditEast2-PH plots). Likewise, we observed similar patterns when the correlation analysis was conducted between the density of mycorrhizal sporocarps and the amount of precipitation (i.e., more significant correlations with summer precipitation) (Tables 3 and A2). Nevertheless, temperature showed weaker correlations with mycorrhizal mushroom biomass than precipitation (Table 3). Indeed, we found a negative correlation between mean summer temperature and mycorrhizal mushroom biomass in one Finnish plot (BorealFinEast), but, on the other hand, this biomass showed a positive correlation with the mean autumn temperature in the western Mediterranean maritime pine forest (MeditWest1-PP) (Table A2).

Furthermore, we found weaker correlations between saprotrophic mushroom biomass and climatic variables (Table 3). The autumn precipitation was the most correlated variable with saprotrophic mushroom biomass, and these correlations were observed in some Mediterranean macrosites (MeditEast, MeditCentral and MeditWest sites). For example, in the central and western Mediterranean maritime pine forests (MeditCentral-PP and MeditWest1-PP, respectively), as well as in the pure and mixed central-eastern Mediterranean Aleppo pine forests (MeditEast2-PH and MeditEast2-PNPH) (Table A2). Similarly as in the relationship between saprotrophic mushroom biomass and climatic variables, the density of saprotrophic sporocarps was better correlated with autumn precipitation than with other climatic variables (Table 3). Indeed, we found more significant correlations (positive and negative) between the autumn precipitation and the density of saprotrophic sporocarps (e.g., negative correlations in MeditWest1-PS and –PP plots) than with mushroom biomass. On the other hand, only the summer temperature showed one significant correlation with the density of saprotrophic sporocarps, as well as with biomass. This negative correlation was found in the MeditWest1-PP plot (Table A2).

3.3. Mushroom yield prediction from climatic and dendrochronological information

All dendrochronological variables (except EWi) were included as significant explanatory variables in the set of models (Table 5). However, autumn precipitation was the only significant variable present in all equations, i.e. in the models of mushroom biomass and sporocarp density. The proportion of variance explained by the fixed plus random factors (R^2c) was higher in the mycorrhizal mushroom models than in the saprotrophic guild equations (Table 5). Actually, the model of density of mycorrhizal sporocarps reached the

highest R^2c by including all climatic predictors and the interaction between autumn precipitation and temperature, as well as the interaction between summer precipitation and temperature (Fig. 4). Although the western Mediterranean plots were among the driest regions, the predictions of density of mycorrhizal sporocarps were the highest. In contrast, the temperate plot in Switzerland showed the lowest density of mycorrhizal sporocarps, although it was the rainiest site with intermediate mean temperatures between boreal and Mediterranean biomes. In addition, the predictions in both boreal plots also revealed high density of mycorrhizal sporocarps, even if these sites were characterized by the lowest summer and autumn temperatures. On the other hand, the fitted model of density of saprotrophic sporocarps included the fixed effect of TRWi, showing a significant increasing-decreasing trend (i.e. extreme TRWi values and therefore very wide tree rings were associated to a reduction in the density of saprotrophic sporocarps; see Fig. 4E). This trend was mathematically represented by two different variables of TRWi, i.e. a negative parameter and a transformed fixed effect. As for mycorrhizal species, the density of saprotrophic sporocarps was predicted to be highest in the western Mediterranean, intermediate in the boreal region and lowest in the temperate site.

The fitted model for mycorrhizal mushroom biomass, based on the data from all plots, included the following positive fixed effects: LWi, autumn precipitation and the interaction of both variables (Table 5 and Fig. A4). When only Scots pine plots were considered, precipitation of summer also emerged as a significant variable.

All models for saprotrophic mushroom yield included the mean autumn temperature as a positive explanatory variable (Table 5).

The mean summer temperature only contributed to explaining two out of six models in the Scots pine forests, namely, having a positive effect on the density of mycorrhizal sporocarps and a negative effect on the saprotrophic mushroom biomass.

Table 5. Significant parameter estimates for the selected models including all plots or those which dominant tree species was Scots pine, with mean annual mycorrhizal and saprotrophic fungi yields ('myco' and 'sapro', respectively) quantified as biomass (kg ha^{-1} year^{-1}) or sporocarp density (No. ha^{-1} year^{-1}) as dependent variables.

		Fixed effects coefficients											Random effects		Pseudo R^2				
		Intercept	log(LWi)	Sqrt(LWi)	TRWi	Sqrt(TRWi)	Paut	Psum	Log(LWi) x Paut	mean Taut	mean Tsum	Paut x meanTaut	Psum x meanTsum	Intercept	Residuals	R^2m[a]	R^2c[b]	**Marginal bias**	**RMSE**	**n**
All plots																				
Biomass (kg ha^{-1} year^{-1})	Sqrt(myco)	8.872	6.009	ns	-	-	0.038	ns	0.050	ns	ns	ns	ns	2.471	2.545	0.38	0.68	-5.47	94.65	16[c]
	Sqrt(sapro)	1.314	ns	1.768	-	-	0.009	ns	ns	0.141	ns	ns	ns	1.376	1.195	0.17	0.64	-0.15	19.14	16[c]
Density (No. ha^{-1} year^{-1})	Sqrt(myco)	100.696	-	-	ns	ns	0.273	0.430	-	3.992	6.601	0.028	0.033	38.542	28.696	0.49	0.82	2945.20	19861.82	18
	Sqrt(sapro)	-405.638	-	-	-454.995	949.248	0.209	ns	-	4.824	ns	ns	ns	34.736	54.638	0.13	0.38	891.96	20597.63	18
Scots pine plots																				
Biomass (kg ha^{-1} year^{-1})	Sqrt(myco)	10.391	4.080	ns	ns	ns	0.034	0.018	0.081	ns	ns	ns	ns	2.832	2.258	0.34	0.74	4.88	104.45	7
	Sqrt(sapro)	2.796	ns	ns	ns	ns	0.010	ns	ns	0.155	-0.227	ns	ns	0.736	1.416	0.12	0.31	-0.07	20.65	7

[a,b] Marginal (proportion of variance explained by the fixed factors, R^2m) and conditional (proportion of variance explained by fixed plus random factors, R^2c) R^2 values were calculated following Nakagawa & Schielzeth (2013).

[c] Biomass models did not include data from Switzerland nor Almazán plots since the latewood width information was not available, as well as biomass data was not measured in Switzerland.

Paut and *Psum* denote autumn and summer precipitations, respectively. *meanTaut* and *meanTsum* denote autumn and summer mean temperatures, respectively. *Marginal bias* is the mean bias error of the marginal predictions while the conditional bias is zero in all models (kg ha^{-1} yr^{-1} in biomass or No. ha^{-1} yr^{-1} in sporocarp density), *RMSE* is the root of mean square error (kg ha^{-1} yr^{-1} in biomass or No. ha^{-1} yr^{-1} in sporocarp density), *n* is the number of observations, and *ns* means non-significant.

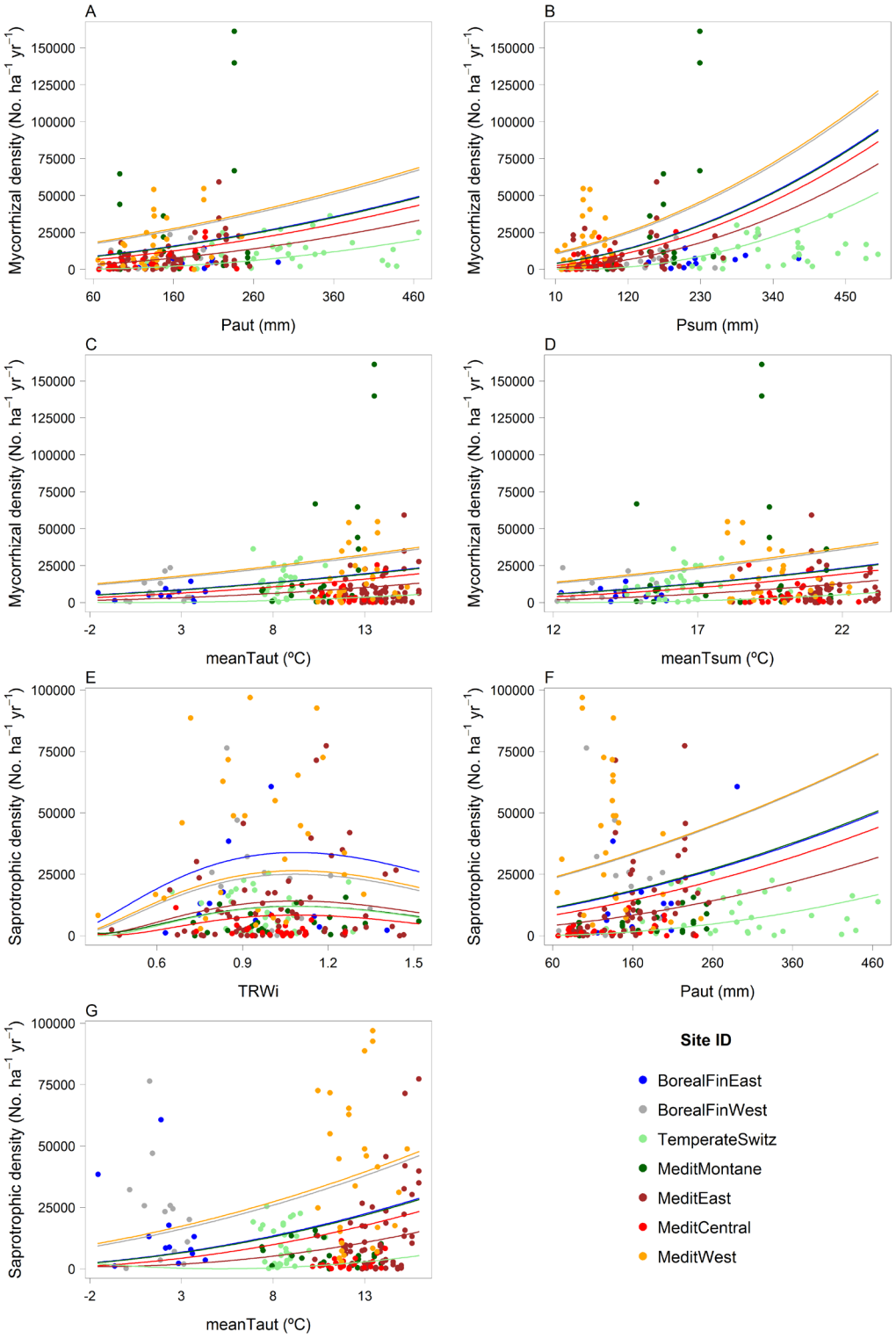

Figure 4: Effect of climatic and dendrochronological variables on the annual density of sporocarps of both mycorrhizal and saprotrophic fungi for each macrosite. The values assigned to the predictors in the simulation correspond to the mean values per each plot in the modeled data. Model predictions (represented as lines) were calculated for each plot using the mean values of predictors during the observation period, and then plot-wise predictions were averaged by macrosite. Dots denote the observed values. Macrosites abbreviations are as in Figure 1. *Paut* and *Psum* denote the total autumn and summer precipitations, respectively, *meanTaut* and *meanTsum* denote autumn and summer mean temperatures, accordingly, and *TRWi* is the tree-ring width index.

4. Discussion

This study provides new insights into the relationships between mushroom productivity and tree growth across different European bioclimatic regions (Mediterranean, temperate and boreal). However, these relationships were not consistent across the different biomes. Only in typically water-limited Mediterranean forests, some positive correlations between latewood production (LWi) and mycorrhizal mushroom biomass was detected in accordance with the first hypothesis of our study. Such linkages may be partly due to the fact that, under water-limited climate conditions, both the seasonal wood production and the mushroom yields are more sensitive to precipitation events during the late growing season, resulting in higher synchrony between tree growth and mushroom yield as a function of water availability in late summer and early autumn. Indeed, we observed differences in the interannual variability of the ring-width indices among forest biomes (Fig. A1). For instance, boreal plots showed lower interannual variation in ring width, resulting in so-called "complacent" series (i.e., similar ring widths for many years consecutively largely due to constant climatic conditions). On the other hand, drought-sensitive tree growth in some eastern Mediterranean plots (e.g., MeditEast2) resulted in marked year-to-year variation in ring width. At the same time, there were differences in the interannual variability among dendrochronological variables, LWi width showing higher year-to-year variation than EWi and TRWi (Figs. 2 and 3), as Miina (2000) also observed in Scots pine trees of eastern Finland.

Our findings across the three different European bioclimatic regions are in line with previous studies conducted at local to regional scales. Primicia et al. (2016) observed higher correlations between mycorrhizal mushroom production and LW width in Mediterranean plots under more severe summer drought conditions. Likewise, Büntgen et al. (2015) observed a significant positive relationship between tree growth (TRW) and fungal fruiting in a Mediterranean pine ecosystem, while Büntgen et al. (2013) did not find any significant correlation under more temperate climatic conditions in Switzerland, similar to our findings for temperate and boreal forest biomes. All these studies are based on the idea that mycorrhizal mushroom production is linked to tree growth, through the carbon allocation from the host trees to mycorrhizal fungi (Högberg et al., 2008), which also depends on climate conditions. However, we did not observe a significant relationship between TRW and density of mycorrhizal sporocarps, which may be due to the fact that this value does not necessarily reflect properly the actual fungal biomass since the number and size of sporocarps may vary between fungal species and may be also driven by environmental conditions. On the other hand, sporocarp biomass can reflect better the carbon allocation patterns of the plant-fungi relationship.

The results of this study also confirmed our second hypothesis, since we found some synchrony between saprotrophic mushroom biomass and tree growth (LW and TRW), but less frequent than for mycorrhizal mushroom biomass. This finding is in accordance with Egli et al. (2010), who observed: (1) an increase of both tree-ring width and density of ectomycorrhizal sporocarps and, to a lesser extent, saprotrophic sporocarps in thinned European beech stands; and (2) significant correlations between the annual growth (i.e., TRW) of two previous years and the current sporocarps production of both fungi guilds, maybe due to the extra supply of litter biomass from the silvicultural operations. Similar findings were also reported by Collado et al. (2018) in a xeric Mediterranean pine forest,

where the ectomycorrhizal mushroom yield was positively correlated with LW production, while saprotrophic mushroom production was only negatively and poorly related to EW formation. Collado et al. (2018) also found a lagged effect of 2 years between increasing LW width and saprotrophic mushroom yield, but showing an increasing-decreasing trend rather than the positive trend found by Egli et al. (2010). Although we did not find lagged effects in our current study, the density of saprotrophic sporocarps was explained by a similar increasing-decreasing trend of TRW width (Fig. 4E). The explanation of this pattern may be that wide rings are usually associated to more open stands with lower stand density and tree-to-tree competition, and this may result in less optimal microclimatic conditions for the fruiting of saprotrophic mushroom, i.e., open forest stands may have higher temperatures and lower relative humidity than stands with higher density of trees, as pointed out by Egli et al. (2010) and Collado et al. (2018) when comparing mushroom productivity of both unthinned vs. thinned plots.

Our study confirmed the important role of the climatic factors driving mushroom production and, moreover, revealed their differential impacts depending on the bioclimatic region and fungal guild (Fig. 4). For instance, the predicted density of saprotrophic sporocarps of western Mediterranean and boreal forest biomes depended highly on autumn precipitation and temperature, unlike in the temperate region. The strong relationship between saprotrophic sporocarp productivity and climatic factors may be explained by the strategy to obtain carbon, since saprotrophic fungi acquire carbon mostly by decomposition processes that are highly dependent on temperature and moisture (Rousk and Bååth, 2011), unlike mycorrhizal species that also depend on the symbiosis with the host tree (Högberg et al., 2001). Although our results barely showed significant correlations between temperature and mushroom yield across the European bioclimatic regions, previous research has shown that temperature may also drive fungal fruiting (e.g., Andrew et al., 2018; Kauserud et al., 2008). Since the available data lacked reliable enough measurements of extreme temperatures for all plots, our results may be explained by the fact that mean monthly temperature was used as a predictor instead of minimum or maximum temperatures, the latter probably being stronger drivers to mushroom productivity. For instance, Taye et al. (2016) and Collado et al. (2018) did not observe any significant relationship between fungal fruiting and mean temperature in a drought-prone Mediterranean maritime pine forest, while minimum and/or maximum temperatures have been reported as significant influential factors in similar sites (Hernández-Rodríguez et al., 2015b; Karavani et al., 2018; Primicia et al., 2016). On the other hand, the mean summer temperature showed a positive effect on saprotrophic mushroom production in a work conducted by Büntgen et al. (2013) in a temperate forest without any water limitation.

Our results were not so obvious due, in part, to the inherent complexity of forest ecosystems and fungal dynamics of this study, where the fungal productivity – tree growth interaction is taking place. Apart from climate, there are other relevant factors not addressed in this work that could affect this relationship, such as the forest management (e.g., Bonet et al., 2012; Egli et al., 2010), the stand age and structure (e.g., Bonet et al., 2004; Fernando Martínez-Peña et al., 2012), the competition among host trees and their physiologies (e.g., hierarchy of carbon allocation) (Waring, 1987), and the influence of the understory (e.g., Nocentini et al., 2004).

Further research must be conducted toward determining the mechanisms driving the interactions between mycorrhizal mushroom production and the host tree growth. This is only possible by the continuous and standardized monitoring of mushroom biomass (of both mycorrhizal and saprotrophic guilds) and tree growth in different biomes together with meteorological information of higher resolution. Moreover, further research would also benefit from an increased number of plots throughout different European forest biomes and ecosystems, as well as from more consistent dendrochronological information across plots by measuring both early- and late-wood formation. Future studies should also try to focus on more mechanistic approaches aiming at exploring the relationship between belowground mycelium biomass production and forest growth, in addition to the aboveground sporocarp production. This could provide new insights into carbon allocation patterns between vegetative fungal growth and reproduction, and contribute to improving scientific knowledge on the fungus-tree-climate relationships.

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Table A1: Additional information on plots.

Macrosite	Site (region, country)	Plots (Site-Species ID)	Lat. N	Long. (-W, +E)	Altitude (m.a.s.l.)	Years of fungi data (period)	Dendrochronological information					
							No. sampled trees	No. cores	Start year	End year	EPS	Available data
BorealFinEast	Kitsi (Lieksa, Finland)	BorealFinEast-PS	63.25	30.76	185	12 (1993-2004)	75 (8)[a]	136 (12)[a]	1799	2015	0.86	TRW, EW, LW
BorealFinWest	Kalimeenoja (Oulu, Finland)	BorealFinWest-PS	65.07	25.51	20	13 (1976-1988)	13	26	1864	2015	0.87	TRW, EW, LW
TemperateSwitz	La Chanéaz (Payerne, Switzerland)	TemperateSwitz-FS	46.82	6.94	575	32 (1975-2006)	78	137	1848	2011	0.89	TRW
MeditMontane	Pre-Pyrenees (Catalonia, Spain)	MeditMontane1-PN	42.18	1.30	903	8 (2007-2014)	16	31	1881	2014	0.96	TRW, EW, LW
		MeditMontane1-PSPN	42.20	1.30	1030		17	32	1915	2014	-	
	Pyrenees (Catalonia, Spain)	MeditMontane2-PS	42.26	1.36	1488	8 (2007-2014)	32	63	1930	2014	0.94	TRW, EW, LW
MeditEast	Prades (Catalonia, Spain)	MeditEast1-PS	41.34	1.05	853	7 (2008-2014)	20	33	1847	2014	0.87	TRW, EW, LW
		MeditEast1-PP	41.35	1.05	807		44	81	1847	2014	0.9	
		MeditEast1-PH	41.38	1.03	465		10	20	1955	2014	0.98	
	Solsonès (Catalonia, Spain)	MeditEast2-PS	42.01	1.62	1033	13 (1997-2001, 2007-2014)	50	95	1847	2014	0.87	TRW, EW, LW
		MeditEast2-PN	42.04	1.54	773		74 (30)[b]	143 (59)[b]	1857	2014	0.98	
		MeditEast2-PH	41.97	1.61	613		43	73	1847	2014	0.94	
		MeditEast2-PNPH	41.85	1.76	408	8 (2007-2014)	29	57	1960	2014	0.98	
MeditCentral	Pinar Grande (Soria, Spain)	MeditCentral-PS	41.83	-2.93	1132	19 (1995-2013)	653	870	1837	2012	0.98	TRW, EW, LW
	Almazán (Soria, Spain)	MeditCentral-PP	41.54	-2.53	1013	8 (2007-2014)	653	658	1837	2012	0.97	TRW
MeditWest	Villaluenga de la Vega (Palencia, Spain)	MeditWest1-PS	42.53	-4.78	985	8 (2008-2015)	17	31	1947	2015	0.92	TRW, EW, LW
		MeditWest1-PP	42.53	-4.78	985	12 (2003-2006, 2008-2015)	19	21	1947	2015	0.95	
	Tudela del Duero (Valladolid, Spain)	MeditWest2-PP	41.55	-4.61	796	9 (2006-2009, 2011-2015)	16	16	1945	2013	0.87	TRW, EW, LW

Abbreviations: Start year: the year of the oldest measured ring of the oldest tree, End year: the year of the newest measured ring, EPS: Expressed Population Signal, a variable quantifying the coherence and replication of the plot chronology. Abbreviations of tree species are as in Table 1.

[a,b] Data between brackets correspond to the No. of sampled trees and cores measured in this study.

[a] The number out of the brackets denote the total number of sampled trees and cores in that plot, including the data between brackets and the cores information from the International Tree-Ring Database (ITRDB; http://www.ncdc.noaa.gov/paleo/treering.html), in order to improve the common signal of the mean series of the plot.

Figure A1: Temporal trends of the tree-ring width index (TRWi) for each plot (i.e., study site – species ID). Legend abbreviations: FS: *Fagus sylvatica*, PS: *Pinus sylvestris*, PN: *Pinus nigra*, PH: *Pinus halepensis*, PP: *Pinus pinaster*, PSPN: *P. sylvestris* and *P.nigra*, PNPH: *P. nigra* and *P. halepensis*. Plot abbreviations are as in Table 1.

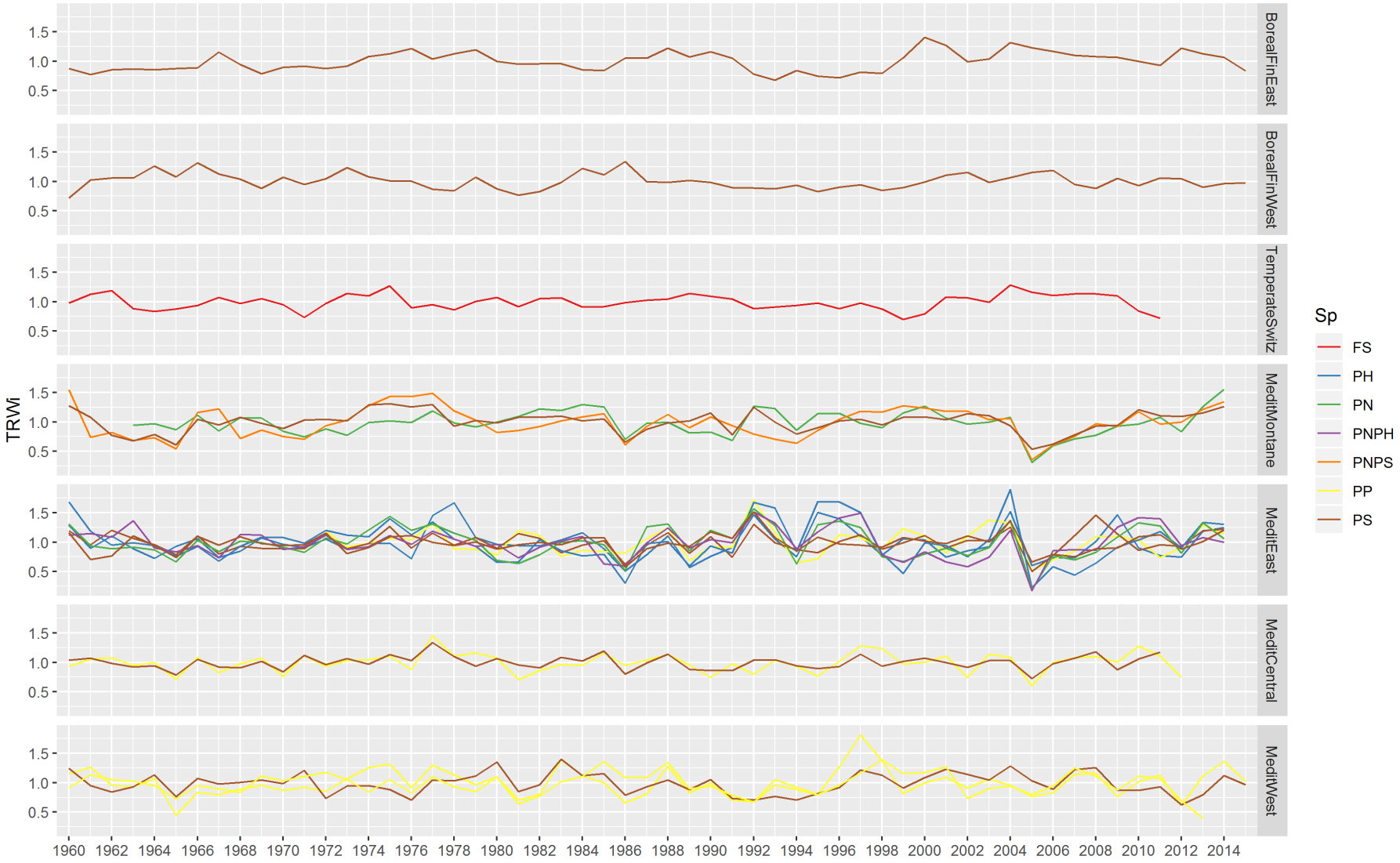


Table A2: Spearman correlation coefficients obtained by relating mushroom biomass (kg ha^{-1} year^{-1}) and sporocarp density (No. ha^{-1} year^{-1}) for both fungi guilds to the seasonal climate and dendrochronological variables for each plot (i.e., study site – species ID).

Site (region, country)	Plot	Biomass mycorrhizal					Biomass saprotrophic					Density mycorrhizal					Density saprotrophic				
		Psum	Paut	Tsum	Taut	LWi	Psum	Paut	Tsum	Taut	LWi	Psum	Paut	Tsum	Taut	TRWi	Psum	Paut	Tsum	Taut	TRWi
Kitsi (Lieksa, Finland)	BorealFinEast-PS	**0.59****	0.27	**-0.53***	0.00	0.06	-0.13	0.33	-0.25	0.29	-0.35	0.47	0.40	-0.31	0.00	0.47	-0.21	0.37	-0.38	-0.38	-0.13
Kalimeenoja (Oulu, Finland)	BorealFinWest-PS	**0.61****	0.37	0.09	-0.09	0.01	0.19	0.38	-0.05	0.05	-0.11	**0.60***	0.38	0.21	-0.21	-0.09	-0.16	0.04	-0.05	-0.31	**-0.54***
La Chanéaz (Payerne, Switzerland)	TemperateSwitz-FS	-	-	-	-	-	-	-	-	-	-	0.19	0.21	0.22	0.18	-0.18	-0.01	-0.02	0.44	0.15	-0.27
Pre-Pyrenees (Catalonia, Spain)	MeditMontane1-PN	**0.74****	0.26	-0.10	0.00	0.62	0.17	0.29	-0.50	0.21	0.07	0.62	0.12	-0.24	0.12	0.52	-0.04	0.35	-0.07	0.40	-0.04
	MeditMontane1-PSPN	**0.76****	0.24	-0.02	0.07	**0.90*****	**0.74****	0.48	0.05	0.10	**0.79****	**0.71***	0.10	-0.14	0.21	**0.74****	0.52	0.60	0.24	0.40	0.21
Pyrenees (Catalonia, Spain)	MeditMontane2-PS	**0.71***	0.19	0.10	0.07	**0.79****	0.29	0.60	-0.17	0.13	0.52	**0.64***	0.10	0.02	0.14	0.50	0.31	**0.69***	0.07	0.40	0.57
Prades (Catalonia, Spain)	MeditEast1-PS	0.32	0.29	0.21	0.07	-0.04	0.25	0.36	0.07	0.00	0.39	0.14	0.29	0.21	0.14	0.21	0.04	**0.79****	-0.25	0.11	0.21
	MeditEast1-PP	0.46	0.00	0.39	-0.07	**0.71***	-0.32	0.61	0.07	0.43	0.04	0.29	0.29	0.43	-0.32	-0.36	-0.14	**0.75****	-0.21	0.43	-0.39
	MeditEast1-PH	0.56	-0.16	0.02	0.00	**0.74***	0.57	0.36	-0.36	-0.14	0.04	0.09	0.31	0.27	0.18	0.23	0.04	**0.79****	-0.25	0.11	-0.36
Solsonès (Catalonia, Spain)	MeditEast2-PS	0.36	**0.75*****	0.02	-0.40	0.20	0.27	0.41	0.37	0.45	0.42	**0.51***	0.36	**0.51***	-0.21	-0.03	0.10	0.32	0.41	0.19	0.38
	MeditEast2-PN	0.19	0.48	0.32	0.31	**0.48***	0.38	0.43	0.16	0.15	**0.48***	0.29	0.36	0.27	0.18	**0.51***	0.04	0.19	0.31	0.42	0.40
	MeditEast2-PH	0.40	**0.73****	0.04	0.06	0.24	-0.01	**0.58****	0.30	0.12	0.03	**0.57****	**0.53***	-0.03	0.12	0.24	0.01	0.36	0.33	0.20	-0.03
	MeditEast2-PNPH	0.10	0.48	0.23	0.50	0.29	0.10	**0.67***	0.24	0.43	0.12	0.33	0.52	0.08	0.40	0.21	0.19	**0.71***	0.19	0.38	0.07
Pinar Grande (Soria, Spain)	MeditCentral-PS	**0.64*****	0.25	-0.10	-0.07	0.33	**0.54****	0.01	-0.10	-0.04	0.25	**0.72*****	0.23	-0.17	-0.28	0.20	**0.52****	0.03	0.03	0.10	-0.10
Almazán (Soria, Spain)	MeditCentral-PP	**0.74****	0.57	0.07	0.14	-	0.52	**0.74****	0.17	0.29	-	0.26	**0.94*****	0.54	-0.31	-0.14	-0.09	0.60	0.37	0.26	0.03
Villaluenga de la Vega (Palencia, Spain)	MeditWest1-PS	0.43	**0.74****	0.10	0.55	0.05	-0.05	0.14	-0.14	0.38	0.12	0.40	0.43	0.02	**0.74****	-0.10	0.24	**-0.64***	-0.21	0.31	-0.21
	MeditWest1-PP	**0.68****	**0.62****	0.20	**0.57***	0.18	0.18	**-0.76*****	**-0.66****	0.08	**0.58****	**0.55***	0.36	-0.08	**0.68****	0.22	0.06	**-0.53***	**-0.67****	0.17	0.38
Tudela del Duero (Valladolid, Spain)	MeditWest2-PP	0.43	0.60	0.03	-0.03	0.31	-0.14	-0.66	0.09	0.20	-0.37	-0.07	0.46	-0.11	-0.29	-0.18	0.43	**0.82****	0.21	0.00	0.29

Abbreviations: Plot abbreviations are as in Table 1. Climate variables: Psum – precipitation of summer (June – August), Paut – precipitation of autumn (September – November), Tsum – temperature of summer (June – August), Taut – temperature of autumn (September – November). Dendrochronological variables: LWi – the latewood width index, TRWi – the tree ring width index.

Table A3: Spearman partial correlation coefficients obtained by relating mushroom biomass (kg ha^{-1} year^{-1}) to latewood-width index (LWi) and sporocarp density (No. ha^{-1} year^{-1}) to tree-ring width index (TRWi) for both fungi guilds, under the controlling effect of climate variables (precipitation and temperature of autumn and summer). Correlations were calculated per each plot (i.e., study site – species ID).

Site (region, country)	Plot	Biomass myco. - LWi				Biomass sap. - LWi				Density myco. - TRWi				Density sap. - TRWi			
		Psum	Paut	Tsum	Taut	Psum	Paut	Tsum	Taut	Psum	Paut	Tsum	Taut	Psum	Paut	Tsum	Taut
Kitsi (Lieksa, Finland)	BorealFinEast-PS	-0.15	0.20	0.21	0.06	-0.33	-0.24	-0.31	-0.35	-0.03	0.33	0.49	**0.53***	-0.11	-0.32	-0.15	0.05
Kalimeenoja (Oulu, Finland)	BorealFinWest-PS	-0.03	-0.29	-0.03	0.02	-0.12	-0.45	-0.10	-0.12	-0.18	-0.23	-0.19	-0.09	**-0.53***	**-0.58****	**-0.57***	**-0.51***
La Chanéaz (Payerne, Switzerland)	TemperateSwitz-FS	-	-	-	-	-	-	-	-	-0.18	-0.15	-0.20	-0.23	-0.27	0.27	-0.34	-0.31
Pre-Pyrenees (Catalonia, Spain)	MeditMontane1-PN	0.59	**0.74***	0.61	**0.86*****	0.02	0.16	0.00	-0.11	0.30	0.53	0.51	0.57	-0.02	-0.02	-0.05	0.40
	MeditMontane1-PSPN	**0.78***	**0.90****	**0.93*****	**0.90****	0.41	**0.81***	**0.82***	**0.78***	0.48	**0.75****	**0.73***	**0.75****	-0.24	0.04	0.27	0.21
Pyrenees (Catalonia, Spain)	MeditMontane2-PS	0.61	**0.80***	**0.79***	**0.82****	0.46	0.55	0.54	0.40	0.13	0.49	0.50	0.49	0.52	0.66	0.58	0.49
Prades (Catalonia, Spain)	MeditEast1-PS	-0.1	-0.10	0.12	-0.02	0.37	0.35	0.55	0.40	0.19	0.22	0.44	0.20	0.21	0.35	0.08	0.21
	MeditEast1-PP	0.71	0.71	0.68	**0.76***	0.11	0.02	0.01	-0.08	-0.53	-0.32	-0.17	-0.32	-0.37	-0.36	-0.62	-0.53
	MeditEast1-PH	0.68	**0.76***	**0.74***	**0.75***	-0.25	0.24	0.02	0.06	0.22	0.47	0.30	0.18	-0.38	0.07	-0.42	-0.43
Solsonès (Catalonia, Spain)	MeditEast2-PS	-0.11	0.14	0.21	0.43	0.34	0.41	**0.57****	0.04	-0.29	-0.18	0.07	0.05	0.37	0.30	**0.50***	0.34
	MeditEast2-PN	**0.56***	**0.53***	**0.57****	0.41	0.33	**0.52***	**0.52***	0.47	0.43	**0.67****	0.47	0.48	0.46	0.48	0.36	0.27
	MeditEast2-PH	-0.04	0.35	0.25	0.26	0.05	0.03	0.10	-0.07	-0.14	0.37	0.23	0.21	-0.04	0.02	0.01	-0.22
	MeditEast2-PNPH	0.29	0.26	0.28	0.22	0.08	0.05	0.11	0.04	0.36	**0.67***	0.43	0.37	-0.02	0.32	0.04	-0.06
Pinar Grande (Soria, Spain)	MeditCentral-PS	0.12	0.29	0.32	0.35	0.07	0.25	0.23	0.27	-0.06	0.15	0.12	0.19	-0.34	-0.11	-0.10	-0.09
Almazán (Soria, Spain)	MeditCentral-PP	-	-	-	-	-	-	-	-	-0.29	0.31	0.08	-0.24	0.07	0.24	0.19	0.10
Villaluenga de la Vega (Palencia, Spain)	MeditWest1-PS	0.01	0.31	0.25	-0.17	0.12	0.15	-0.01	-0.01	-0.11	-0.11	-0.09	-0.25	-0.23	-0.28	-0.34	-0.26
	MeditWest1-PP	-0.05	**0.65****	0.30	0.14	**0.56***	0.41	0.45	**0.58***	0.08	0.32	0.21	0.15	0.38	0.33	-0.03	0.37
Tudela del Duero (Valladolid, Spain)	MeditWest2-PP	0.26	0.12	0.39	0.31	-0.35	-0.18	-0.39	-0.37	-0.19	-0.22	-0.32	-0.30	-0.06	0.45	0.57	0.30

Abbreviations: Plot abbreviations, as well as the fungi ones, are as in Table 1. Climate variables: Psum – precipitation of summer (June – August), Paut – precipitation of autumn (September – November), Tsum – temperature of summer (June – August), Taut – temperature of autumn (September – November). Dendrochronological variables: LWi – the latewood width index, TRWi – the tree-ring width index.

Significance levels: '*' $0.05 < P \leqslant 0.1$, '**' $0.01 < P \leqslant 0.05$, '***' $P \leqslant 0.01$.

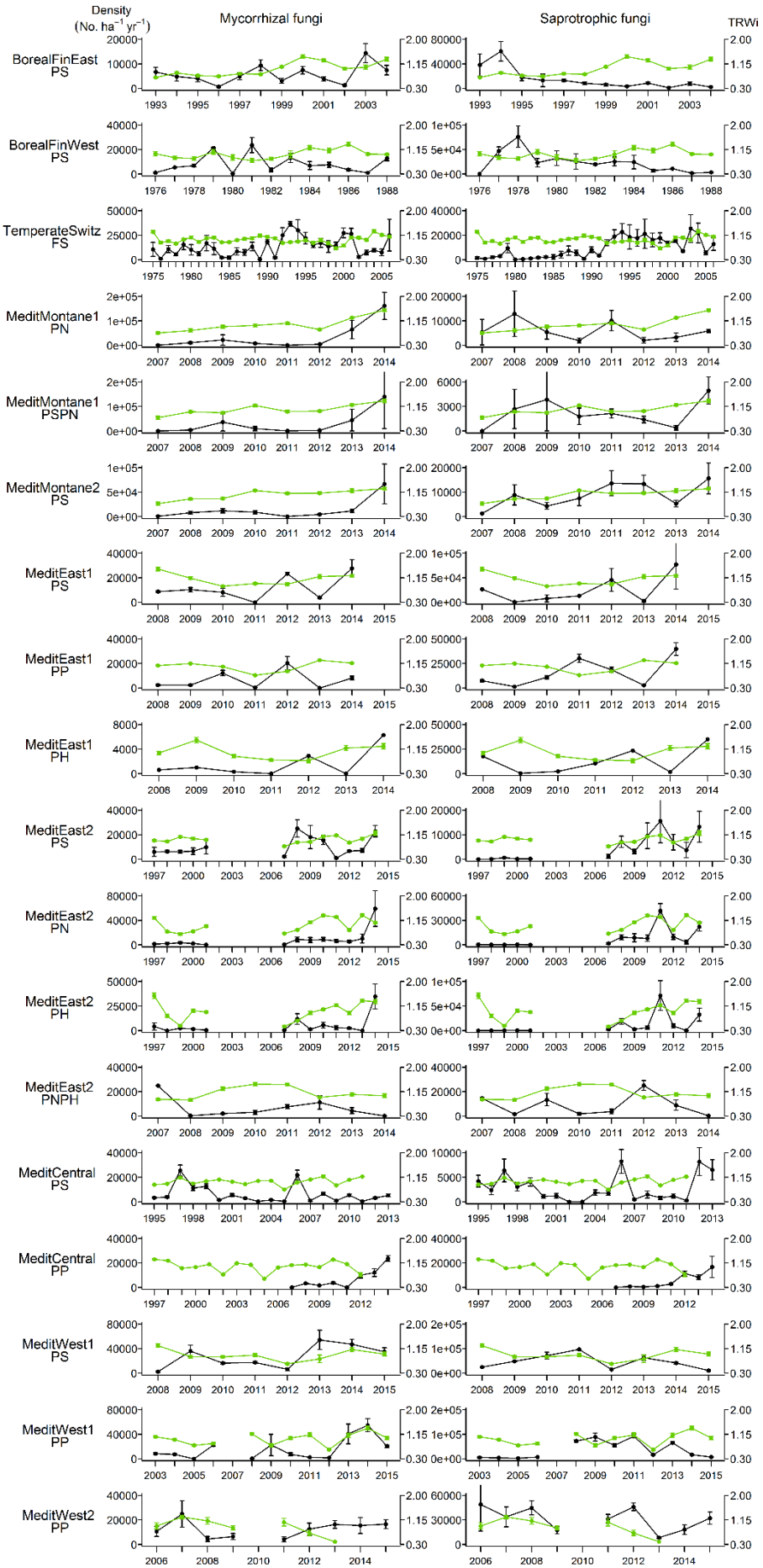


Figure A2: Temporal trends of mean annual mycorrhizal and saprotrophic fungi sporocarps (No. ha^{-1} year^{-1}) in black line and tree-ring width index (TRWi, green line) in the plots (i.e., the study site – species IDs). Sites and species abbreviations are as in Table 1.

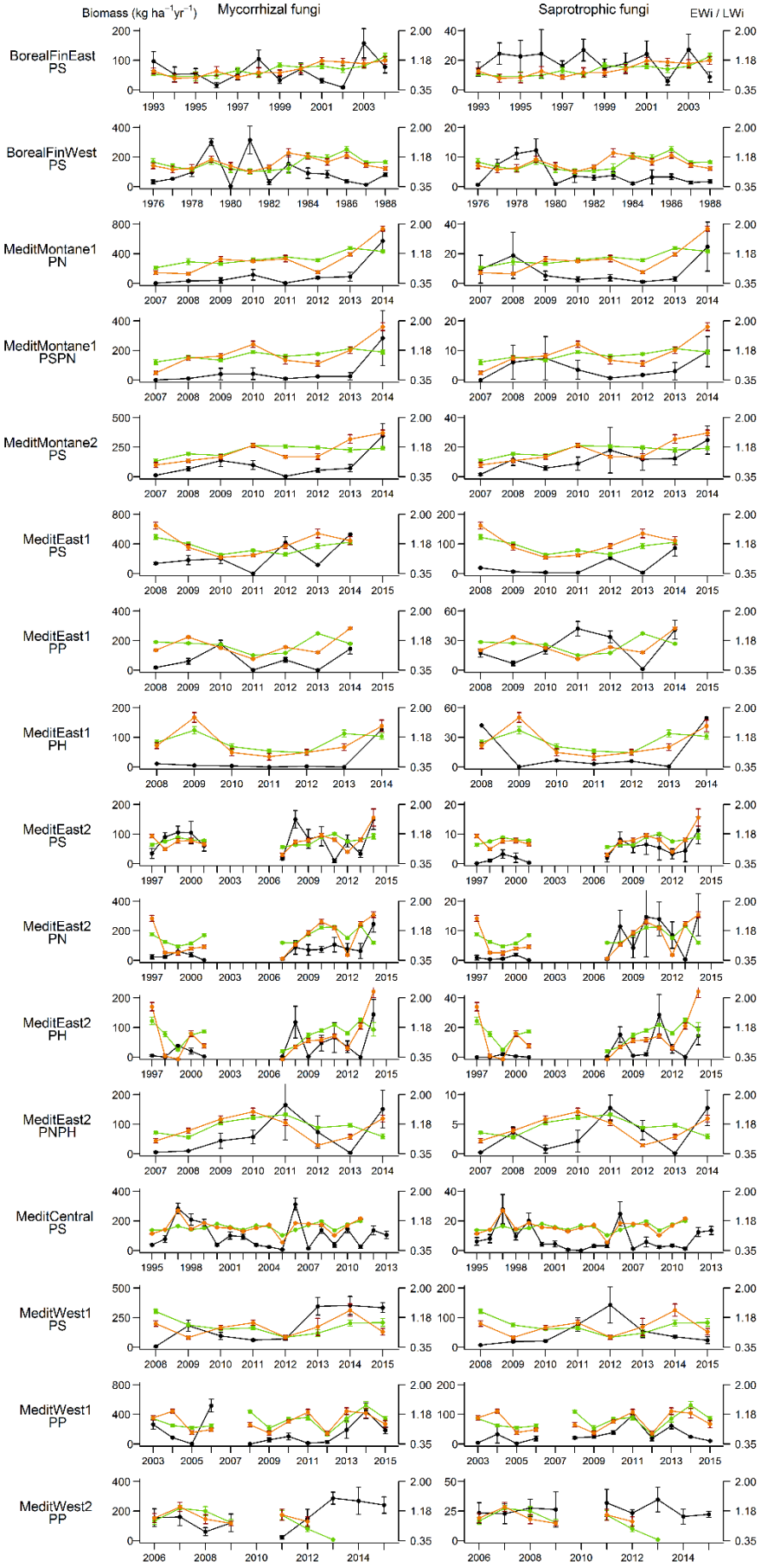


Figure A3: Temporal trends of mean annual mycorrhizal and saprotrophic fungi biomass (kg ha^{-1} year^{-1}) in black line, and earlywood (EW) and latewood (LW) width indices (green and brown lines, respectively) in the plots (i.e., the study site – species IDs). Sites and species abbreviations are as in Table 1.

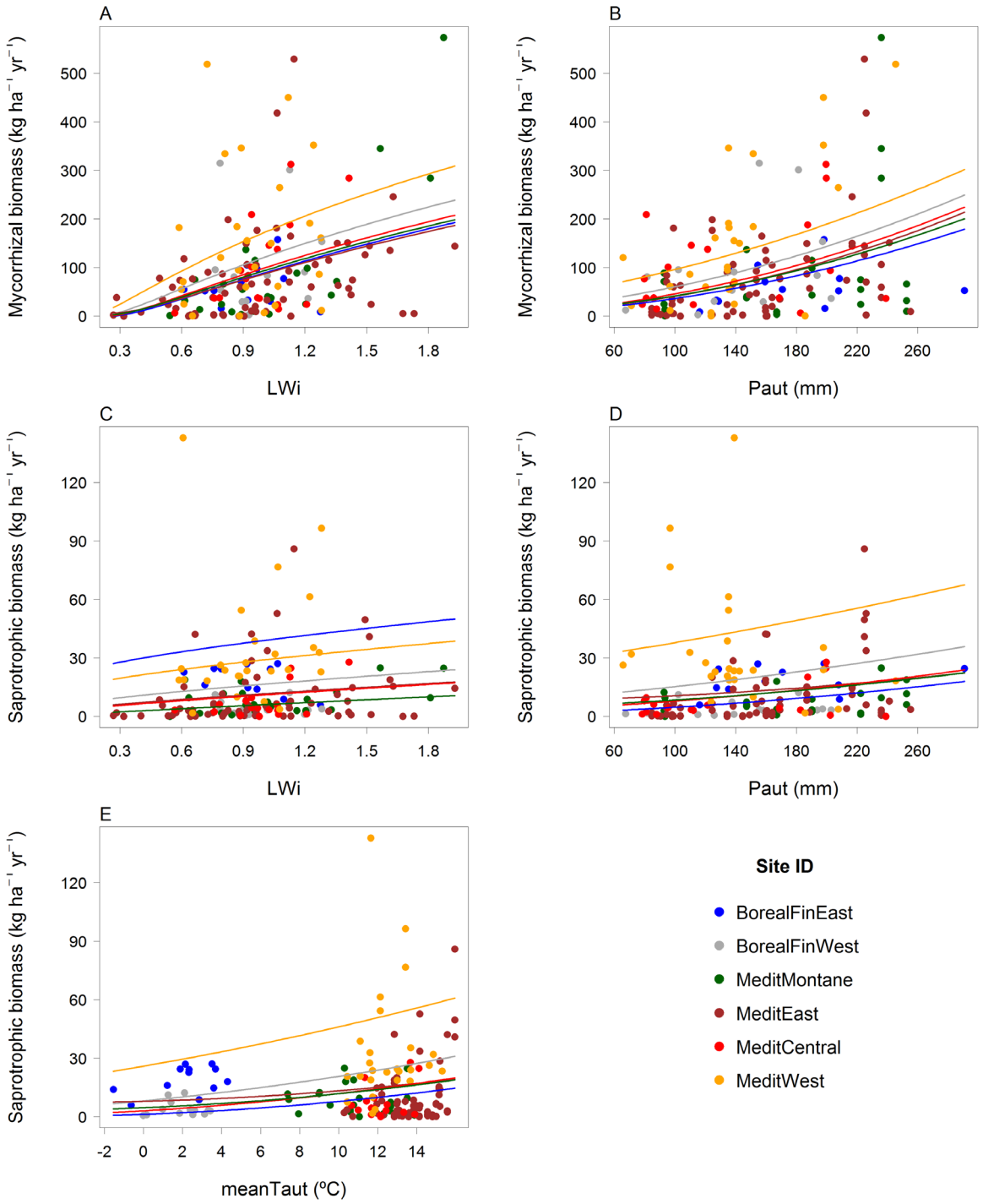
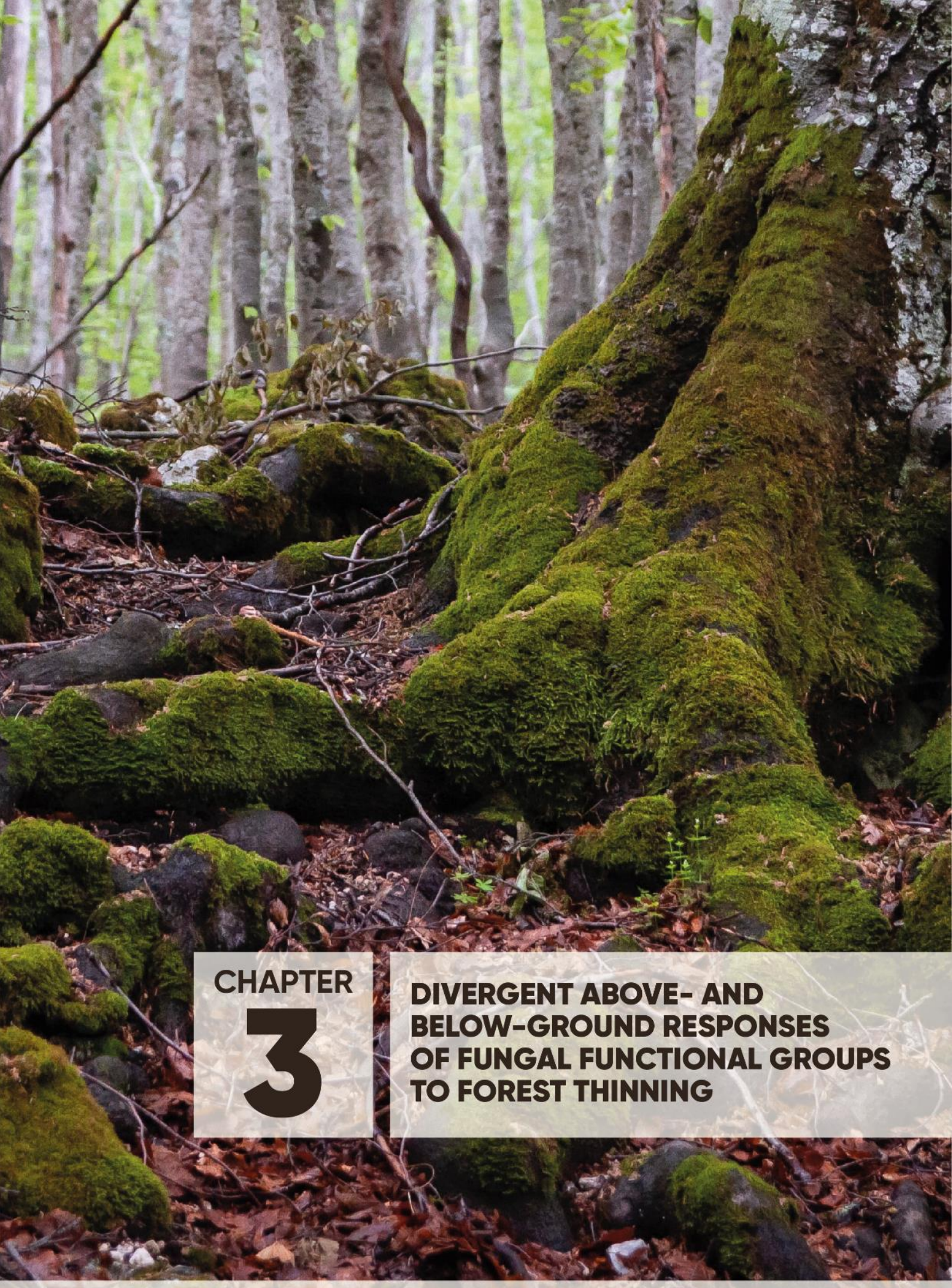


Figure A4: Effect of climatic and dendrochronological variables on the annual biomass of both mycorrhizal and saprotrophic fungi for each macrosite. The values assigned to the predictors in the simulation correspond to the mean values per each plot in the modeled data. Model predictions (represented as lines) were calculated for each plot using the mean values of predictors during the observation period, and then plot-wise predictions were averaged by macrosite. Dots denote the observed valued. Macrosites abbreviations are as in Figure 1. *Paut* denotes the total autumn precipitation, *meanTaut* denotes mean temperature of autumn, and *LWi* is the latewood width index.



CHAPTER

3

DIVERGENT ABOVE- AND BELOW-GROUND RESPONSES OF FUNGAL FUNCTIONAL GROUPS TO FOREST THINNING

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Divergent above- and below-ground responses of fungal functional groups to forest thinning

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Abstract

Forest disturbances have a strong effect on soil fungal communities and associated ecosystem processes. However, little is known about the response of mycelial biomass to disturbances, and how fungi reallocate carbon into different fungal structures under environmental stressors. We investigated above- and below-ground fungal biomass shifts in response to different intensities of forest management in Mediterranean *Pinus pinaster* forests. Soil fungal biomass was estimated by ergosterol quantification and production of sporocarps was estimated from repeated field samplings during 5 years in 26 experimental plots. Abundance of mycorrhizal and saprotrophic fungi belowground was determined using Pacific Biosciences sequencing of fungal ITS2 amplicons. Thinning had a prolonged negative effect belowground, inter- and intra-annually, on total fungal biomass and on the biomass of ectomycorrhizal fungi, but not on saprotrophic fungi. Total and ectomycorrhizal mushroom yields were negatively correlated with the total and the ectomycorrhizal mycelial biomass, respectively. Thinning also correlated positively with the aboveground/belowground ratio of both total and ectomycorrhizal fungal biomass. We show potential short-term shifts in resource allocation of fungi from below- to above-ground structures under disturbances such as forest thinning. Ectomycorrhizal fungi may respond to disturbances by increasing reproduction rather than colonizing the surrounding soil.

Keywords: fungal dynamics, ectomycorrhizal, saprotrophic, ergosterol, high throughput sequencing

1. Introduction

Fungi are pivotal drivers of soil processes in forest ecosystems and their functions include the assimilation and release of nutrients, contributing to soil organic carbon (C) dynamics and forest growth (Rayner and Boddy, 1988; Smith and Read, 2008). Ectomycorrhizal (ECM) symbiosis is the most widespread form of fungal symbiosis with tree roots, where photosynthetically fixed carbohydrates are allocated to the fungi in exchange for improved nutrient uptake (Ekblad et al., 2013; Smith and Read, 2008; Steidinger et al., 2019). In forest ecosystems, about half of the photosynthetic C supply is allocated belowground to roots and ECM fungi (Gill and Finzi, 2016). The extramatrical mycelium (EMM) is the main belowground fungal structure foraging for nutrients in soils and supplying them to their

tree host (Cairney, 2012). Production and turnover of EMM represents a significant belowground C flux with impact on soil nutrient cycling and belowground C storage (Clemmensen et al., 2015; Ekblad et al., 2013; Fernandez et al., 2019, 2016), and relates to variation in fungal community composition and dynamics (Baskaran et al., 2016; Clemmensen et al., 2015; Hagenbo et al., 2018). Since forest management has a strong effect on forest C allocation, fungal community composition and belowground processes (Jones et al., 2003), forest management is likely to contribute to changes in mycorrhizal C dynamics and functions (Kohout et al., 2018; Kyaschenko et al., 2017). However, information of how this forest disturbance may affect EMM dynamics is not known, and the extent to which fungal communities may redirect C fluxes into either reproductive or vegetative structures in response to disturbances is uncertain.

Ectomycorrhizal fungi sporocarps account for a large proportion of the fungal biomass, being strongly influenced by host performance, and allocation of C to belowground (e.g., Bonet et al., 2012; De la Varga et al., 2012; Egli et al., 2010). Both aboveground and belowground fungal structures are sensitive to weather and site conditions (e.g., Castaño et al., 2018b; Karavani et al., 2018; Martínez de Aragón et al., 2007; Taye et al., 2016), as well as to changes in forest stand structure (Hagenbo et al., 2017). Altering the stand structure by forest management practices may modify mushroom biomass production either directly, through interfering in the C flux (Högberg et al., 2001), or indirectly by changing the microclimate conditions (Karavani et al., 2018; Pilz and Molina, 2002). However, forest management treatments have so far shown contrasting effects on mushroom production (Tomao et al., 2017). For example, several studies have observed non-linear responses of mushroom yields to forest management intensity, with low to moderate thinning treatments resulting in the maximum yields (e.g., Ayer et al., 2006; Bonet et al., 2012; Kropp and Albee, 1996; Salerni and Perini, 2004). Conversely, heavy thinning (e.g., Salerni and Perini, 2004) or clear-cutting (e.g., Durall et al., 2006; Ohenoja, 1988) drastically reduced the mushroom production due to removal of the host trees and accelerated drying of the soil (Pilz and Molina, 2002).

While the aboveground fungal production has been widely studied, little is known about the mycelial biomass and its response to disturbances. To date, previous research has shown contrasting results concerning how forest management affects soil fungal communities (Tomao et al., 2020). For instance, heavy disturbances (e.g., clear-cutting) have been shown to severely alter the soil fungal community composition (Hartmann et al., 2012; Kohout et al., 2018; Kyaschenko et al., 2017; Parladé et al., 2019; Varenius et al., 2016), whereas less intensive disturbances (e.g., thinning, foliage defoliation) have demonstrated to have limited effects on the belowground fungal communities (e.g., Castaño et al., 2018a; Sterkenburg et al., 2018) or fungal biomass (e.g., Hendricks et al., 2016; Parladé et al., 2019). Heavy disturbances that interrupt the mycelium contact with the C source of the host, may decrease the relative abundance of the ECM fungal guild while increasing the relative abundance of non-ECM fungi (e.g., saprotrophs) (Kyaschenko et al., 2017; Parladé et al., 2019). This pattern may be reversed with forest development as an effect of re-colonisation of resilient root-associated communities, as observed by Chen et al. (2019) and Kyaschenko et al. (2017). However, other studies suggest that the belowground fungal biomass does not change as long as a certain number of host trees remain after the disturbance and the fungal networks are preserved (cf. Mediavilla et al., 2017; Parladé et al., 2017; Sterkenburg et al., 2019). Additionally, fungal responses to disturbances may depend on the traits of a given

species or community. For example, it seems that fungal response to several disturbances (e.g., nitrogen deposition, drought) promote mycorrhizal fungal species with a smooth mantle and few emanating hyphae (Castaño et al., 2018a; Ekblad et al., 2013; Fernandez et al., 2016).

Current studies on the effect of forest management on both aboveground and belowground fungal biomass components are scant and only focused on specific species, with still non-conclusive results. For example, several studies, focused on specific species, report no relationships between the biomass of mycelium and sporocarps (De la Varga et al., 2013; Parladé et al., 2017), whereas others observed a positive correlation between mushroom growth and the mycelial biomass (Mediavilla et al., 2017; Suz et al., 2008). Additionally, Pestaña and Santolamazza-Carbone (2011) found that 75% defoliation in a temperate *Pinus pinaster* forest modified the mycorrhizal community, whereas mushroom biomass or abundance was not affected. Uncoupled above- and below-ground responses of fungi under environmental stressors may respond to a resource allocation strategy of fungi to cope with such stressors, so that fungi may prioritize either to reproduce or to colonize the surrounding soil, but this question has received little attention in the literature.

In the present study, we investigated the response of the belowground fungal biomass to different thinning intensities over time, both inter- and intra-annually (up to 5 years and 12 months, respectively), and compared it with the effect of thinning on aboveground fungal biomass (sporocarps). We collected and analysed total fungal biomass data, as well as separately quantified biomass data for different functional guilds (i.e., ECM and saprotrophic fungi) in Mediterranean *P. pinaster* forests. Mushroom yield was assessed by repeated sampling of epigeous sporocarps, while belowground fungal biomass was quantified using ergosterol analysis from soil samples. We hypothesized that (i) in the short term, there will be a decrease of mycelium biomass in the total and ECM fungi after thinning treatment, but the thinning effect will disappear over time. This hypothesis was based on the assumption that thinning may change C allocation to roots and associated symbionts belowground. We further hypothesized that (ii) the belowground biomass of the saprotrophic fungal guild will not show a clear response to thinning since they are not energetically dependent on photosynthetic C, as opposed to ECM fungi.

2. Material and methods

2.1. Study area

In 2008, we established a long-term experimental setup with 26 plots, located in the Natural Protected Area of Poblet (Northeast Spain, 41° 21′ 06.5″ N and 1° 02′ 25.8″ E), at an altitude of 400-1201 m a.s.l. The average annual rainfall is 659 mm and the average annual temperature is 11.8 °C (data from L' Espluga de Francolí station, 41° 23′ 47″ N, 1° 06′ 10″ E, 412 m) with a summer drought lasting approximately three months (Ogaya et al., 2015). The overstorey is dominated by *Pinus pinaster* Aiton trees, aged 60 years-old, and the understorey is dominated by few isolated *Quercus ilex* L. trees with some sparse occurrences of other woody species such as *Arbutus unedo* L. and *Phillyrea latifolia* L. The soils are classified as a cambisol (FAO, 1998), and are characterized by siliceous minerals with sandy loam textures, pHs ranging from 6.1 to 6.6 and organic matter contents ranging from 2.95 to 10.51 (Castaño et al., 2017).

2.2. Thinning experiment

The experimental design consisted of 26 permanent inventory plots of 100 m^2 (10 × 10 m), of which 13 were thinned during summer 2009 and the other 13 served as paired un-thinned plots (thinning intensities ranged from 26% to 71% in stand basal area). Plots were covering different aspects, altitudes (from 594 to 1013 m a.s.l.), slopes (3-23%), stand densities (350-2657 trees ha^{-1}) and basal areas (ca. 18-80 m^2 ha^{-1}), as described in Table 1. In order to avoid edge effects, each thinned plot was around 1600 m^2 in area (40 m × 40 m) with a central 100 m^2 sampling area. The trees of the thinned plots were systematically felled using a chainsaw and removed from the plot with minimum disturbance of the soil. Further information about the thinning procedure and the stand variables are available in Bonet et al. (2012), while Castaño et al. (2018a) provide, in the supplementary material, a schematic diagram of the experimental design.

Table 1: Summary of the main data on site characteristics and the aboveground and belowground fungal biomass of total fungi and ectomycorrhizal (ECM) guild. Values between brackets denote standard deviations. The inter-annual data were obtained in 2009 and from 2012 to 2015 (ECM fungi data did not include 2015), and the intra-annual data were obtained monthly from May 2013 to April 2014 (ECM data started and finished one month after).

							Average belowground fungal biomass (mg mycelia g soil^{-1})				Average aboveground fungal yield (kg ha^{-1})			
							Total		ECM		Total		ECM	
Paired plot	Plot	Alt (m)	Asp (°)	Slo (%)	Basal area (m^2 ha^{-1})	Thinning intensity (%)	Inter-annual	Intra-annual	Inter-annual	Intra-annual	Inter-annual	Intra-annual	Inter-annual	Intra-annual
301	301	1010	110	19	77.75 (0.12)	0	4.87 (1.43)	4.80 (1.01)	3.14 (1.33)	2.79 (0.66)	2.84 (2.78)	0.023 (0.04)	1.97 (2.39)	0.00 (0.00)
	301t				30.15 (1.93)	55	3.86 (1.44)	3.75 (1.07)	1.36 (1.06)	1.79 (0.58)	1.00 (1.99)	0.01 (0.01)	0.34 (0.76)	0.00 (0.00)
302	302	1013	135	22	80.42 (0.94)	0	3.67 (1.41)	3.21 (1.32)	2.64 (1.00)	1.77 (0.93)	4.02 (3.79)	0.19 (0.34)	2.47 (2.79)	0.00 (0.00)
	302t				42.61 (2.58)	28	4.59 (1.03)	3.97 (1.33)	3.09 (1.71)	2.24 (0.89)	4.43 (4.99)	0.79 (1.05)	3.44 (4.37)	0.08 (0.14)
303	303	903	20	19	49.77 (0.13)	0	3.31 (0.97)	4.10 (1.18)	1.80 (0.89)	2.65 (0.73)	4.67 (7.34)	0.31 (0.51)	4.27 (6.49)	0.00 (0.00)
	303t				35.73 (2.94)	47	2.01 (0.65)	1.68 (0.37)	1.13 (0.49)	1.12 (0.34)	2.64 (2.74)	0.25 (0.44)	2.60 (2.74)	0.00 (0.00)
304	304	879	360	22	35.53 (0.34)	0	3.86 (0.80)	3.60 (0.88)	2.79 (0.98)	2.32 (0.78)	1.05 (1.36)	0.02 (0.04)	0.99 (1.33)	0.00 (0.00)
	304t				30.23 (3.25)	47	3.38 (1.72)	2.80 (1.01)	1.94 (0.93)	2.08 (0.73)	1.89 (2.55)	0.07 (0.12)	1.46 (2.24)	0.00 (0.00)
305	305	744	90	18	64.36 (1.26)	0	2.72 (0.85)	2.65 (0.77)	-	1.32 (0.38)	2.90 (3.81)	0.03 (0.03)	1.63 (3.14)	0.00 (0.00)
	305t				49.51 (2.94)	33	4.28 (5.07)	3.23 (2.78)	-	1.42 (0.35)	4.80 (6.35)	0.26 (0.40)	4.26 (6.05)	0.00 (0.00)
306	306	759	40	23	60.05 (0.38)	0	2.58 (0.49)	2.16 (0.70)	2.17 (0.50)	1.39 (0.49)	2.64 (3.26)	0.03 (0.06)	2.07 (2.33)	0.00 (0.00)
	306t				25.85 (2.14)	58	2.30 (0.99)	2.19 (0.66)	1.57 (0.77)	1.17 (0.41)	3.27 (6.06)	0.01 (0.02)	2.97 (5.91)	0.00 (0.00)
307	307	796	60	18	36.23 (0.23)	0	3.26 (0.98)	3.56 (1.32)	2.18 (0.49)	1.98 (0.56)	2.87 (3.12)	0.08 (0.11)	2.12 (2.23)	0.00 (0.00)
	307t				24.03 (2.52)	31	2.37 (0.40)	2.55 (0.74)	1.72 (0.76)	1.51 (0.48)	8.29 (15.15)	0.06 (0.06)	7.46 (15.58)	0.00 (0.00)
308	308	835	65	15	32.35 (0.06)	0	3.54 (0.87)	3.24 (1.10)	2.49 (1.07)	2.25 (0.76)	3.94 (4.60)	0.14 (0.25)	3.01 (4.56)	0.00 (0.00)
	308t				23.38 (1.77)	36	3.47 (1.49)	2.23 (0.58)	1.50 (0.66)	1.56 (0.50)	1.83 (2.03)	0.06 (0.09)	1.28 (1.92)	0.00 (0.00)
309	309	852	20	13	31.79 (0.36)	0	3.18 (0.74)	3.31 (0.80)	1.92 (0.88)	2.19 (0.49)	2.21 (4.70)	0.03 (0.05)	1.85 (3.96)	0.00 (0.00)
	309t				19.41 (2.60)	71	3.51 (0.82)	2.72 (0.79)	2.06 (1.17)	1.98 (0.70)	5.07 (7.43)	0.75 (1.27)	4.42 (7.81)	0.00 (0.00)
312	312	633	10	23	30.92 (0.08)	0	2.02 (0.59)	2.21 (0.72)	1.41 (0.15)	0.96 (0.40)	6.48 (9.92)	0.00 (0.01)	5.61 (8.84)	0.00 (0.00)
	312t				45.20 (8.18)	32	2.27 (0.79)	1.77 (0.44)	1.80 (0.66)	1.01 (0.37)	10.31 (13.14)	0.04 (0.05)	9.75 (13.09)	0.00 (0.00)
313	313	609	340	5	42.43 (0.15)	0	3.28 (2.04)	3.23 (1.71)	1.35 (0.53)	1.39 (0.94)	1.09 (0.73)	0.06 (0.11)	0.60 (0.56)	0.00 (0.00)
	313t				33.59 (3.83)	63	2.77 (0.41)	2.68 (0.72)	2.04 (0.59)	1.40 (0.58)	4.17 (4.85)	0.35 (0.56)	2.78 (4.85)	0.00 (0.00)
315	315	626	260	23	42.24 (2.28)	0	2.92 (1.14)	3.08 (1.21)	1.57 (0.92)	0.72 (0.61)	1.88 (1.81)	0.03 (0.04)	0.00 (0.00)	0.00 (0.00)
	315t				51.74 (4.14)	26	2.67 (0.53)	1.96 (0.58)	1.49 (0.67)	1.09 (0.35)	0.84 (0.64)	0.00 (0.01)	0.42 (0.53)	0.00 (0.00)
316	316	644	30	3	34.29 (0.39)	0	3.77 (1.61)	3.04 (1.24)	2.27 (1.09)	1.70 (0.87)	0.91 (0.73)	0.02 (0.03)	0.49 (0.80)	0.00 (0.00)
	316t				35.53 (3.75)	61	1.59 (0.74)	1.95 (0.71)	0.81 (0.42)	0.66 (0.38)	3.04 (3.38)	0.21 (0.26)	2.26 (3.61)	0.00 (0.00)

Note: Plots with letter 't' denotes thinned plot, otherwise control plot. ' Alt' is the altitude above the sea level, 'Asp' is the aspect, 'Slo' is the slope, 'Total' stands for total fungal biomass and 'ECM' denote the ectomycorrhizal fungal biomass. Thinning intensity is given as a percentage of the stand basal area. Aboveground fungal yield includes ECM and saprotrophic mushrooms, while belowground fungal biomass comprises ECM, moulds, yeasts, black yeasts, litter saprotrophs, soil saprotrophs pathogens, moss-associated fungi and root-associated ascomycetes. Basal area and inter-annual values are averaged by years (n = 5 years for total and n = 4 for ECM fungal biomass), while intra-annual values are averaged by months (n = 12 months). The inter-annual data from the aboveground fungal yield represents the total mushroom production in November.

2.3. Quantification of belowground fungal biomass

2.3.1. Soil sampling

To investigate inter-annual variation in belowground fungal biomass, soil samples were systematically taken once every year at the month of November in all the 26 plots, starting in 2009 and continuing from 2012 to 2015. No sampling was conducted in 2010-2011 due to insufficient funding. Eight soil cores (two along each side of the plot) of 12 cm deep and 5 cm in diameter were extracted from each plot. The upper litter layer was discarded from all soil cores to reduce sampling of needle-associated saprotrophs (Voříšková et al., 2014). Soil samples were stored at 4 °C for < 24 h and then sieved using a 3-mm mesh. Sieved soils were freeze-dried and pooled to obtain a composite sample representing each plot for each of the sampling time-points. Each composite soil sample was homogenized using a pestle and mortar, resulting in a fine powder, and stored at -20 °C before DNA extraction and molecular analyses. In total, 416 composite soil samples were used to study inter- and intra-annual variation in soil fungal biomass, the intra-annual period ranging between May 2013 and April 2014.

2.3.2. Ergosterol analyses

Total fungal biomass in the soil samples was estimated by quantifying the fungal-specific biomarker ergosterol in 1 g of soil. Ergosterol was extracted as described by Nylund & Wallander (1992) and was chromatographically analysed as described by Hagenbo et al. (2017). Ergosterol data was converted to total soil fungal biomass using the a conversion factor of 3 μg ergosterol mg^{-1} dry matter (Salmanowicz and Nylund, 1988), and a correction factor (1/0.62) was applied to account for unextracted ergosterol (Montgomery et al., 2000). Technical replicates were included and results were consistent across samples, with SD ~ 10%.

2.3.3. Sequence analyses

Fungal DNA was extracted from 500 mg of soil using the NucleoSpin® NSP soil kit (Macherey-Nagel, Duren, Germany) following the manufacturer's protocol with a modification; 900 μl of buffer was added for sample lysis. Samples for sequencing were prepared following an optimized metabarcoding protocol according to Castaño et al., (2020). The fungal internal transcribed spacer 2 (ITS2) region was amplified in a 2720 Thermal Cycler (Life Technologies, Carlsbad, CA, USA) using the primers gITS7 (Ihrmark et al., 2012), ITS4 (White et al., 1990) and ITS4A (Sterkenburg et al., 2018). To identify switched tags, both primers were fitted with unique 8-bp tags, with each tag differing at least in three positions. The number of PCR cycles was optimised for each soil sample to reduce size-length biases (Castaño et al., 2020), with most of the samples amplifying well at 21–24 cycles. The final concentrations in the 50 μL PCR reactions were: 200 μM of each nucleotide, 2.75 mM $MgCl_2$, primers at 500 nM (gITS7) and 300 nM (ITS4 and ITS4A) and 0.025 U μL^{-1} of DreamTaq Green polymerase (Thermo Fisher Scientific, Waltham, MA) in the buffer supplied by the manufacturer. PCR cycling conditions were as follows: 5 min at 95°C, followed by 21–30 cycles of 30 s at 95°C, 30 s at 56°C, 30 s at 72°C and a final extension step at 72°C for 7 min before storage at 4°C. Samples were amplified in triplicates with negative extraction and PCR controls. Amplicons were purified using the AMPure kit (Beckman Coulter Inc., Brea,

CA, USA) and quantified using the Qubit high sensitivity (0.01-100 ng/µl) DNA quantification kit on a Qubit Fluorometer. Equal amounts of DNA from each sample were pooled, and the mix was further purified using the EZNA Cycle Pure kit (Omega Bio-Tek). Samples were sequenced at SciLifeLab NGI, Uppsala, Sweden, on a PacBio RS II system (Pacific Biosciences, Menlo park, CA, USA) using 26 SMRT cells.

2.3.4. Bioinformatic analysis

Sequences were quality filtered and clustered using the SCATA pipeline (https://scata.mykopat.slu.se/). Global singletons and sequences with length of <200 bp were first removed and remaining sequences were screened for primers (requiring 90% primer match) and sample tags (100% match). After collapsing homopolymers to 3 bp, sequences were pair-wise compared using 'usearch' (Edgar, 2010). Pairwise alignments were scored using a mismatch penalty of 1, gap open penalty of 0 and a gap extension penalty of 1. Sequences were clustered using single linkage clustering with a minimum similarity of 98.5% to the closest neighbour required to enter clusters.

2.3.5. Taxonomic and functional identification

We assigned putative taxonomy to the 550 most abundant species hypotheses (SHs; Kõljalg et al. (2013)), which represented 93% of the total sequences (Table S1 in Castaño et al. (2018b)). Then, SHs were assigned to the following functional guilds: ECM, moulds, yeasts, black yeasts, litter saprotrophs, soil saprotrophs (saprotrophic taxa commonly found in mineral soils), pathogens, moss-associated fungi and root-associated ascomycetes. Taxonomic identities at species level were assigned based on > 98.5% similarity with references in the UNITE (Abarenkov et al., 2010), International Nucleotide Sequence Database consortium (INSDc) databases, supported by neighbour joining phylogenetic trees (Castaño et al., 2018b). Finally, the proportion of sequences assigned to ECM and saprotrophic fungi was multiplied with the ergosterol-derived biomass estimates to calculate the separate biomass of ECM and saprotrophic fungi. Sequence data are archived at NCBI's Sequence Read Archive under accession number PRJNA309233 (ncbi.nlm.nih.gov/sra) and community data is available at the Dryad Digital Repository (doi: 10.5061/dryad.s71c1tp). Due to funding limitations, the fungal community analysis was conducted in 2009 and from 2012 to 2014, i.e., one year less than the biomass quantification of total fungi.

2.4. Quantification of aboveground fungal biomass

Over 2008-2015, all epigeous sporocarps (except parasitic fungi) were collected in each plot on a weekly basis throughout the autumn fruiting season, spanning over early September to late December. The sporocarps were taken to the laboratory for identification at species level (otherwise, at genus level) following the nomenclature of Hansen and Knudsen (1997; 1992) and classified as saprotrophic (including both wood and soil saprotrophs) or ectomycorrhizal, according to Agerer (2006) and Tedersoo et al. (2014). The dry weight was measured by weighting the sporocarps after drying in an air-vented oven at 35-40°C. Further

details regarding the mushroom productivity sampling and quantification can be obtained from Martínez de Aragón et al. (2007).

2.5. Statistical analysis

Inter- and intra-annual variation in biomass over thinned and control plots, was evaluated for statistical significance using linear mixed-effects models, accounting for repeated sampling and plot-level random variations. These models are able to elucidate the effect over time of different thinning intensities on the fungal biomass, as well as to avoid time-space dependence from the experimental design. Linear mixed-effects models are also capable to avoid repeated significance testing and pseudo-replication of the data, which are likely to contribute to both type I and type II errors (Harrison et al., 2018). All statistical analyses were conducted in R statistical software (R Core Team, 2014), and linear mixed effect models where done using the lme4 package (Bates et al., 2014) and correlation analyses where done using the psych-package (Revelle, 2015).

Concerning the mixed-effects models describing inter-annual variation in biomass, we fitted two models on total fungal biomass and ectomycorrhizal fungal biomass. Specifically, one model focused on the below-ground biomass (mycelia) and a second model which was aimed at predicting the ratio of above/below-ground biomass (i.e., the ratio between the total mushroom yield of November and the mycelial biomass collected in November). We also tried to fit similar models for saprotrophic fungal guild (including both litter and soil saprotrophs altogether). The models for saprotrophic biomass are also suitable as a benchmark to better evaluate the hypothesized effect of thinning on ECM fungal biomass, i.e., assuming that saprotrophic fungi, unlike ECM fungi, are not directly related to thinning as they do not depend on the C allocation from the host. Thinning intensity and time after thinning were the predictor variables in the mixed-effects models, while the paired plot and the year were considered the random effects. The unit of the belowground fungal biomass was converted from mg mycelia g $soil^{-1}$ to kg ka^{-1} in order to compute the ratio in the same units (Kyaschenko et al., 2017). This conversion was computed based on the area (radius 2.5 cm), the weight (62.5 g) and the length (12 cm) of the cylindrical soil cores. Concerning the intra-annual models, we only fitted belowground biomass while using the intensity of thinning as the only fixed effect and paired plot and months as the random factors. For all models, Snowdon’s bias correction factor was used to correct the predictions for the back-transformation bias to the original scale (Snowdon, 1991). Additionally, we performed Spearman correlation analysis in order to complement the mixed-effect models on the aboveground/belowground ratio.

The best-fit models were selected considering largely the lowest Akaike Information Criterion (AIC) values (Burnham and Anderson, 2003) by means of the Multi-Model Inference (*MuMIn*) package (Bartoń, 2013). We also used the likelihood comparisons to test the significance of the random effects by the “ANOVA” function (Chambers and Hastie, 1992). We also estimated a pseudo-R^2 of the selected models following Nakagawa & Schielzeth (2013), which includes both marginal (R^2m, accounting for the proportion of variance explained by the fixed factors) and conditional (R^2c, accounting for the proportion of variance explained by the whole model) R^2 values. Additionally, we considered the following criteria in model evaluation: parsimony, robustness, statistical significance of parameters (*t-value* $\geqslant$ 2), consistency with current ecological knowledge, mean bias (from

both marginal and conditional predictions), precision, homoscedasticity, normal distribution of residuals and root-mean-square error (RMSE), and absence of multicollinearity among predictor variables (assessed by Variance Inflation Factor – VIF).

3. Results

3.1. Inter-annual effect of thinning intensity on below- and above-ground fungal biomass

Thinning had a prolonged negative effect on the total belowground fungal biomass and on the biomass of ECM fungi (Figs. 1C, 1D, 2A, 2B and Table 2). On average over the years, the total mycelial biomass decreased significantly ($P = 0.01$) from 3.4 ± 0.5 to 2.6 ± 0.4 mg g soil^{-1}, and the ECM mycelial biomass decreased significantly ($P = 0.04$) from 2.2 ± 0.7 to 1.4 ± 0.5 mg g soil^{-1}. The total belowground fungal biomass was lowest at the year of thinning (year-0; 2.4 ± 0.2 mg g soil^{-1}), reaching a maximum at the third year after thinning (3.5 ± 0.3 mg g soil^{-1}) and decreasing over the following years (e.g., 2.9 ± 0.3 mg g soil^{-1} in year-5) (Figs. 1C and 2A). A linear increasing trend was detected from the lowest ECM mycelial biomass in year-0 (1.1 ± 0.2 mg g soil^{-1}) until a maximum standing biomass was reached in the 4th and 5th year after thinning (2.4 ± 0.4 mg g soil^{-1}) (Figs. 1D and 2B). No significant model was found for the belowground biomass of saprotrophic fungi as it remained relatively constant throughout the years, and only displayed a low inter-annual variability in biomass (Fig. S1C).

Total and ECM mushroom yields correlated negatively with the total- and the ECM soil mycelial biomass, respectively. In the case of total fungal biomass, the correlation was -0.18 in control plots ($P = 0.004$) and -0.24 in thinned plots ($P = 0.003$); and in the case of ECM fungi, the correlation coefficients were -0.25 in control plots ($P = 0.001$) and -0.39 in thinned plots ($P < 0.001$). Additionally, thinning intensity correlated positively with the aboveground/belowground ratio of total and ECM fungal biomass, respectively (Table 2 and Figs. 2C-D). The effect of thinning intensity on these ratios was higher right after thinning and then tended to fade over time. On average over the years, the aboveground/belowground ratio of total fungal biomass increased significantly ($P = 0.05$) with increasing thinning intensity from 3.50E^{-3} ± 3.53E^{-3} to 7.61E^{-3} ± 7.66E^{-3}. This ratio was highest at the year of thinning (year-0; 0.01 ± 0.00) and decreased to 2.47E^{-4} ± 2.80E^{-5} at the fourth year after thinning (Fig. 2C). Similarly, the aboveground/belowground ratio of ECM fungal biomass increased significantly ($P = 0.01$) with increasing thinning intensity from 0.006 ± 0.005 to 0.03 ± 0.05. A linear decreasing trend was detected from the highest ratio of ECM fungal biomass in year-0 (0.03 ± 0.03) until a minimum value for this ratio was reached in the last year of the ECM study campaign (year-5; 2.1E^{-3} ± 7.4E^{-4}), as denoted by the negative interaction between thinning intensity and time after thinning ($P_{Intensity\ x\ Time} = 0.010$; Fig. 2D; Table 2). Similar to the belowground fungal biomass results, no significant model was found for the aboveground/belowground ratio of saprotrophic fungi.

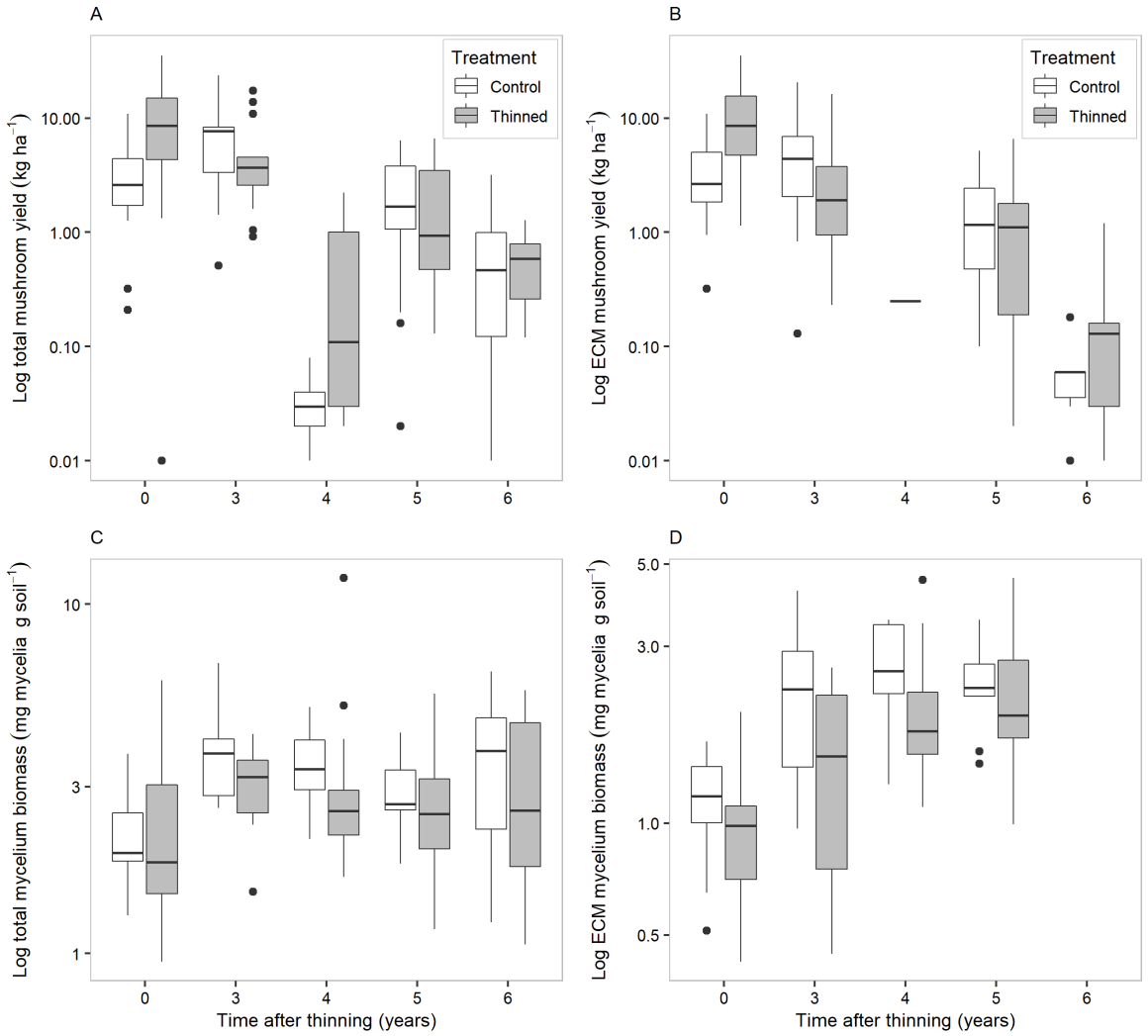

Figure 1: The aboveground and belowground thinning effect along the years since the thinning treatment in summer 2009 on: total fungi (A, C), ectomycorrhizal (ECM) fungi (B, D). Dots denote outlier values (i.e., values that fall below Q1 – 1.5 IQR or above Q3 + 1.5 IQR). There is not available data in the sixth year after thinning in the belowground ECM biomass (D), and there is only one value from one plot in the fourth year after thinning in the ECM mushroom yield (B). The yield data arise from the total production of November, while the belowground biomass data were obtained in a single day in November.

Table 2: Summary of fitted models for the belowground biomass (mg mycelia g soil^{-1}) of total and ectomycorrhizal (ECM) fungi, and for aboveground/belowground ratio of total and ECM fungi, over the years after thinning.

		Fixed effects coefficients				Random effects				Pseudo R^2				
						Paired plot		Year	Residuals					
	Fungal biomass	Intercept	Thinning intensity	Time	Thinning intensity x Time	Intercept	Thinning intensity	Intercept	Intercept	R^2m^a	R^2c^b	**Marginal bias**	**RMSE**	**n**
Belowground	Total fungi	1.128***	-0.353**	-	-	0.034	-	0.031	0.129	0.04	0.36	-0.070	0.34	127
	ECM	0.666*	-0.623*	-	-	0.059	0.546	0.137	0.122	0.07	0.64	-0.100	0.31	95
Ratio	Total fungi	-7.092***	1.091*	-	-	0.161	-	2.640	2.004	0.02	0.59	-0.003	1.36	114
	ECM	-4.813***	2.902*	-0.310**	-0.874*	0.137	-	-	1.874	0.39	0.44	0.000	1.293	66

Fungal biomass is the dependent variable and was log-transformed. Thinning intensity (%, expressed as a decimal), time (years after thinning treatment) and the interaction of both are the independent variables. Marginal bias is the mean bias error of the marginal predictions while the conditional bias is zero in all models (mg mycelia g soil^{-1} in belowground models), *RMSE* is the root of mean square error (mg mycelia g soil^{-1} in belowground models) and *n* is the number of observations.

[a,b] Marginal (proportion of variance explained by the fixed factors, R^2m) and conditional (proportion of variance explained by fixed plus random factors, R^2c) R^2 values were computed following Nakagawa and Schielzeth (2013).

Significance levels: '***' $P < 0.001$; '**' $P < 0.01$; '*' $P < 0.05$.

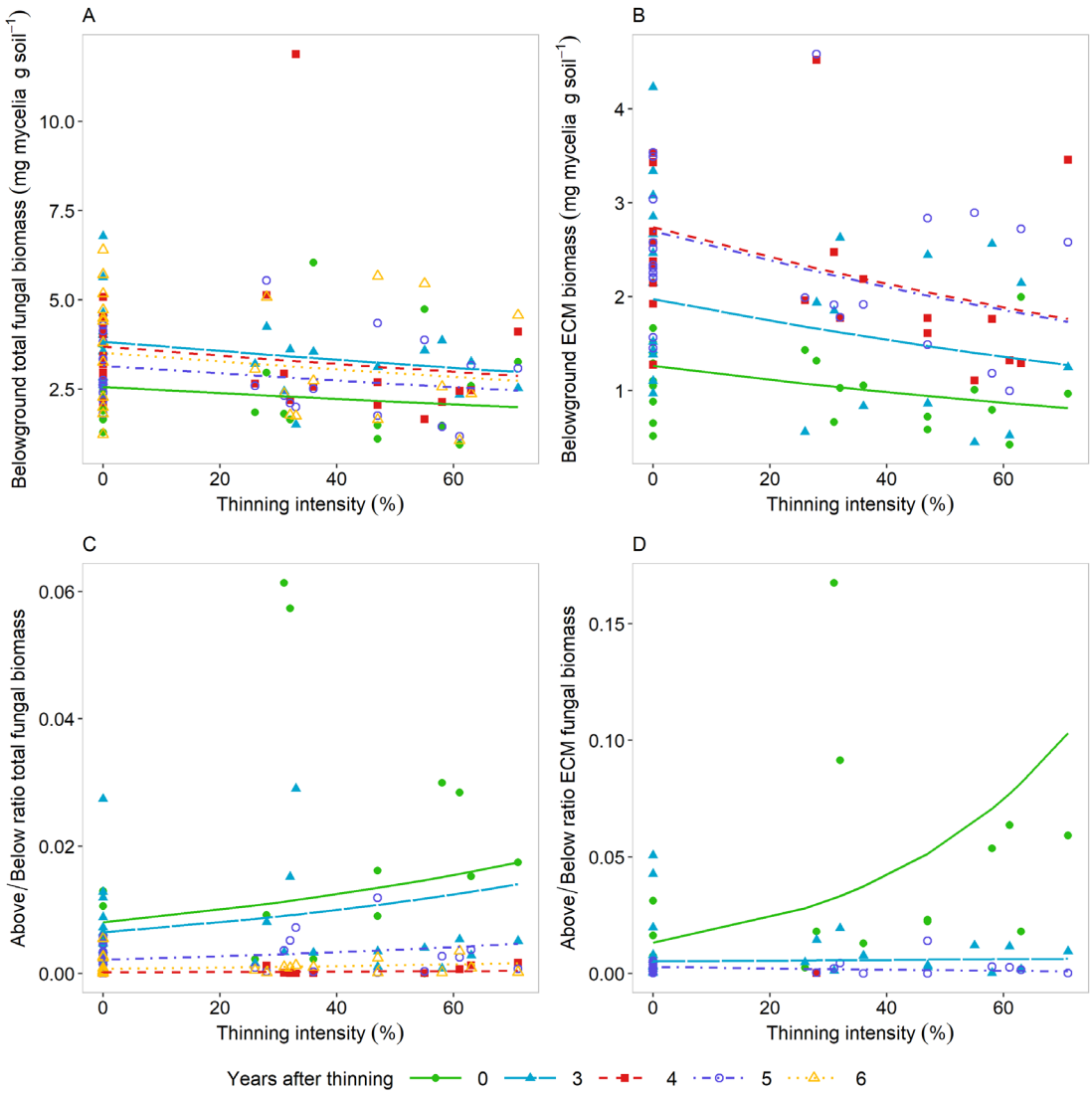

Figure 2: Inter-annual variation in predicted biomass of total and ectomycorrhizal (ECM) fungal biomass and their relationships with thinning intensity in Mediterranean *Pinus pinaster* forest stands. Figures A and B show the belowground biomass, while figures C and D show the ratio between aboveground biomass (sporocarps) and belowground biomass. Straight lines indicate the predicted changes in biomass over time and dots denote the observed fungal biomass over time.

3.2. Intra-annual effect of thinning intensity on belowground fungal biomass

Both total and ECM belowground biomass correlated negatively ($P < 0.001$) with thinning intensity, over an annual cycle (spring 2013 – spring 2014), while no correlation was observed between thinning intensity and biomass of saprotrophic fungi (Figs. 3C, 3D, 4A, 4B, S1D and Table 3). On average over the months, the belowground total fungal biomass decreased from 3.2 ± 0.5 to 2.2 ± 0.4 mg g soil^{-1}, while the belowground ECM fungal biomass declined from 1.8 ± 0.3 to 1.2 ± 0.2 mg g soil^{-1}. Both total and ECM biomass varied monthly in control and thinned plots, reaching the maximum in October-December (Figs. 4A and 4B). Mushroom productivity was low during October-November 2013 (Fig. 3A) and only a negligible growth of ECM sporocarps (0.25 kg ha^{-1}) was observed during this period (Fig. 3B).

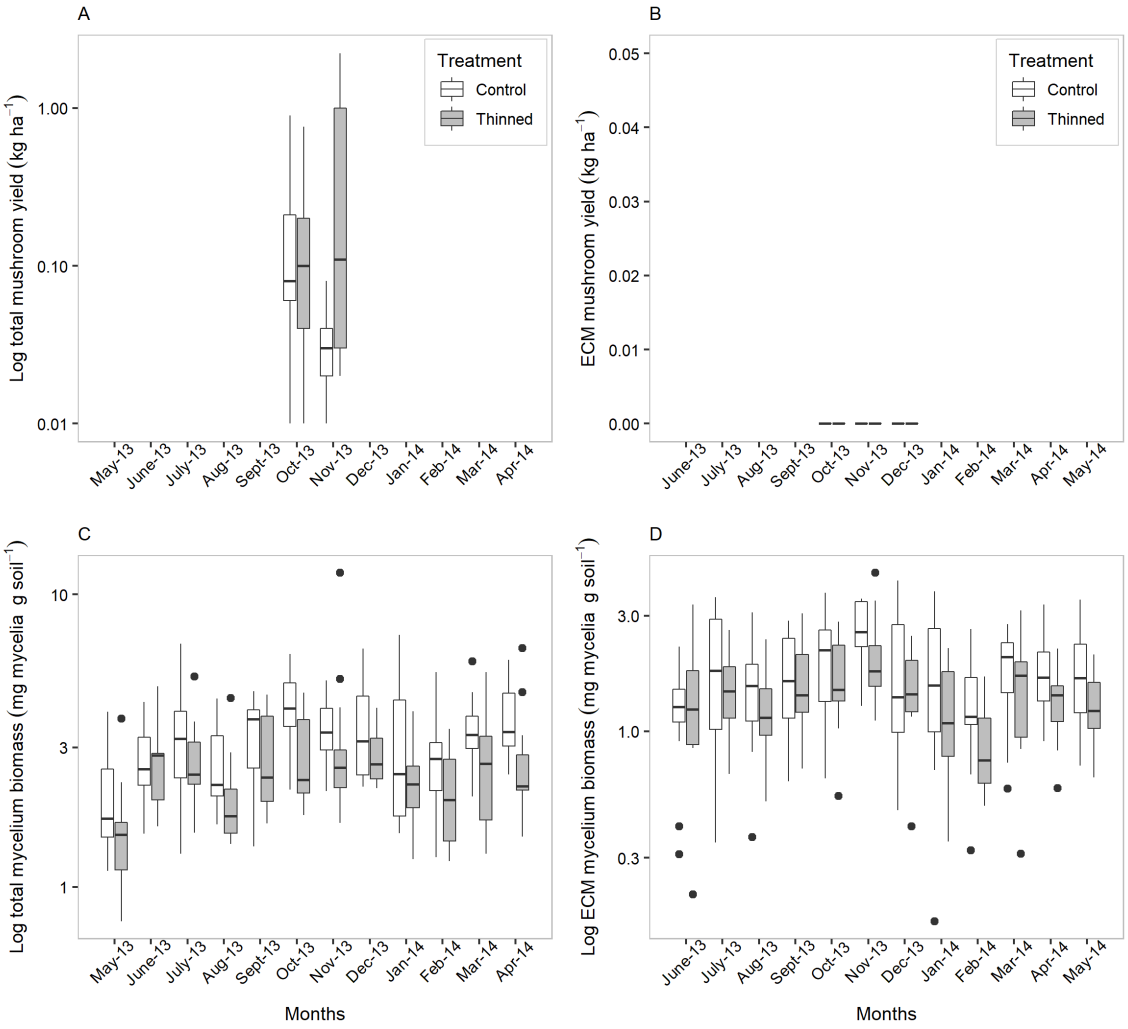

Figure 3: Effects of thinning in *Pinus pinaster* forests on aboveground and belowground fungal biomass dynamics over a year (May 2013 to April 2014): total fungi (A, C) and ectomycorrhizal (ECM) fungi (B, D). The annual cycle in total fungi ranged monthly from May 2013 to April 2014, while ECM fungi guild included from June 2013 to May 2014. Dots denote outlier value (i.e. values that fall below Q1 – 1.5 IQR or above Q3 + 1.5 IQR). One outlier with a value of 0.25 kg ha^{-1} was removed from the plot B.

Table 3: Results of linear mixed effect models testing relationships between different intensities of thinning and monthly belowground total biomass and biomass of ectomycorrhizal fungi (ECM).

	Fixed effects coefficients		**Random effects**			**Pseudo R²**				
Fungal biomass	Intercept	Thinning intensity	Paired plot (intercept)	Month (intercept)	Residuals (intercept)	R^2m^a	R^2c^a	**Marginal bias**	**RMSE**	**n**
Total	1.095***	-0.501***	0.042	0.035	0.096	0.08	0.49	-0.07	0.30	306
ECM	0.474***	-0.485***	0.115	0.036	0.153	0.05	0.52	-0.08	0.38	304

Thinning intensity (%, expressed as a decimal) is the independent variable, while fungal biomass (mg mycelia g soil^{-1}) is the dependent variable and was log-transformed. The annual cycle in total fungi ranged from May 2013 to April 2014, while ECM fungi guild included from June 2013 to May 2014.
[a,b] Marginal (proportion of variance explained by the fixed factors, R^2m) and conditional (proportion of variance explained by fixed plus random factors, R^2c) R^2 values were computed following Nakagawa and Schielzeth (2013). Marginal bias is the mean bias error of the marginal predictions while the conditional bias is zero in all models (mg mycelia g soil^{-1}), *RMSE* is the root of mean square error (mg mycelia g soil^{-1}) and *n* is the number of observations. Significance level: '***' $P < 0.001$.

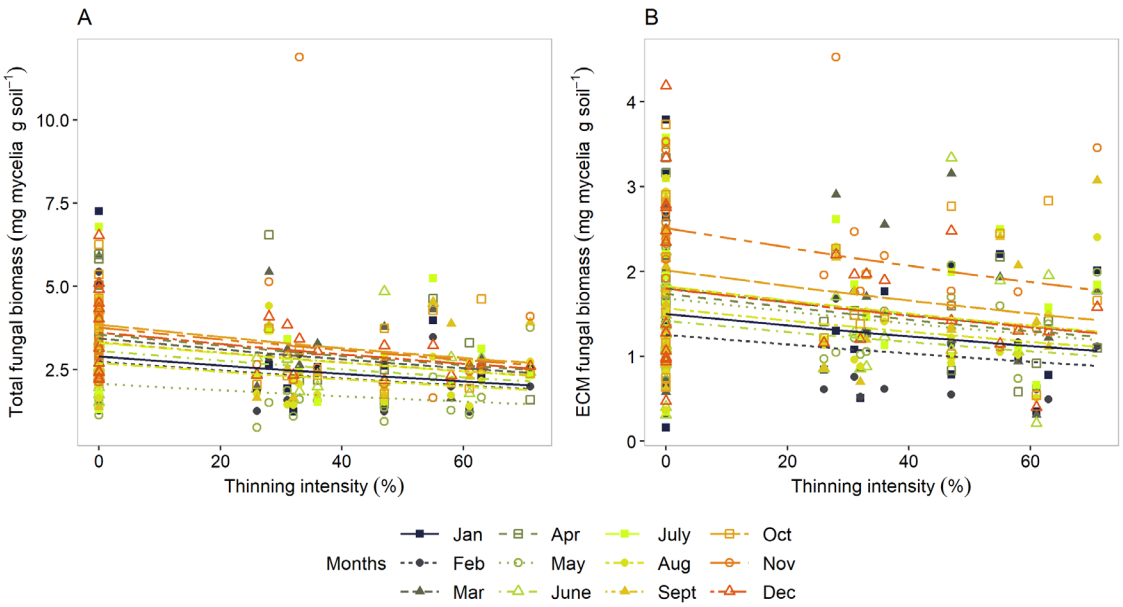

Figure 4: Predicted intra-annual effect (lines) of thinning intensity on belowground total fungal biomass (A) and ectomycorrhizal (ECM) biomass (B). The annual cycle for biomass of total fungi ranged from May 2013 to April 2014, while for ECM fungi the study period ranged from June 2013 to May 2014. Dots denote the observed fungal biomass over time.

4. Discussion

In this study we investigated how different thinning intensities of Mediterranean *P. pinaster* forest stands relates to variation in above- and below-ground fungal biomass. In support of our first hypothesis, we found that thinning reduced the total belowground fungal biomass, mainly driven by a reduction in belowground ECM biomass. We also observed that higher thinning intensities were related to a long-lasting reduction of total- and ECM biomass. In the short term (⩽3 years) thinning also increased the proportion of aboveground biomass (sporocarps) relative to the belowground biomass. Reduced belowground biomass was observed from spring 2013 to spring 2014.

The results are consistent with the findings of previous studies focused on single fungal species. For example, in Mediterranean *Pinus sylvestris* L. forest stands, Parladé et al. (2017) reported a lower mycelial biomass of *Boletus edulis* in clearcut and thinned forests, compared to control forest. Similarly, Mediavilla et al. (2017) also observed a decrease in the mycelial biomass of *B. edulis* after eliminating the dominant shrubs of *Cistus ladanifer* L. by a final felling and controlled burning. Similar to our results, both Parladé *et al.* (2017) and Mediavilla et al. (2017) did not observe any recovery over time of the mycelial biomass after thinning. Kyaschenko et al. (2017) and Kohout et al. (2018) also found that clear-cutting negatively affected the relative abundance and/or diversity of ECM fungi, but ECM communities could at least partially recover as forest aged. The survival capacity of a particular fungal species to a disturbance was also addressed by Gordon & Van Norman (2014), who could detect belowground mycelia of *Phaeocollybia* 12 years after thinning. This is in line with Castaño et al. (2018a) who highlighted that the remaining trees after thinning may act as a 'refuge' and may provide sufficient photosynthetic C to support the belowground ECM community (Amaranthus and Perry, 1987; Varenius et al., 2016).

Similarly, Sterkenburg et al., (2018) showed that a significant fraction of the ECM community is preserved when 30-60% of the trees are retained. In this study, the negative effect of thinning on belowground biomass is likely driven by a decrease in ECM biomass component. Although the mycelial biomass of ECM fungi was estimated from the total fungal biomass (by ergosterol quantification), and the ECM fungal composition was estimated from community profiling (using high-throughput sequencing of fungal ITS2 amplicons), ECM fungi is the only functional guild that has been clearly shown to be sensitive to host tree disturbances (cf. Collado et al., 2018). Furthermore, we did not observe any effect of thinning on the biomass of saprotrophic fungi, thus confirming our second hypothesis. Previous studies showed how opportunistic saprotrophic fungi, after heavy disturbances, may be stimulated by reduced competition or elimination of ECM through the so-called 'Gadgil effect', resulting in higher nitrogen mineralization and C losses (Fernandez and Kennedy, 2016; Gadgil and Gadgil, 1975; Kyaschenko et al., 2017; Sterkenburg et al., 2019). However, we did not observe such an effect in the present study, suggesting the possibility of absence of resources limitation (particularly nitrogen) that could promote the saprotrophic proliferation in deeper layers. Saprotrophic fungi are influenced by weather conditions and litter inputs (Rayner and Boddy, 1988), while ECM fungi are, in addition to the previous factors, also sensitive to the photosynthetic C supply from the host tree, which is affected by changes in climatic conditions and forest stand structure (Högberg et al., 2010, 2001). Thinning may also alter soil microclimatic conditions which may contribute to the observed reduction in belowground fungal biomass. For example, Castaño et al. (2018a) found that changes in community composition are partly driven by inter-annual variation in temperature and precipitation, while thinning treatment did not cause any effect to the fungal community composition. Similarly, De la Varga et al. (2013) reported a positive correlation between the mycelial biomass of *L. deliciosus* and relative air humidity, whereas the biomass correlated negatively with mean temperature and solar radiation.

Thinning had a negative effect on the mycelial biomass of both total and ECM fungi but an initial positive effect on the production of sporocarps which faded over time. Lower mycelial biomass coupled with a higher mushroom production reflected on the ratio between aboveground and belowground fungal biomass. In particular, thinning caused a positive effect on the aboveground/belowground ratio, increasing with higher thinning intensities. These results pinpoint to a shift in the fungal biology from vegetative growth to reproduction under disturbances, similar to what Suz et al. (2008) observed for *Tuber melanosporum* Vittad. However, the extent to which fungi improve their reproductive capacity by reallocating resources from mycelium to sporocarps is not known and deserves further investigation. Contrary to our results, increase in sporocarp production after thinning was not observed by Parladé et al. (2017) nor De la Varga et al. (2013) on sporocarp formation of *B. edulis* and *L. deliciosus*, respectively. However, when De la Varga et al. (2013) compared their results with those obtained from a previous work (De la Varga et al., 2012), they observed a negative relationship between the mycelial biomass and the productivity of *B. edulis* sporocarps, similar to our findings. In contrast, Mediavilla et al. (2017) detected a recovery of both belowground biomass and the production of sporocarps of *B. edulis* three-four years after total clearing of *C. ladanifer* shrubs. Furthermore, De la Varga et al. (2013) observed the minimum mycelium biomass before or during the fruiting season, whereas we found that the mushroom fruiting season and the maximum

belowground fungal biomass of total and ECM fungi occurred simultaneously. However, barely any ECM sporocarp emerged during that fruiting season due to the low precipitation. Regarding the C reallocation during autumn, Teramoto et al. (2012) and Lamhamedi et al. (1994) detected that recently photosynthesised C strongly contributed to metabolic activities and sporocarp production.

Finally, incorporation of biomass data (obtained by ergosterol analyses) emerged inter- and intra-annual patterns of the fungal biomass dynamics related to thinning. In previous works, fungal community composition was not affected by thinning, and therefore no compositional changes in the fungal community were observed (Castaño et al., 2018a). Here, incorporation of ergosterol data into our models highlighted negative effects of thinning to the ECM biomass. Assessing fungal community composition together with the fungal biomass may yield complementary information about the ecology and biology of fungal species and guilds.

5. Conclusions

This study shows how forest management negatively affects ECM and total fungal biomass belowground, which feedbacks on sporocarp production, resulting in higher mushroom productivity in the short term. Additionally, the inter- and intra-annual observation of belowground fungal biomass fluctuations, resulted in similar annual and monthly patterns in fungal biomass shifts. We demonstrate that effects of forest management on fungal biomass dynamics may extent over several years. We also show that after thinning, soil fungi may respond by increasing reproduction rather than colonizing the surrounding soil, and that thinning may exacerbate resource allocation of fungal biomass towards reproductive structures (sporocarps). Thus, this work provides further insights into the functioning of fungi, fungal resource allocation and C allocation patterns between fungi and host trees, as well as into the effect of management-related disturbance on fungi in forest ecosystems.

Acknowledgements

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Supplementary material

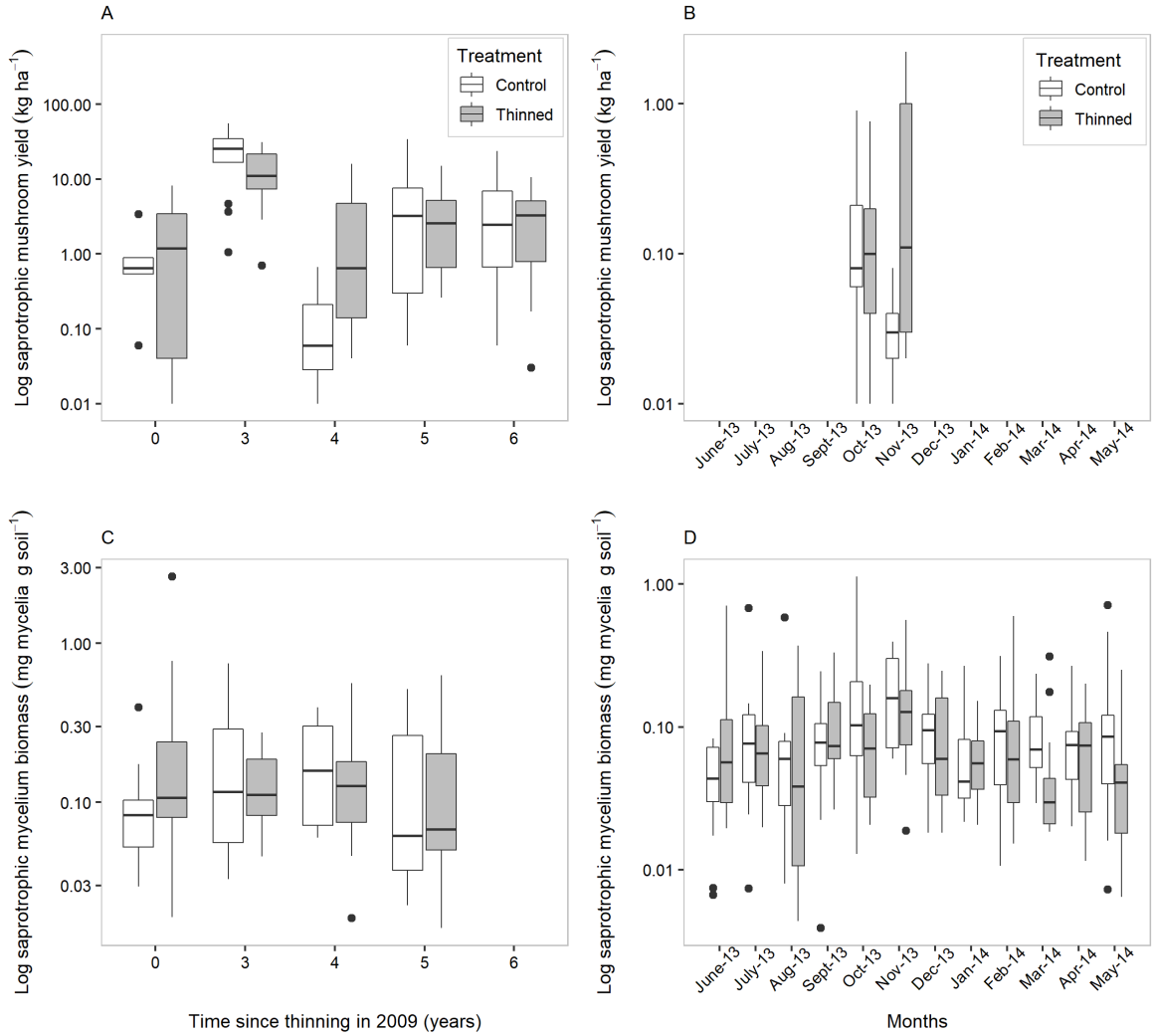
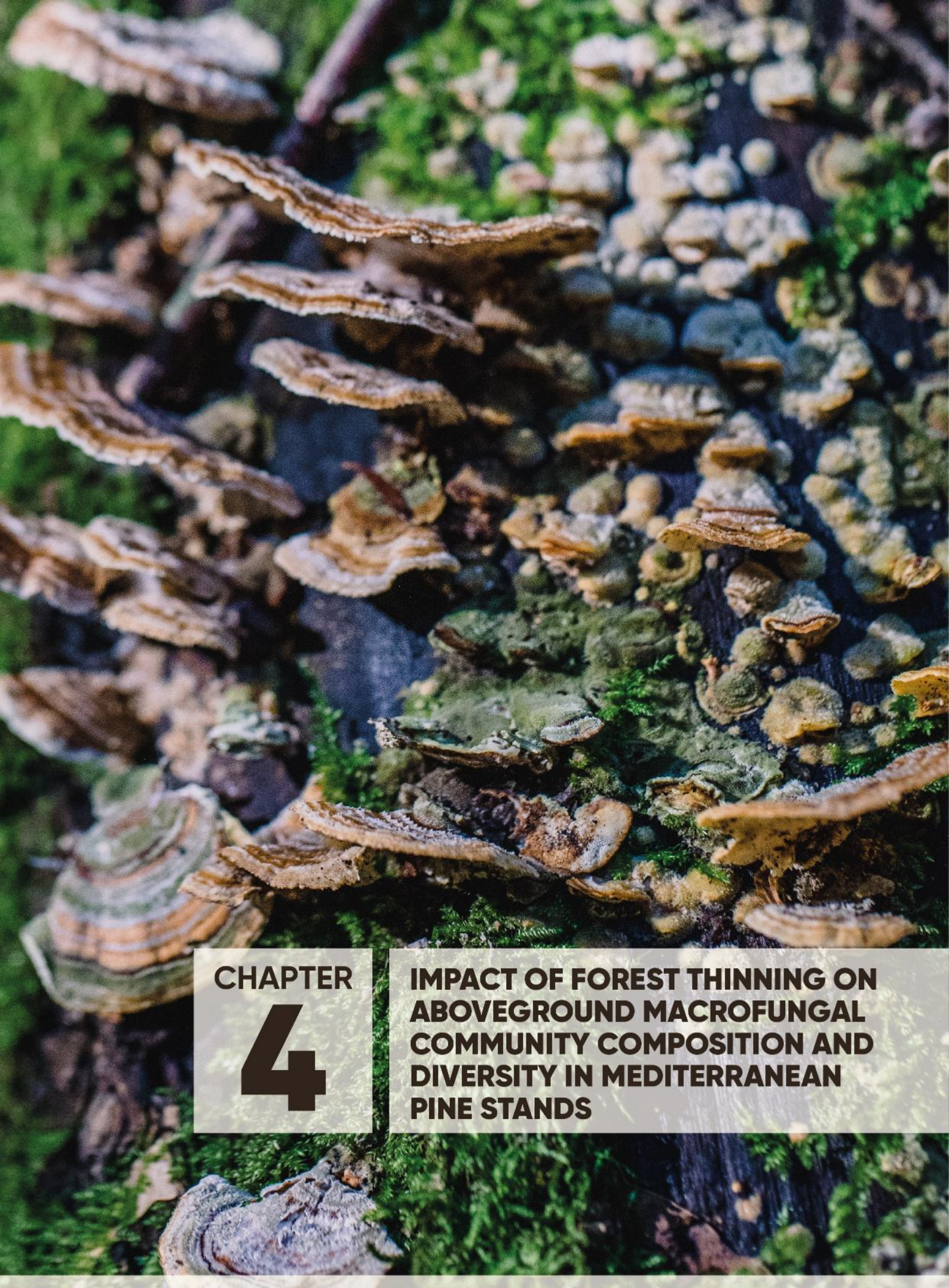


Figure S1: Boxplots reflecting the lack of significant above- and belowground thinning effect on saprotrophic fungi (including both litter and soil saprotrophs) both inter-annually since the thinning treatment in summer 2009 (A, C) and intra-annually (June 2013 to May 2014; B, D). There was no data available for belowground saprotrophic biomass in the sixth year after thinning. Inter-annual mushroom yield (A) represents the total production of November in different years based on weekly mushroom sampling. Inter-annual belowground biomass (C) was obtained from one-day sampling in the same month (November) in different years. Similarly, intra-annual mushroom yield (B) represents the total aboveground production of saprotrophic fungi between June 2013 and May 2014, while intra-annual belowground biomass (D) was obtained from one-day sampling in every month for the same period. Dots denote outlier value (i.e., values that fall below Q1 – 1.5 IQR or above Q3 + 1.5 IQR).



CHAPTER 4

IMPACT OF FOREST THINNING ON ABOVEGROUND MACROFUNGAL COMMUNITY COMPOSITION AND DIVERSITY IN MEDITERRANEAN PINE STANDS

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Impact of forest thinning on aboveground macrofungal community composition and diversity in Mediterranean pine stands

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Abstract

1. Fungal communities are especially relevant in Mediterranean regions, a 'hotspot' of fungal diversity, and where the value of edible commercial sporocarps may be much higher than the income from timber products. Assessing the effects of forest management practices together with the modulating role of climate on sporocarp community composition and diversity is crucial for understanding their impacts on fungal-related ecosystem services. Yet, previous research on forest management impacts on aboveground fungal diversity and community composition is scant, sometimes contradictory and mainly focused on rather short-term impacts.
2. We quantified the long-term response of the sporocarp community composition and diversity to different forest thinning intensities in Mediterranean *Pinus pinaster* forest stands, and the interactions with weather conditions in modulating the fungal response. We relied on 28 permanent plots representing a thinning intensity gradient, monitored for sporocarp diversity on a weekly basis during eleven consecutive years. Weather conditions of each plot were obtained through interpolation from different meteorological stations.
3. Overall, the fungal sporocarp community composition showed short-term (< 2 years) changes mainly under both heavy and light thinning intensities compared to unthinned plots. The unexpected compositional change caused by light thinning intensities affected only certain ectomycorrhizal fungi (*Lactarius* group *deliciosus*). Climatic factors, mostly the mean temperature of September and October, contributed to enhancing or diminishing the compositional response of macrofungi to forest thinning.
4. There was no effect of forest thinning on sporocarp species diversity (i.e., richness and evenness). Both ectomycorrhizal and saprotrophic species richness and ectomycorrhizal species evenness increased over time.
5. *Synthesis and applications*. Forest thinning in Mediterranean pine stands may lead to short-term changes in sporocarp community composition, with the highest thinning intensities triggering the greatest and most long-lasting changes. Particular commercial fungal species are capable to benefit from immediate post-treatment conditions by producing large amount of sporocarps. Moreover, forest thinning with a careful and low-impact removal of trees does not jeopardize sporocarp diversity.

Keywords: Ectomycorrhizal, forest disturbance, forest management, fungi, mushroom, *Pinus pinaster*, saprotrophic, silviculture

1. Introduction

Fungal communities play an essential and manifold role in forest ecosystem services. Distinct roles are addressed by different fungal functional guilds differing in their strategy to obtain energy. Ectomycorrhizal (ECM) fungi provide nutrients to host trees in exchange for organic carbon (Högberg et al., 2001; Smith and Read, 2008), and increase access to soil water (Allen, 2007) and, indirectly, water retention by improving soil conditions (structure and porosity) (Querejeta, 2017). Although ECM fungi may also oxidize organic matter to obtain nitrogen (Lindahl and Tunlid, 2015), the saprotrophic guild are the main decomposers of dead organic matter, thus driving the carbon cycle (Rayner and Boddy, 1988). In addition to their role in regulating and supporting ecosystem services (e.g., soil carbon sequestration and soil formation, respectively), ECM and saprotrophic fungi also provide important cultural and provisioning ecosystem services, such as recreational and socioeconomic benefits from picking and trading edible sporocarps, respectively (Boa, 2004; Gorriz-Mifsud, Secco, Da Re, Pisani & Bonet, 2017). This is especially relevant in Mediterranean regions, considered as a 'hot spot' of fungal diversity (Tedersoo et al., 2014), and where the value of edible commercial sporocarps may be much higher than the income from timber products (Palahí et al., 2009; Pettenella and Secco, 2006). Therefore, the conservation of fungal communities and diversity in Mediterranean ecosystems is central to the provision of key ecosystem services.

Fungal communities are determined by multiple factors such as inter-annual fluctuations in precipitation and temperature (e.g., Alday, Martínez de Aragón, de-Miguel & Bonet, 2017; Castaño et al., 2018). Indeed, climate arises as the foremost driver of sporocarp emergence and yield, acting as a limiting or mediating factor according to local conditions (Büntgen, Kauserud & Egli, 2012). Moreover, the forest stand structure is another important factor in fungal dynamics that, unlike climate, can be modified by human activities (Tomao, Bonet, Castaño & de-Miguel, 2020). Accordingly, assessing the effects of forest management practices together with the modulating role of climate on Mediterranean fungal communities and diversity is crucial for understanding their impacts on fungal related ecosystem services.

At belowground level, the remaining trees or stumps are essential for fungal survival after heavy forest disturbances (e.g., clear-cutting), acting as a 'refuge' for the ECM fungal community, until a new cohort of trees is established (Varenius, Lindahl & Dahlberg, 2017). Heavy forest disturbances may trigger reductions in ECM fungal diversity (Jones, Durall & Cairney, 2003; Parladé et al., 2019) and changes in soil fungal community composition (Kyaschenko, Clemmensen, Hagenbo, Karltun & Lindahl, 2017). Sterkenburg, Clemmensen, Lindahl and Dahlberg (2019) found that belowground ECM species richness decreased linearly with increasing reduction of tree retention three years after logging in a boreal *P. sylvestris* forest, so that half of ECM species remained after maintaining 30% of retention trees as 'lifeboats'. Conversely, one of the few studies conducted in a Mediterranean pine forest observed no effect of heavy thinning, neither on belowground fungal species richness and diversity nor on soil fungal community composition (Castaño

et al., 2018). However, previous works have demonstrated that belowground mycelium can react differently to forest disturbances compared to aboveground fruiting patterns. For example, Collado et al. (2020) observed that total and ECM mushroom yields were negatively correlated with mycelial biomass after forest thinning in *Pinus pinaster* stands.

At aboveground level, previous research has generally shown reductions in sporocarp diversity of ECM and saprotrophic fungi under reduced tree cover (Tomao et al., 2020). Santos-Silva, Gonçalves and Louro (2011) found that reduced canopy cover in cork and holm oak stands led to changes in sporocarp community composition and to reduced mycorrhizal sporocarp richness. The latter findings were partly explained by the author as a result of alterations in microclimatic conditions (e.g., increase in soil temperatures and sun exposition). Other studies have suggested that changes in microclimatic conditions shape, in particular, the diversity of wood-inhabiting fungi (Bässler, Müller, Dziock & Brandl, 2010; Rayner & Boddy, 1988). Sporocarp richness of wood-inhabiting species may be also boosted after forest thinning due to new specific organic matter such as stumps (Müller, Engel & Blaschke, 2007). However, forest thinning has shown, in different ecosystems, contrasting effects on sporocarp richness. For instance, Egli, Ayer, Peter, Eilmann and Rigling (2010) detected an increase in ECM and saprotrophic sporocarp richness four years after the thinning of a mixed temperate forest, whereas Lin et al. (2015) observed a decline in saprotrophic sporocarp richness in the first year of post-thinning in a tropical plantation. The latter study also found that higher thinning intensity had greater impact on the sporocarp community. In another tropical plantation, Lin, Chen and Wang (2011) also detected higher saprotrophic sporocarp richness in light-thinned stands than in those heavily thinned plots. Conversely, Shaw, Kibby and Mayes (2003) did not observe, in temperate coniferous stands, any community-level response of ECM sporocarps to thinning in the five years after the removal of 50% of pine trees. Therefore, both the intensity of the disturbance and the forest ecosystem characteristics may differently shape the aboveground macrofungal sporocarp composition and diversity over time.

In a nutshell, the scientific knowledge on the effect of forest management-related disturbance on Mediterranean fungal communities is very limited and unclear. Moreover, while previous research has mainly focused on the impact of forest management-related tree removal on belowground fungal community composition, the existent literature on aboveground community composition is even more scant and mainly focused on rather short-term impacts (< 5 years). Thus, how aboveground macrofungal community and diversity change over time after forest thinning remains largely unknown, especially under Mediterranean conditions and over longer time periods (Tomao et al., 2020).

In this study, we quantify the long-term response of the aboveground macrofungal sporocarp community composition and diversity to different forest thinning intensities in Mediterranean *Pinus pinaster* forest stands, disentangling in turn how climate conditions modulate such fungal response. For this purpose, we relied on 28 permanent plots representing a thinning intensity gradient, monitored for sporocarp diversity on a weekly basis during eleven consecutive years. Based on the general trends of the aforementioned scant previous research, we hypothesized: (i) that forest thinning lead to changes in aboveground (i.e., sporocarps) macrofungal community composition and species diversity affecting both saprotrophic and ECM fungi, with the highest thinning intensities triggering the greatest and most long-lasting changes as well as reductions in fungal diversity; and (ii)

a fast recovery (< 5 years after thinning) of the aboveground macrofungal community composition and diversity after the thinning treatment. The latter was based on findings from previous research on sporocarp productivity that suggest short-term disturbance effects on mushroom abundance (e.g., Hintikka, 1988; Pilz, Molina & Mayo, 2006). Additionally, we hypothesized that (iii) both accumulated precipitation and temperature, as crucial factors in fungal fructification, modulate the responses to thinning of both sporocarp community composition and diversity.

2. Material and methods

2.1. Study area

The study was conducted in the Natural Protected Area of Poblet (Northeast Spain, 41° 21′ 06.5″ N and 1° 02′ 25.8″ E), located within an altitudinal range of 400-1201 m a.s.l. (Fig. S1). The climate is characterised by a drought-prone summer season, typical from Mediterranean areas, with an average annual temperature of 14 °C and an average annual rainfall of 524 mm (data obtained for the study period from L'Espluga de Francolí weather station, 41° 23′ 47″ N, 1° 06′ 10″ E, 446 m a.s.l.). The plots represent *P. pinaster* stands, planted between 1963 and 1968, with presence of isolated *Quercus ilex* L. trees or shrubs, while the understorey is dominated by *Arbutus unedo* L., *Calluna vulgaris* (L.) Hull., *Phillyrea latifolia* L. and *Erica arborea* L.

2.2. Experimental design

The macrofungal diversity sampling was based on 28 permanent sporocarp inventory plots of 100 m^2 (10 m x 10 m) (Fig. S1). 15 control (unthinned) plots were established in 2008, whereas the other 13 plots were set up in the summer (July and August) of 2009. The forest thinning intensity gradient (in stand basal area) represented in the experimental design was as follows: light (20-30%, 5 plots), medium (31-50%, 3 plots) and heavy (51-70%, 5 plots). The sporocarp inventory plots were located in the centre of larger forest plots (40 m x 40 m) in order to prevent edge effects (Fig. S1). All felled trees were cut using chainsaw and removed carefully to avoid soil disturbance. Additionally, a forest inventory was performed in all plots before and after silvicultural treatments in 2008 and 2010, respectively. Plots were also established representing different gradients in altitude (594 – 1013 m a.s.l.), aspect (north, west, east), terrain slope (3 – 23%), remaining stand basal area (control plots: 21 – 82 m^2 ha^{-1}, thinned plots: 17 – 47 m^2 ha^{-1}) and remaining stand density (control plots: 446 – 2657 trees ha^{-1}, thinned plots: 350 – 1528 trees ha^{-1}). Further details on experimental design and plot characteristics can be found in Bonet et al. (2012).

2.3. Sporocarp sampling

A total of 89,153 epigeous sporocarps were collected from 2009 to 2019 (11 years). All sporocarps were collected in each plot on a weekly basis over the autumn fruiting season (i.e., from September to the end of December). The sampling day was always Wednesday or Thursday to reduce potential sampling bias associated to sporocarp removals by recreational weekend mushroom pickers. Sampling was performed carefully to avoid soil

disturbance and compaction. In the same sampling day, all sporocarps were identified in the lab at species level (otherwise, at genus level) and weighted them fresh to the nearest 0.01 g. Sporocarps were also dried in an air-vented oven at 30 - 40 °C in order to reduce biomass variability owing to water content, obtaining comparable biomass data. The 421 species collected over the study period were then classified into two functional guilds based on expert and current scientific knowledge (e.g., Agerer, 2006; Hobbie & Agerer, 2010; Tedersoo et al., 2014; Tedersoo & Nara, 2010): ectomycorrhizal (168 species in total) and saprotrophic (253 species in total, including both wood and soil saprotrophs). No ECM fungi were found neither in 2013 nor in 2017. Further details on the sporocarp sampling procedure and sporocarps identification can be found in Martínez de Aragón et al. (2007).

2.4. Climate data

Climatic variables, i.e., temperature and precipitation, were obtained for each plot from 2009 to 2019 by means of the DAYMET methodology (Thornton et al., 2000; Thornton and Running, 1999) implemented in the R package "meteoland" (De Cáceres et al., 2017). Such methodology consisted of estimating daily temperature and precipitation for each plot by averaging the values of different local meteorological stations. Additionally, these estimates were firstly weighted according to the geographical nearness to the target plot and subsequently corrected for the elevation differences between such plots and the meteorological stations. Finally, we used the mean temperature and the accumulated precipitation per each month. Further details about the methodology can be found in Karavani et al. (2018).

2.5. Statistical analysis

Principal Response Curves (PRC) analysis was used to test the effect over time of forest thinning intensity on sporocarp community composition. This multivariate analysis allows to describe the treatment effect on species composition over time (van den Brink et al., 2009). To better understand the fruiting compositional dynamics and patterns we performed PRC analysis on two different sporocarp datasets: i) the sporocarp abundance of each fungal species (i.e., dry biomass quantitative abundance, kg in dry weight ha^{-1}), and ii) the presence/absence of sporocarps of each fungal species (i.e., qualitative abundance). Thinning intensity (relative to stand basal area) was considered as a factor with four levels (control: 0% thinned, light: 20–30% thinned, medium: 30–50% thinned, and heavy: 50–70% thinned), while the sampling year was set as a factor with 11 levels (i.e., from 2009 to 2019). The significance of thinning intensity effect in the main axis was assessed by Monte Carlo simulation (999 permutations). PRC analysis was performed iteratively, either including or excluding the less abundant species and the most common species, in order to better evaluate treatment effects on the overall community. The same procedure was also conducted for ECM and saprotrophic sporocarp species, separately, since previous research has shown that their fruiting response may depend on disturbance intensity (e.g., Collado et al., 2018). Moreover, partial Redundancy analysis (RDA) was used to evaluate whether monthly accumulated precipitation and mean temperature, from August to December, interacted with thinning intensity, further modulating the sporocarps responses to thinning. In these models, the climate-thinning interaction was controlled for the over-all

temporal trend using time as a covariable to consider the repeated observations collected from same plot (Alday et al., 2013). The significance of the environmental effect over the main axis was assessed using Monte Carlo simulation (999 permutations).

Differences in sporocarp diversity between thinning intensities and years were analysed using sporocarp richness (*S*) (i.e., the total number of taxa observed per plot) and evenness (*J*) (i.e., the equitability of sporocarp species abundances per plot) (Magurran, 2004). While richness informs about the total amount of species, evenness is crucial for understanding their relative abundances, with further implications on the functioning of fungal communities and their reproductive structure (Alday, Martínez de Aragón, de-Miguel, & Bonet, 2017). Evenness was calculated using Pielou's evenness index (Pielou, 1966). Linear mixed-effects models (LME) were used to test significance shifts in sporocarp richness and evenness between thinning intensities and years. Thinning intensity and time (years) after thinning were considered as fixed effects, with random plot effects. LME was also used to evaluate if monthly accumulated precipitation and mean temperature, from August to December, interacted with thinning intensity. All these analyses were also conducted separately for ECM and saprotrophic sporocarp species. The suitability of the models was evaluated by manifold criteria (e.g., parsimony, robustness, statistical significance of parameters, homoscedasticity, absence of bias, normality among residuals) (Zuur et al., 2009).

All statistical analyses were performed in R software 3.6.3 (R Core Team, 2014). The statistical analyses on fungal sporocarp community composition (multivariate analyses) and diversity (richness and evenness) were carried out using the "vegan" package (Oksanen et al., 2013), while linear mixed-effects models were performed using the "nlme" package (Pinheiro and Bates, 2000).

3. Results

3.1. Fungal community responses to thinning intensity

PRC analysis showed a significant effect of thinning intensity on total sporocarp community composition, both quantitatively (i.e., abundance) and qualitatively (i.e., presence/absence) (Table 1, Fig. 1). Ectomycorrhizal and saprotrophic sporocarp communities responded differently to thinning intensity according to the type of composition data (i.e., quantitative or qualitative) (Table 1). Namely, the effect of thinning intensity was only significant on the ECM quantitative sporocarp composition (Fig. S4A) and the saprotrophic qualitative sporocarp composition (Fig. 2B).

Table 1: Summary of the statistical significance and percentage of variance explained by the first axis in the PRC analysis of each functional fungal guild, under different type of composition data (quantitative: abundance in dry biomass [kg ha^{-1}]; qualitative: presence and absence of species).

Data	Trophic group	Axis 1	*F*-ratio	$p_{(999)}$
Quantitative	Total (ECM-Saprotrophic)	18.37	15.57	0.002
	ECM	24.79	16.04	0.001
	Saprotrophic	3.52	14.29	0.495
Qualitative	Total (ECM-Saprotrophic)	7.81	4.34	0.001
	ECM	3.93	3.58	0.151
	Saprotrophic	5.85	5.09	0.001

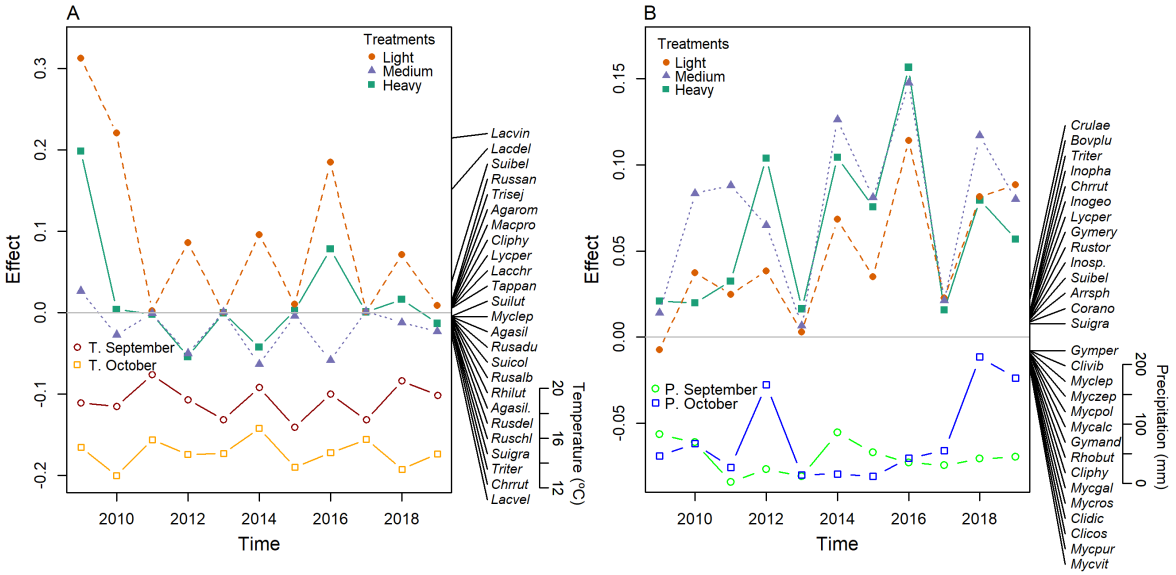

Figure 1: Principal response curves (PRC) analysis showing the effect of thinning intensity on total sporocarp community composition over 11 years after the thinning conducted in 2009 for (A) quantitative (i.e., species abundance) data and (B) qualitative (species presence-absence) data. Treatment (thinning) intensities in stand basal area were classified as: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). 'P' denotes the accumulated precipitation of each month and 'T' is the mean temperature of a given month. Species codes are (sorted alphabetically): Agarom = *Agaricus romagnesii*, Agasil = *Agaricus sylvaticus*, Agasil. = *Agaricus sylvicola*, Arrsph = *Arrhenia sphagnicola*, Bovplu = *Bovista plumbea*, Chrrut = *Chroogomphus rutilus*, Clicos = *Clitocybe costata*, Clidic = *Clitocybe dicolor*, Cliphy = *Clitocybe phyllophila*, Clivib = *Clitocybe vibecina*, Corano = *Cortinarius anomalus*, Crulae = *Crucibulum laeve*, Gymand = *Gymnopus androsaceus*, Gymper = *Gymnopus peronatus*, Gymery = *Gymnopus erythropus*, Inogeo = *Inocybe geophylla*, Inopha = *Inocybe phaeodisca*, Inosp. = *Inocybe* sp., Lacchr = *Lactarius chrysorrheus*, Lacdel = *Lactarius deliciosus*, Lacvel = *Lactarius vellereus*, Lacvin = *Lactarius vinosus*, Lycper = *Lycoperdon perlatum*, Macpro = *Macrolepiota procera*, Mycalc = *Mycena alcalina*, Mycgal = *Mycena galericulata*, Myclep = *Mycena leptocephala*, Mycpol = *Mycena polygramma*, Mycpur = *Mycena pura*, Mycros = *Mycena rosella*, Mycvit = *Mycena vitilis*, Myczep = *Mycena zephirus*, Rhilut = *Rhizopogon luteolus*, Rhobut = *Rhodocollybia butyracea*, Rusadu = *Russula adusta*, Rusalb = *Russula albonigra*, Ruschl = *Russula chloroides*, Rusdel = *Russula delica*, Russan = *Russula sanguinea*, Rustor = *Russula torulosa*, Suibel = *Suillus bellinii*, Suicol = *Suillus collinitus*, Suigra = *Suillus granulatus*, Suilut = *Suillus luteus*, Tappan = *Taminella panuoides*, Trisej = *Tricholoma sejunctum*, Triter = *Tricholoma terreum*.

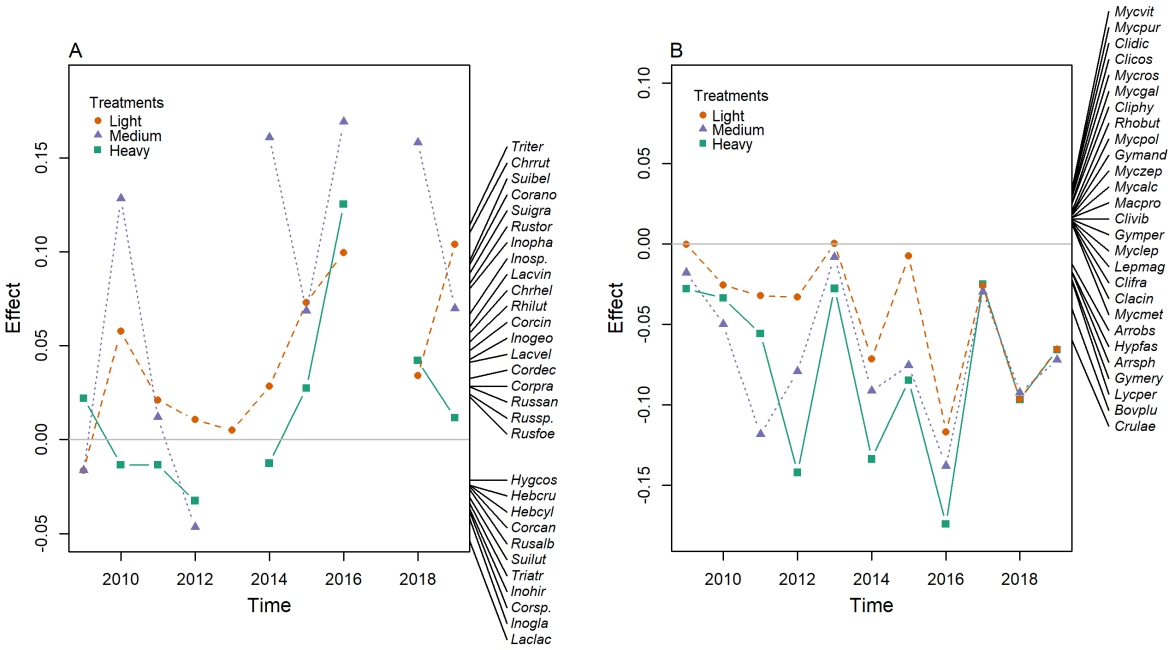

Figure 2: Principal response curves (PRC) analysis showing the effect of thinning intensity on ectomycorrhizal (A) and saprotrophic (B) sporocarp community composition over 11 years after the thinning conducted in 2009. Macrofungal community composition was described based on qualitative data (i.e., presence-absence of species). Treatments (thinning) intensities in stand basal area were classified as: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). No ECM sporocarp emerged in medium- and heavy-thinned plots during 2013 nor in any of the thinned plots during 2017. Species codes are (sorted alphabetically): Arrobs = *Arrhenia obscurata*, Arrsph = *Arrhenia sphagnicola*, Bovplu = *Bovista plumbea*, Chrhel = *Chroogomphus helveticus*, Chrrut = *Chroogomphus rutilus*, Clacin = *Clavulinopsis cinerioides*, Clicos = *Clitocybe costata*, Clidic = *Clitocybe dicolor*, Clifra = *Clitocybe fragrans*, Cliphy = *Clitocybe phyllophila*, Clivib = *Clitocybe vibecina*, Corano = *Cortinarius anomalus*, Corcan = *Cortinarius caninus*, Corcin = *Cortinarius cinnamomeus*, Cordec = *Cortinarius decipiens*, Corpra = *Cortinarius pratensis*, Corsp. = *Cortinarius* sp., Crulae = *Crucibulum laeve*, Gymand = *Gymnopus androsaceus*, Gymper = *Gymnopus peronatus*, Gymery = *Gymnopus erythropus*, Hebcru = *Hebeloma crustuliniforme*, Hebcyl = *Hebeloma cylindrosporum*, Hygcos = *Hygrophorus cossus*, Hypfas = *Hypholoma fasciculare*, Inogeo = *Inocybe geophylla*, Inogla = *Inocybe glabripes*, Inohir = *Inocybe hirtella*, Inopha = *Inocybe phaeodisca*, Inosp. = *Inocybe* sp., Laclac = *Laccaria laccata*, Lacvel = *Lactarius vellereus*, Lacvin = *Lactarius vinosus*, Lepmag = *Lepiota magnispora*, Lycper = *Lycoperdon perlatum*, Macpro = *Macrolepiota procera*, Mycalc = *Mycena alcalina*, Mycgal = *Mycena galericulata*, Myclep = *Mycena leptocephala*, Mycmet = *Mycena metata*, Mycpol = *Mycena polygramma*, Mycpur = *Mycena pura*, Mycros = *Mycena rosella*, Mycvit = *Mycena vitilis*, Myczep = *Mycena zephirus*, Rhilut = *Rhizopogon luteolus*, Rhobut = *Rhodocollybia butyracea*, Rusalb = *Russula albonigra*, Rusfoe = *Russula foetens*, Russan = *Russula sanguinea*, Russp. = *Russula* sp., Rustor = *Russula torulosa*, Suibel = *Suillus bellinii*, Suigra = *Suillus granulatus*, Suilut = *Suillus luteus*, Triatr = *Tricholoma atrosquamosum*, Triter = *Tricholoma terreum*.

3.1.1. Thinning effects on abundance-based macrofungal community composition

PRC showed an immediate total sporocarp compositional effect two months after thinning (in 2009), so that both the light- and heavy-thinned plots exhibited the highest differences in sporocarp composition compared to control plots (Fig.1A). These trends are related with high abundance of the *Lactarius* group *deliciosus* (i.e., *L. vinosus* and *L. deliciosus*). However, in 2010 this compositional change was maintained only in light-thinned plots, while in 2011 the compositional differences between all thinned treatments and control plots disappeared. In the following years, the total sporocarp community composition of thinned plots differed from that of the control plots due exclusively to interannual meteorological conditions (Fig. 1A, 1B).

When *Lactarius* group *deliciosus* was removed from the analysis to prevent its dominant effect on the community composition, the PRC results (Fig. S2A) showed different patterns over time compared to the PRC with the genus *Lactarius* (Axis 1: F-value$_{[2,261]}$ = 7.08, p = 0.394). Here, (i) only sporocarp composition on heavy thinning showed an immediate effect in 2009, (ii) the light treatment barely caused an effect along the years on the sporocarp composition, (iii) the effect over time of heavy and medium thinning intensity resulted in different sporocarp composition among them, and (iv) the latter effect was related to the interannual precipitation (Fig. 1B). Additionally, such removal of species revealed that heavy thinning intensities favoured species such as *Suillus bellinii* and *Leucopaxillus gentianeus*, while medium intensities promoted, largely, *Macrolepiota procera* and *Lactarius vellereus*. As more abundant species were ruled out from the total quantitative composition, thinning showed less effect on the community (Fig. S2B).

The PRC of ECM quantitative abundance also showed an immediate positive compositional reaction in 2009 under light and heavy thinning due to the high emergence of *L. vinosus* and *L. deliciosus* (Fig. S4A), while the thinning effect disappeared from 2010 onwards. From 2011 to 2015, the ECM quantitative composition of medium and heavily thinned differed significantly from control and light thinned plots, due to the interannual precipitation variability (Fig. 1B). However, the ECM quantitative composition of heavy thinned plots behaved erratically in the last years, i.e., changes in the ECM quantitative composition every year from 2016 to 2019. Interestingly, after filtering out 10% of the most abundant species from the ECM quantitative composition, there was a lack of compositional differences between harvest intensities and controls (F-value$_{[1,200]}$ = 4.21, p = 0.84; Fig. S4B), emphasizing that the significant compositional effect of harvest in quantitative ECM composition was mainly conditioned by the genus *Lactarius*.

Our results also showed that both total and ECM sporocarp community composition shifted compared to the control plots as a result of the interaction with the meteorological conditions of a given year (Fig. 1). Regarding total sporocarp community composition, the mean temperature of September and October interacted significantly with thinning intensity. This interaction either enhanced or diminished the effect caused by the thinning treatment (F-value$_{[3,217]}$ = 2.32, p = 0.002; F-value$_{[3,217]}$ = 2.31, p = 0.001, respectively). The interactions of total sporocarp composition with accumulated precipitation of September and October were not significant (F-value$_{[3,217]}$ = 0.95, p = 0.539; F-value$_{[3,217]}$ = 0.57, p = 0.928, respectively). Similarly to the total fungal community, only the mean temperature of both September and October resulted in a significant effect on the ECM composition, its

interaction with the treatment being also significant (F-value$_{[3,165]}$ = 2.33, p = 0.002; F-value$_{[3,165]}$ = 2.31, p = 0.002, respectively).

3.1.2. Thinning effects on presence-absence macrofungal community composition

The PRC analysis of total sporocarp community composition in terms of qualitative abundance did not show any immediate compositional response to thinning effect (Fig. 1B). From 2012, all thinning treatments caused a positive effect on qualitative sporocarp species composition in comparison with controls. This positive effect was more pronounced by the medium and heavy thinning intensities. Thinning especially favoured saprotrophic species such as *Crucibulum laeve* and *Bovista plumbea*. The reduction of 10% of the most abundant species in the presence-absence data showed similar results as whole community (Fig. S3A). As more abundant species were ruled out from the total qualitative composition, thinning showed less effect on the community (Fig. S3B).

The PRC analysis on the saprotrophic qualitative community composition over time (mostly from 2012 to 2016) showed that, at higher thinning intensities, saprotrophic sporocarp composition moved further away from the community of control plots (Fig. 2B). The fructification of species such as *Crucibulum laeve* and *Bovista plumbea* were strongly favoured by higher thinning intensities. Treatment effect became even more non-significant as more abundant saprotrophic species were excluded from the composition, i.e., ruling out 25% of the most abundant species (Axis 1: F-value$_{[1,259]}$ = 3.23, p = 0.369; Fig. S7).

All climatic variables of both September and October caused an effect on both the total and saprotrophic sporocarp community composition in terms of species presence-absence (p = 0.001), either favouring or impairing the emergence of certain fungal species. In the total sporocarp community composition, only the mean temperature of September and October interacted with the treatment effect (F-value$_{[3,217]}$ = 1.70, p = 0.001; F-value$_{[3,217]}$ = 1.71, p = 0.001, respectively). In the saprotrophic sporocarp community composition, the mean temperature of September and October interacted with the treatment effect (F-value$_{[3,215]}$ = 1.83, p = 0.001; F-value$_{[3,215]}$ = 1.84, p = 0.001, respectively), as did the accumulated precipitation of October (F-value$_{[3,215]}$ = 1.43, p = 0.026). Namely, all of these interactions with climate variables enhanced or diminished the effect caused by treatment.

3.2. Fungal diversity responses to thinning intensity

Total, ectomycorrhizal and saprotrophic sporocarp species richness and evenness were not significantly affected by thinning intensity (Table 2, Fig. 3, S8, S9), nor by the interaction between thinning intensity and meteorological variables (i.e., the accumulated precipitation and the mean temperature). However, total species (both ECM and saprotrophic fungi) richness and ECM species evenness increased significantly over time (p < 0.001 and p = 0.002, respectively). Over the years and on average over all plots, the total sporocarp species richness increased from 11 to 24, the saprotrophic sporocarp species richness increased from 5 to 17 and both ECM sporocarp species richness and evenness increased from 4 to 12 and from 0.44 to 0.79, respectively.

Meteorological variables of particular months interacted significantly with time, enhancing or diminishing the positive effect caused by time on species richness. Regarding total species richness, the accumulated precipitation of September and October and the mean temperature of September and November interacted with time ($t(305) = 3.83$, $p < 0.001$; $t(305) = -2.15$, $p = 0.032$; $t(305) = 5.64$, $p < 0.001$; $t(305) = 5.03$, $p < 0.001$, respectively). Concerning ECM species richness, the accumulated precipitation of August, October and November interacted with time ($t(242) = -3.86$, $p < 0.001$; $t(242) = -3.71$, $p < 0.001$; $t(242) = 4.08$, $p < 0.001$, respectively), as did the mean temperature of September, October and November ($t(242) = 4.50$, $p < 0.001$; $t(242) = 2.58$, $p = 0.011$; $t(242) = 4.19$, $p < 0.001$, respectively). Regarding saprotrophic species richness, the accumulated precipitation and the mean temperature of September and November interacted with time ($t(304) = 5.16$, $p < 0.001$; $t(304) = 2.90$, $p = 0.004$; $t(304) = 3.69$, $p < 0.001$; $t(304) = 4.96$, $p < 0.001$, respectively).

Only the interaction between the accumulated precipitation of particular months and time caused a significant effect on species evenness (total and ECM). Namely, for total species evenness, the accumulated precipitation of August interacted positively with time ($t(289) = 2.15$, $p = 0.033$). The negative interaction between the accumulated precipitation of September and time had a significant effect on the ECM species evenness ($t(223) = -2.83$, $p = 0.005$). The latter precipitation diminished the positive effect caused by time on the ECM species evenness.

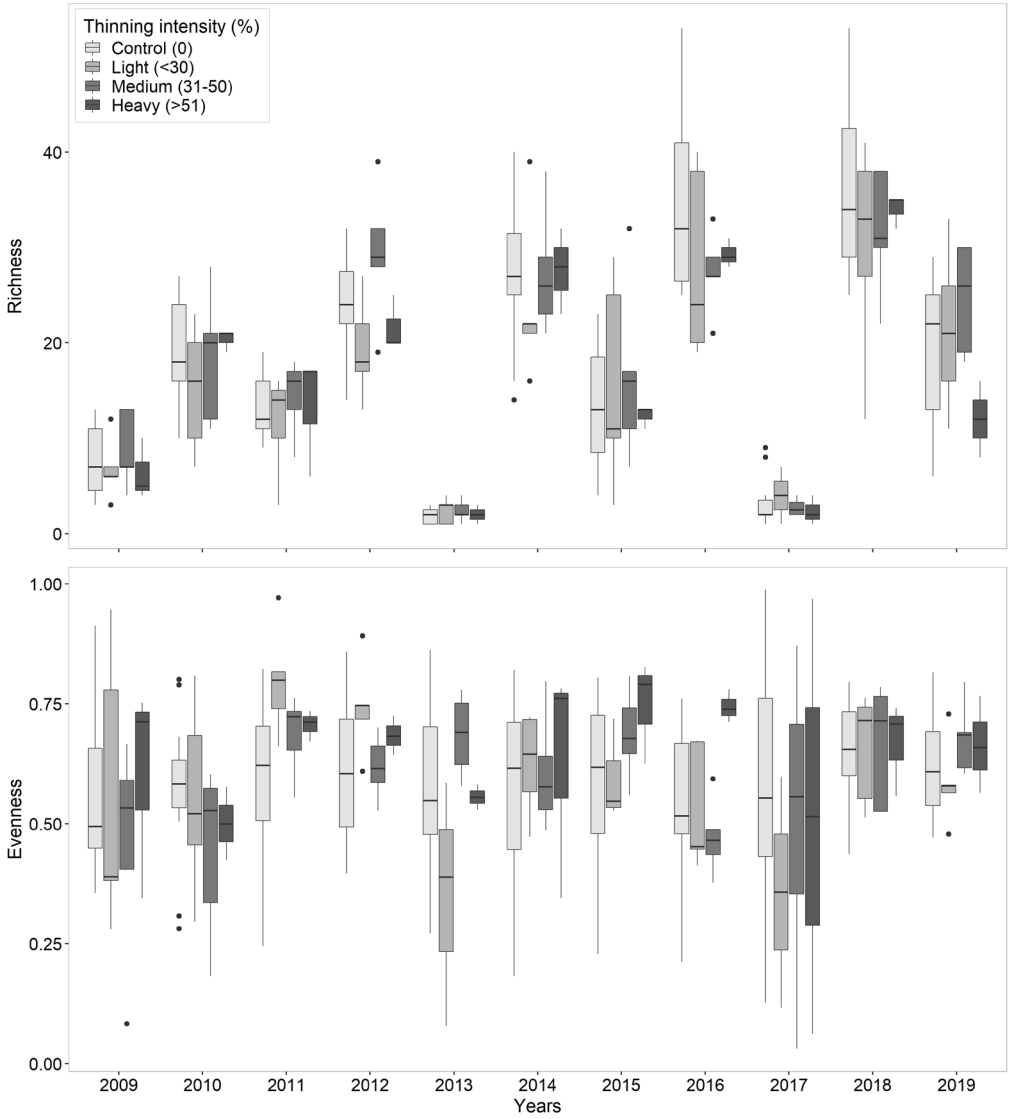

Figure 3: Total sporocarp species richness and evenness under different thinning intensities in stand basal area: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). Dots denote outlier values (i.e., values that fall below Q1 – 1.5 IQR or above Q3 + 1.5 IQR).

Table 2: Summary of fitted models for the sporocarp richness and evenness of total, ectomycorrhizal (ECM) and saprotrophic fungi over the years after thinning.

		Fixed effect coefficients				Random effect		Pseudo R^2				
						Plot	Residuals					
	Trophic group	Intercept	Thinning intensity	Time	Thinning intensity x Time	Intercept	Intercept	R^2m[a]	R^2c[b]	Marginal bias	RMSE	n
Richness	Total fungal sp.	18.239**	-0.021	3.417**	0.008	2.784	125.097	0.09	0.11	-0.005	11.02	305
	ECM	8.058**	0.004	1.409**	-0.003	3.667	18.939	0.08	0.23	-0.010	4.17	242
	Saprotrophic	11.880**	-0.025	2.453**	9.31E-04	6.383	49.937	0.10	0.20	-0.009	6.84	304
Evenness	Total fungal sp.	0.596**	1.95E-04	0.0148	-1.55E-04	0.005	0.024	0.01	0.16	2.30E+04	0.15	289
	ECM	0.588**	5.29E-04	0.047*	1.30E-04	0.008	0.031	0.07	0.27	-0.002	0.17	223
	Saprotrophic	0.623**	1.39E-04	-0.017	2.89E-04	0.008	0.032	0.00	0.20	0.002	0.17	283

Thinning intensity (%, expressed as a decimal), time (years after thinning treatment) and the interaction of both are the independent variables. Marginal bias is the mean bias error of the marginal predictions while the conditional bias is zero in all models, *RMSE* is the root of mean square error and *n* is the number of observations.

[a,b] Marginal (proportion of variance explained by the fixed factors, R^2m) and conditional (proportion of variance explained by fixed plus random factors, R^2c) R^2 values were computed following Nakagawa and Schielzeth (2013).

Significance levels: '**' $p < 0.001$; '*' $p < 0.01$.

4. Discussion

In this study we have investigated how different forest thinning intensities, carried out in Mediterranean *P. pinaster* forest stands, influence the macrofungal sporocarp species composition and diversity. Thinning resulted in short-term quantitative and qualitative changes of the macrofungal community composition, also reflecting the different dynamics of the ectomycorrhizal and saprotrophic functional guilds. Overall, the total fungal sporocarp community composition showed short-term (< 2 years) changes mainly under heavy and light thinning intensities compared to control plots, while there was no effect of thinning on sporocarp species diversity (i.e., richness and evenness). The unexpected compositional change caused by light thinning intensities has been exclusively related to a specific fungal genus (*Lactarius*). Namely, only after excluding *Lactarius* group *deliciosus* from the total and ECM quantitative sporocarp composition, the heavy thinning intensity induced the greatest and most long-lasting changes, thereby partly confirming our first hypothesis. These changes may be explained either by the high alteration of microclimatic conditions after reducing drastically the canopy cover (e.g., Santos-Silva et al., 2011) and/or by the interference in the carbon flux from trees to fungi as a result of very few standing trees (Högberg et al., 2001). Moreover, the new forest stand structure after the light thinning treatment could lead to suitable conditions for the fructification of *Lactarius* group *deliciosus*, such as the increase of effective water availability used directly by the fungus and the low evaporation rates (i.e., as compared to those in heavily thinned stands). In this context, control plots represented very dense stands, resulting in a high competition between trees for water and nutrients. The response of such particular ECM species has been previously described by Bonet et al. (2012), who already observed a sharp increase in sporocarp abundance of *Lactarius* group *deliciosus* after thinning (mostly light intensity). Additionally, some species of the genus *Lactarius* have been found to be favoured by disturbances due to their ECM mycelial exploration type (Ekblad et al., 2013; Guignabert et al., 2018). Namely, contact explorers, e.g., *Lactarius* sp., may easily regenerate their reduced system of extramatrical mycelium (i.e., the main belowground fungal structure), resulting in a higher resilience in the face of disturbances (Tedersoo & Smith, 2013).

We also assumed in the first hypothesis that thinning would lead to changes in ECM and saprotrophic sporocarp diversity but, surprisingly, the results showed no statistically significant thinning effects on aboveground macrofungal diversity. Namely, despite thinning intensity caused different effects on different macrofungal species, favouring particular species at the expense of others, the total number and relative abundance of fungal species remained constant. However, these findings are in contrast to previous short-/mid-term studies that found that forest management tends to reduce sporocarp richness (Kouki and Salo, 2020; Lin et al., 2015), albeit with some exceptions. For instance, Egli et al. (2010) observed, in a long term study of 32 years in temperate Swiss forests, an increasing trend in sporocarp richness (particularly in ECM fungi) in the fourth year after thinning and over 17 years. In the unmanaged stands of the latter study, Egli (2011) found an unexpected declining trend during those 32 years in the percentage of mycorrhizal species. By contrast, other studies showed increasing trends in sporocarp species richness (mostly in ECM fungi) with increasing stand age (e.g., Keizer & Arnolds, 1994; Senn-Irlet & Bieri, 1999). In this sense, we also found that ECM and saprotrophic species richness increased non-linearly over the eleven-years study period, that increment being further either enhanced or diminished depending on the meteorological conditions of a given year.

The increment of saprotrophic sporocarp richness through time could be related to increases in abundance and variety of soil organic matter (e.g., litter, stumps) derived from the increasing forest maturity (Straatsma et al., 2001). The temporal variation observed in fungal sporocarp diversity, modulated by weather conditions, was also reported in previous studies conducted in Mediterranean forests. For instance, Alday et al. (2017) detected along an elevation gradient significant decreasing and increasing trends over eight consecutive years for total and ECM sporocarp richness, as well as an increasing trend in saprotrophic fungal richness.

The results also showed a fast recovery (< 3 years) of the aboveground macrofungal community composition after the thinning treatment, thus confirming our second hypothesis. Namely, particular fungal species may quickly benefit from the forest disturbance to perpetuate themselves by reallocating resources from mycelia to sporocarps (Collado et al., 2020). A possible explanation for such a fast recovery could be the lack of soil disturbances (e.g., soil compaction; Amaranthus, 1996) during harvest, since the felled trees were removed carefully from the plots. For instance, Egli et al. (2010) attributed the low sporocarp production in the two years after the forest thinning to the intervention itself, while the sporocarp production of unthinned stands remained stable. Other works have also reported a short-/mid-term recovery of sporocarp productivity after heavy forest management. For example, Hintikka (1988) detected a recovery of sporocarp yields in the first years after the regeneration cut, whereas Pilz et al. (2006) found that the effect of different thinning intensities on the sporocarp production of *Cantharellus lutescens* persisted less than six years. Nevertheless, the silvicultural treatment effects over time on the sporocarp community composition still remain quite unknown (Tomao et al., 2020).

We found that short-term thinning effects on the community composition interacted with the mean monthly temperature (September and October), thereby confirming our third hypothesis on the modulating effect of weather conditions on the fungal community response to forest thinning. In the mid-/long-term, the differences observed in community composition between thinned and control plots arose exclusively from inter-annual differences in meteorological conditions (temperature and precipitation). Soil moisture is one of the most important factors shaping the sporocarp community in Mediterranean regions, but moisture is highly conditioned by evapotranspiration and, therefore, by temperature (Ágreda, Águeda, Olano, Vicente‐Serrano & Fernández‐Toirán, 2015). In this context, the soil of the site barely retains the moisture since it is characterized by sandy loam textures. In the same plots, Karavani et al. (2018) observed significant correlations between the probability of marketed mushroom occurrence (ECM species) and climatic variables such as the precipitation of September and October. Similarly, Gassibe, Oria-de-Rueda and Martín-Pinto (2015) found in other Mediterranean-continental *P. pinaster* stands that sporocarp community composition was largely related to minimum and maximum temperature and precipitation variables. Therefore, the sporocarp fructification in Mediterranean regions is heavily dependent on the meteorological conditions, to the extent that such conditions may disguise the reduction of carbon flow caused by forest thinning.

Our results also show no impact of thinning intensity on the presence-absence of ECM species (i.e., qualitative abundance), indicating that the same ECM species occur regardless of thinning intensity. Actually, the increase over time in fungal species evenness indicates a gradual reduction of dominance in the fructification of particular ECM species, such as

the initial short-term dominance of *Lactarius* group *deliciosus*. A plausible reason behind these findings may be the high influence of the tree species composition on the ECM fungal composition (Tomao et al., 2020), since different host trees provide unique habitats for host-specific fungi (Tedersoo et al., 2012). In this sense, our study site is characterized by a similar tree species composition in both control and thinned plots. Additionally, previous studies concluded that the soil ECM fungal community does not change as long as enough host trees are retained to provide carbon to such fungi (Sterkenburg et al., 2019; Varenius et al., 2017), as it was the case in our experimental plots (i.e., with at least 30% of remaining trees, in stand basal area).

The lack of response of quantitative composition to thinning may lie in the fact that the quantitative abundance of saprotrophic sporocarps is more sensitive to weather events in Mediterranean regions, rather than to forest thinning (Collado et al., 2018). However, climatic factors together with the thinning activity resulted in changes in the qualitative saprotrophic composition, as hypothesized. In particular, the medium- and heavy-thinning intensities caused the largest changes in the community composition. This may be explained by the fructification of less-abundant specialist fungal species facilitated by the new conditions established in the thinned stands after treatment: (i) the new microclimate, i.e., higher temperatures, sun exposition and evaporation as forest thinning was intensified (Pilz and Molina, 2002); and (ii) the additional available resources (Boddy, Frankland & Van West, 2008; Gebauer & Taylor, 1999). Namely, the fructification of macrofungi –especially saprotrophic species– relies on water availability (particularly in Mediterranean biomes) and on the quality and quantity of resources, which may possibly be altered by anthropogenic disturbances (Krah et al., 2018; Tomao et al., 2020). This alteration may create new niches for a particular fungal community. The new resources that might be used by saprotrophic species may arise either from the organic matter supplied by tree removal and/or from less competition between trees for the resources. Indeed, although we tried to remove the trees carefully, additional organic matter (e.g., branches, litter) was inevitably left in the plots as well as the stumps with their root system. Stumps are niches for specialized fungal species, these fungi profiting the exposed cut surface area and the root system of the stump to colonize them via airborne spores and mycelia, respectively (Berglund, Jönsson, Penttilä & Vanha-Majamaa, 2011; Parisi et al., 2018). For instance, Müller, Engel and Blaschke (2007) observed in a beech forest that with higher management intensities the sporocarps of species with preference for stumps increased significantly. Conversely, other studies found higher fungal sporocarp diversity in unmanaged stands, due to the high amount of deadwood, than in disturbed stands (Dvořák et al., 2017; Juutilainen, Mönkkönen, Kotiranta & Halme, 2016). In the light of the different saprotrophic groups with preference for diverse organic matter, further research in this area must include such groups in order to have a whole and precise picture of the saprotrophic community and its response to disturbances.

5. Conclusions

In this long-term experimental study, we show how the post-treatment conditions following forest thinning facilitated short-term successional changes in both ECM and saprotrophic fungal assemblages. Particular ECM fungal species (i.e., *Lactarius* group *deliciosus*) quickly reacted to the anthropogenic forest disturbance by producing a significantly larger amount of sporocarps. Once such immediate reaction disappeared, the macrofungal community showed absence of dominance of particular fungal species and, in turn, an increasing sporocarp species richness over time. We also found that weather conditions, as crucial factors involved in fungal fructification, either enhance or diminish the effect caused by forest thinning on the sporocarp community composition. Lastly, this study provides a sounder base for building tools oriented toward assessing the impact of forest management and silvicultural practices on ecosystem biodiversity and services provided by fungi.

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Authors' contributions

JAB, JMA and SdM conceived the ideas and designed methodology; JMA and EC collected the data; EC, JA and SdM analysed the data; EC led the writing of the manuscript. JAB and SdM supervised the overall research work. All authors contributed critically to the drafts and gave final approval for publication.

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Supplementary material

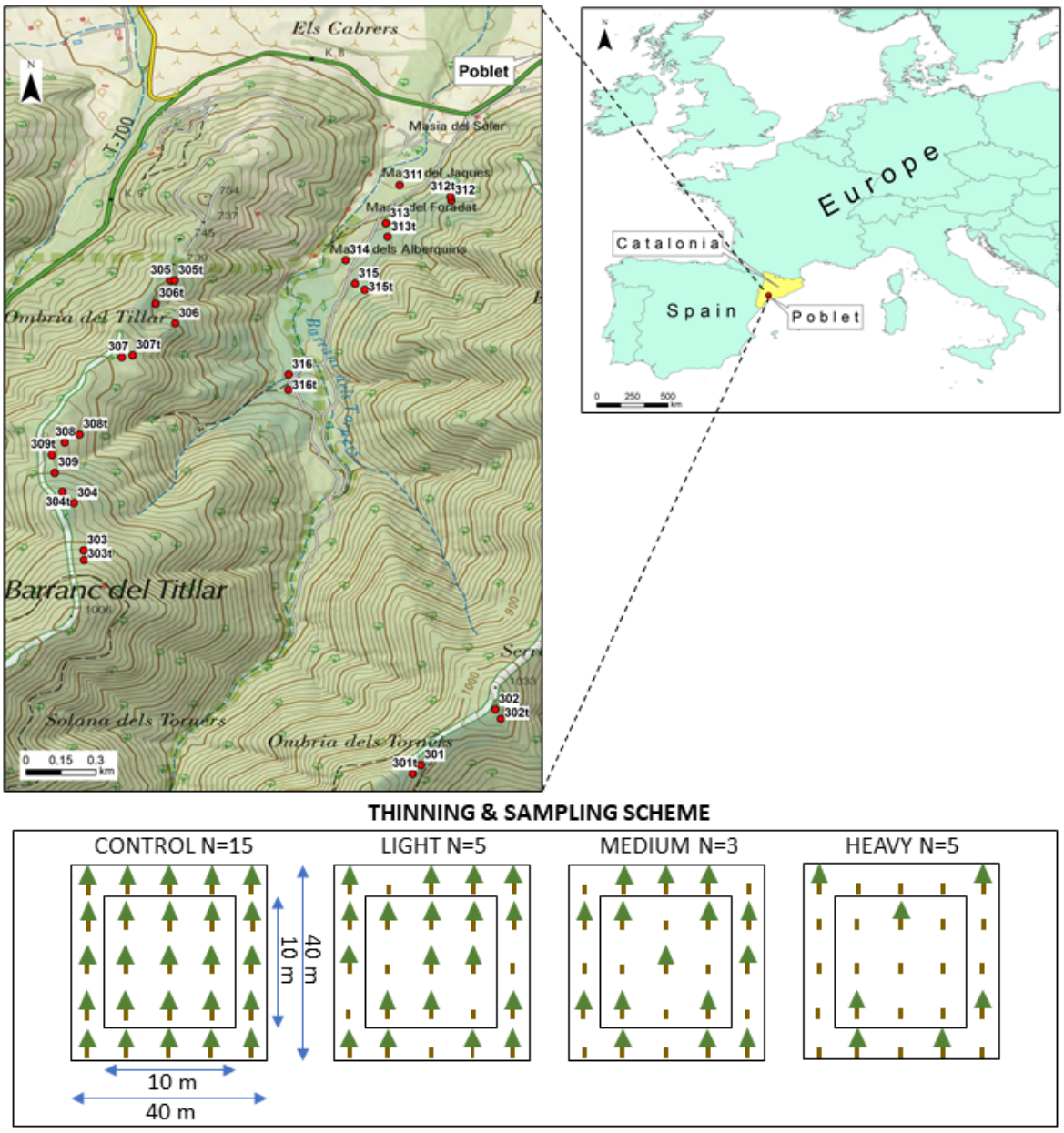

Figure S1: Geographical location of the 28 permanent sporocarp inventory plots of 100 m^2 (10 x 10 m). 15 control (unthinned) plots were established in 2008, whereas the other 13 plots were set up in summer of 2009 representing different thinning intensities. The forest thinning intensity gradient (in stand basal area) represented in the experimental design was as follows: light (20-30%, 5 plots), medium (31-50%, 3 plots) and heavy (51-70%, 5 plots). The thinned plots were located in the centre of larger thinning plots (40 m x 40 m) in order to prevent edge effects. Image source: the Spanish National Mapping Agency (Instituto Geográfico Nacional).

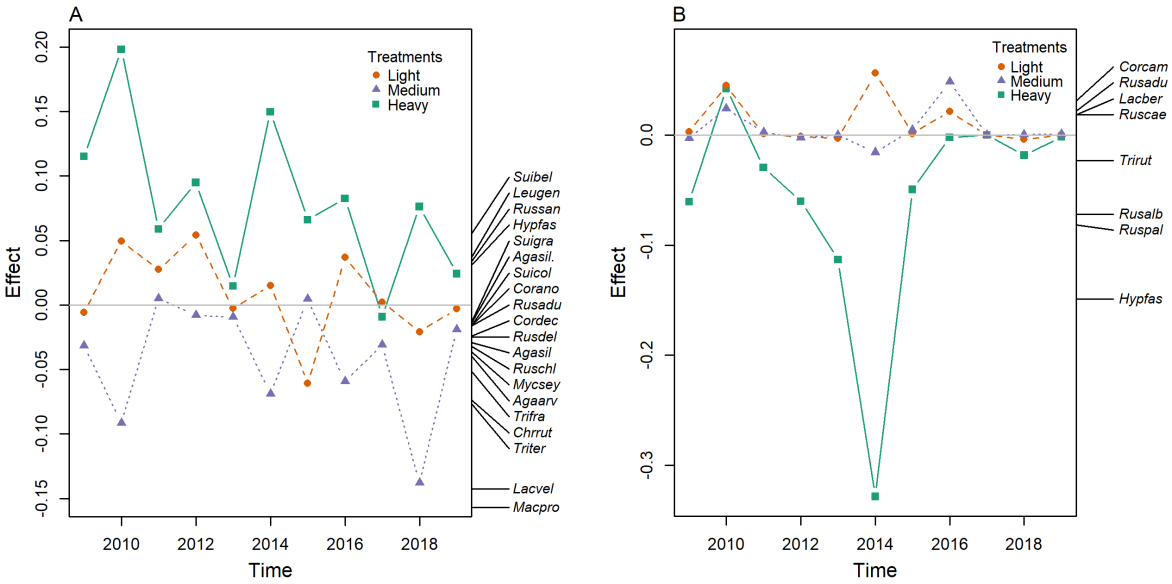

Figure S2: Principal response curves analysis of the changes over 11 years and after different thinning intensities (conducted in 2009) in total fungal sporocarp composition, under different reductions of the most abundant species. Such reductions consisted of ruling out both *Lactarius deliciosus* and *L. vinosus* (A), as well as 15% of the most abundant species (B). The fungal composition was based on the production of sporocarps (kg in dry weight ha^{-1}). Treatments (thinning) intensities in stand basal area were classified as: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). Species codes are (sorted alphabetically): Agaarv = *Agaricus arvensis*, Agasil = *Agaricus sylvaticus*, Agasil. = *Agaricus sylvicola*, Chrrut = *Chroogomphus rutilus*, Corano = *Cortinarius anomalus*, Corcam = *Cortinarius camphoratus*, Cordec = *Cortinarius decipiens*, Hypfas = *Hypholoma fasciculare*, Lacber = *Lactarius bertillonii*, Lacvel = *Lactarius vellereus*, Leugen = *Leucopaxillus gentianeus*, Macpro = *Macrolepiota procera*, Mycsey = *Mycena seynii*, Rusadu = *Russula adusta*, Rusalb = *Russula albonigra*, Ruscae = *Russula caerulea*, Ruschl = *Russula chloroides*, Rusdel = *Russula delica*, Ruspal = *Russula paludosa*, Russan = *Russula sanguinea*, Suibel = *Suillus bellinii*, Suicol = *Suillus collinitus*, Suigra = *Suillus granulatus*, Trifra = *Tricholoma fracticum*, Trirut = *Tricholomopsis rutilans*, Triter = *Tricholoma terreum*.

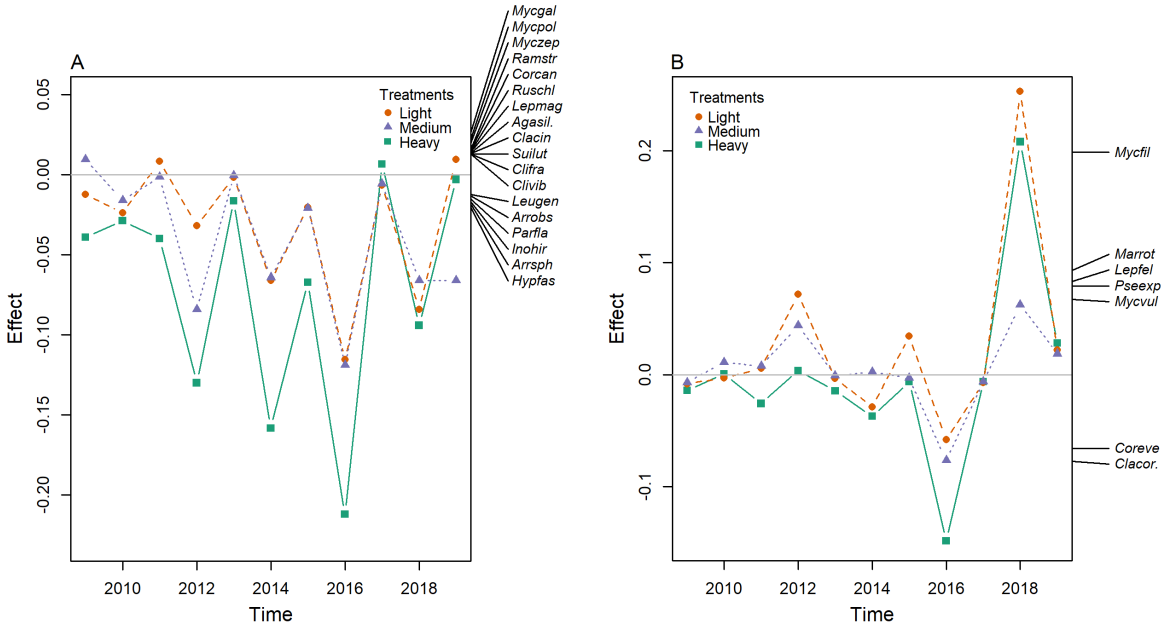

Figure S3: Principal response curves analysis of the changes over 11 years and after different thinning intensities (conducted in 2009) in total fungal sporocarp composition, under different reductions of the most abundant species. Such reductions consisted of ruling out both 10% and 20% of the most abundant species (A and B, respectively). The fungal composition was based on the presence-absence of sporocarps. Treatments (thinning) intensities in stand basal area were classified as: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). Species codes are (sorted alphabetically): Agasil. = *Agaricus sylvicola*, Arrobs = *Arrhenia obscurata*, Arrsph = *Arrhenia sphagnicola*, Clacin = *Clavulinopsis cinerioides*, Clacor. = *Clavulina coralloides*, Clifra = *Clitocybe fragrans*, Clivib = *Clitocybe vibecina*, Corcan = *Cortinarius caninus*, Coreve = *Cortinarius evernius*, Hypfas = *Hypholoma fasciculare*, Inohir = *Inocybe hirtella*, Leugen = *Leucopaxillus gentianeus*, Lepfel = *Lepiota felina*, Lepmag = *Lepiota magnispora*, Marrot = *Marasmius rotula*, Mycfil = *Mycena filopes*, Mycgal = *Mycena galericulata*, Mycpol = *Mycena polygramma*, Mycvul = *Mycena vulgaris*, Myczep = *Mycena zephirus*, Parfla = *Paralepista flaccida*, Pseexp = *Pseudoclitocybe expallens*, Ramstr = *Ramaria stricta*, Ruschl = *Russula chloroides*, Suilut = *Suillus luteus*.

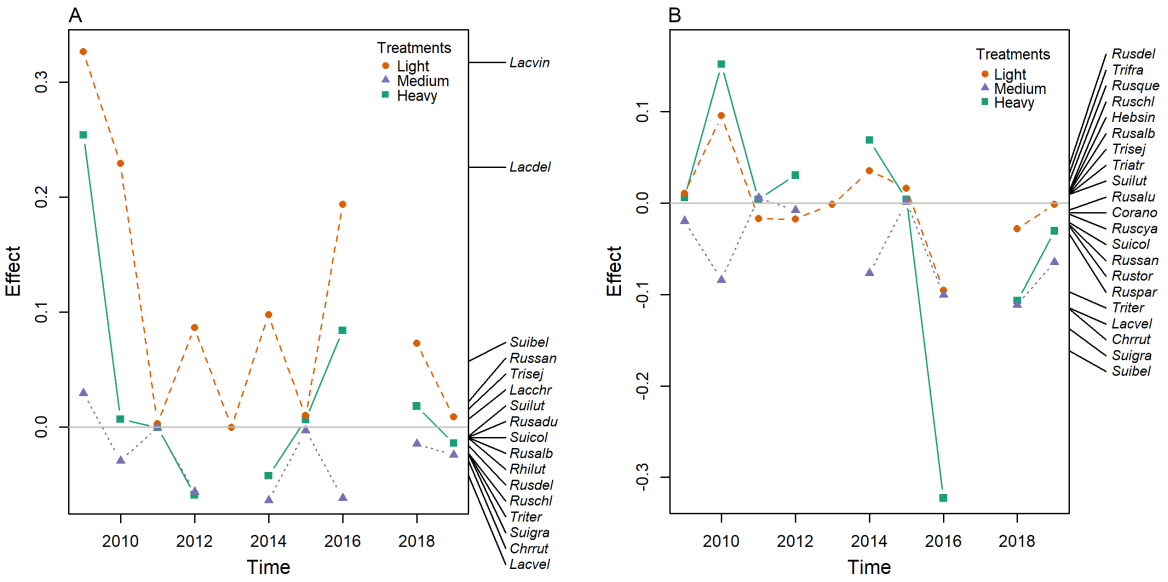

Figure S4: Principal response curves analysis of the changes over 11 years and after different thinning intensities (conducted in 2009) in the ectomycorrhizal sporocarp composition (A), and with a reduction of 10% of the most abundant species (B). The fungal composition was based on the production of sporocarps (kg in dry weight ha^{-1}). Those years without data corresponded to the absence of ECM fructification. Treatments (thinning) intensities in stand basal area were classified as: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). Species codes are (sorted alphabetically): Chrrut = *Chroogomphus rutilus*, Corano = *Cortinarius anomalus,* Hebsin = *Hebeloma sinapizans*, Lacchr = *Lactarius chrysorrheus*, Lacdel = *Lactarius deliciosus*, Lacvel = *Lactarius vellereus*, Lacvin = *Lactarius vinosus*, Rhilut = *Rhizopogon luteolus*, Rusadu = *Russula adusta*, Rusalb = *Russula albonigra*, Rusalu = *Russula alutacea*, Ruschl = *Russula chloroides*, Ruscya = *Russula cyanoxantha*, Rusdel = *Russula delica*, Ruspar = *Russula parazuela*, Rusque = *Russula queletii*, Russan = *Russula sanguinea*, Rustor = *Russula torulosa*, Suibel = *Suillus bellinii*, Suicol = *Suillus collinitus*, Suigra = *Suillus granulatus*, Suilut = *Suillus luteus*, Triatr = *Tricholoma atrosquamosum*, Trifra = *Tricholoma fracticum*, Trisej = *Tricholoma sejunctum*, Triter = *Tricholoma terreum*.

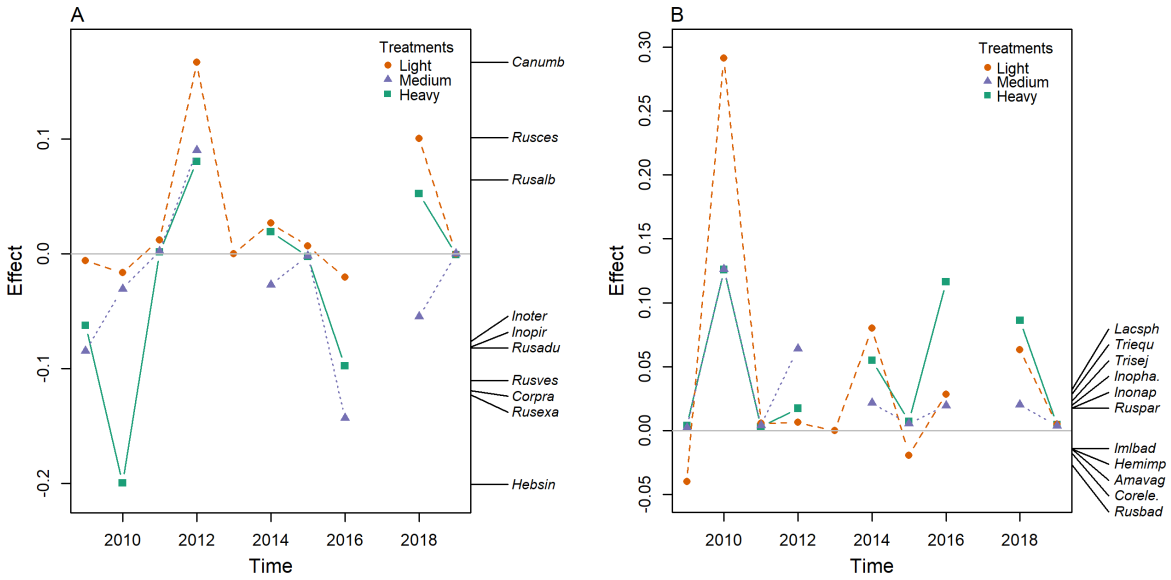

Figure S5: Principal response curves analysis of the changes over 11 years and after different thinning intensities (conducted in 2009) in the ectomycorrhizal sporocarp composition, under different reductions of the most abundant species. Such reductions consisted of ruling out both 10% and 25% of the most abundant species (A and B, respectively). The fungal composition was based on the presence-absence of species. Those years without data corresponded to the absence of ECM fructification. Treatments (thinning) intensities in stand basal area were classified as: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). Species codes are (sorted alphabetically): Amavag = *Amanita vaginata*, Canumb = *Cantharellula umbonata*, Corele. = *Cortinarius elegantissimus*, Corpra = *Cortinarius pratensis*, Hebsin = *Hebeloma sinapizans*, Hemimp = *Hemileccinum impolitum*, Imlbad = *Imleria badia*, Inonap = *Inocybe napipes*, Inopha. = *Inocybe phaeoleuca*, Inopir = *Inocybe piriodora*, Inoter = *Inocybe terrigena*, Lacsph = *Lactarius sphagneti*, Rusadu = *Russula adusta*, Rusalb = *Russula albonigra*, Rusbad = *Russula badia*, Rusces = *Russula cessans*, Rusexa = *Russula exalbican*, Ruspar = *Russula parazuela*, Rusves = *Russula vesca*, Triequ = *Tricholoma equestre*, Trisej = *Tricholoma sejunctum*.

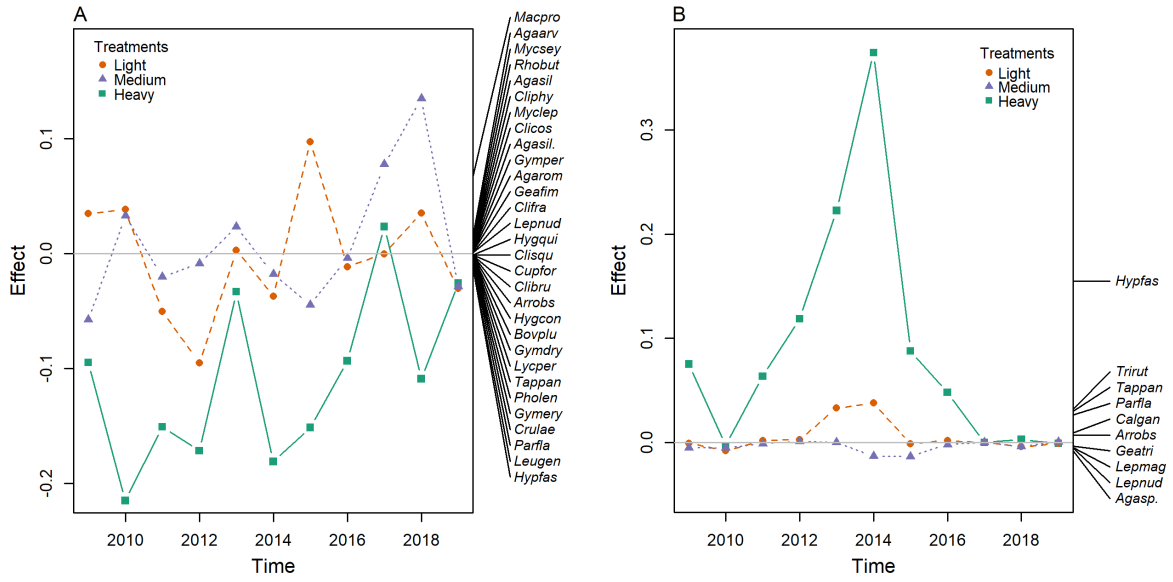

Figure S6: Principal response curves analysis of the changes over 11 years and after different thinning intensities (conducted in 2009) in the saprotrophic sporocarp composition (A), and with a reduction of 10% of the most abundant species (B). The fungal composition was based on the production of sporocarps (kg in dry weight ha^{-1}). Treatments (thinning) intensities in stand basal area were classified as: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). Species codes are (sorted alphabetically): Agaarv = *Agaricus arvensis*, Agarom = *Agaricus romagnesii*, Agasil = *Agaricus sylvaticus*, Agasil. = *Agaricus sylvicola*, Agasp. = *Agaricus* sp., Arrobs = *Arrhenia obscurata*, Bovplu = *Bovista plumbea*, Calgan = *Calocybe gangraenosa*, Clibru = *Clitocybe brumalis*, Clicos = *Clitocybe costata*, Clifra = *Clitocybe fragrans*, Cliphy = *Clitocybe phyllophila*, Clisqu = *Clitocybe squamulosa*, Crulae = *Crucibulum laeve*, Cupfor = *Cuphophyllus fornicatus*, Geafim = *Geastrum fimbriatum*, Geatri = *Geastrum triplex*, Gymdry = *Gymnopus dryophilus*, Gymper = *Gymnopus peronatus*, Gymery = *Gymnopus erythropus*, Hygcon = *Hygrocybe conica*, Hypfas = *Hypholoma fasciculare*, Hygqui = *Hygrocybe quieta*, Lepmag = *Lepiota magnispora*, Lepnud = *Lepista nuda*, Leugen = *Leucopaxillus gentianeus*, Lycper = *Lycoperdon perlatum*, Macpro = *Macrolepiota procera*, Myclep = *Mycena leptocephala*, Mycsey = *Mycena seynii*, Parfla = *Paralepista flaccid*, Pholen = *Pholiota lenta*, Rhobut = *Rhodocollybia butyracea*, Tappan = *Taminella panuoides*, Trirut = *Tricholomopsis rutilans*.

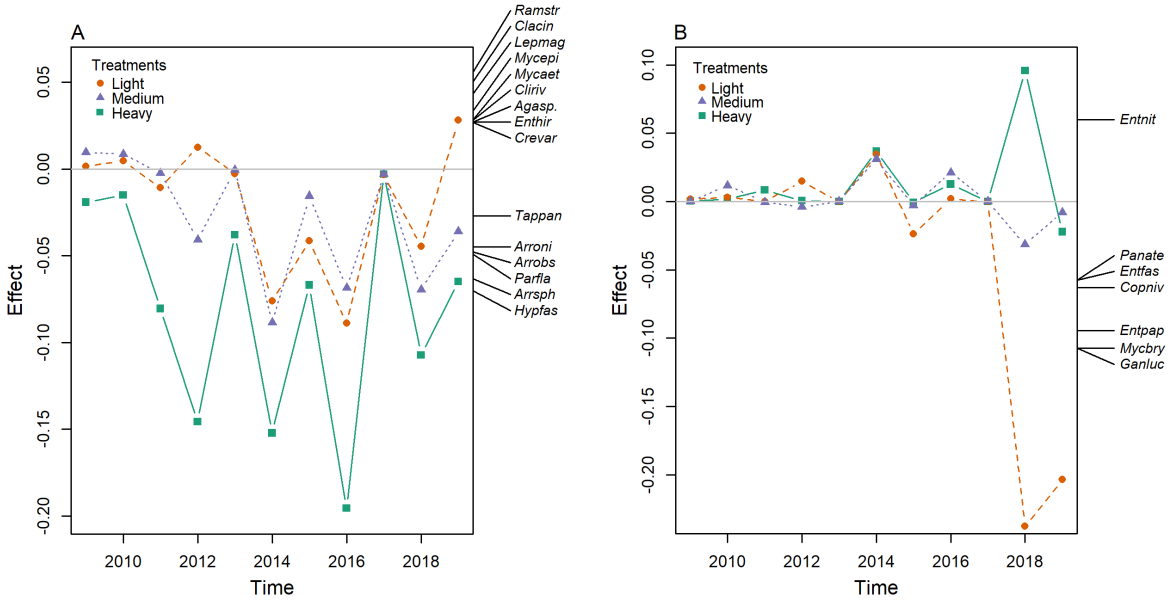

Figure S7: Principal response curves analysis of the changes over 11 years and after different thinning intensities (conducted in 2009) in the saprotrophic sporocarp composition, under different reductions of the most abundant species. Such reductions consisted of ruling out both 10% and 25% of the most abundant species (A and B, respectively). The fungal composition was based on the presence-absence of species. Treatments (thinning) intensities in stand basal area were classified as: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). Species codes are (sorted alphabetically): Agasp. = *Agaricus* sp., Arrobs = *Arrhenia obscurata*, Arroni = *Arrhenia onisca*, Arrsph = *Arrhenia sphagnicola*, Clacin = *Clavulinopsis cinerioides*, Cliriv = *Clitocybe rivulosa*, Copniv = *Coprinopsis nivea*, Crevar = *Crepidotus variabilis*, Entfas = *Entoloma fastigiatum*, Enthir = *Entoloma hirtipes*, Entnit = *Entocybe nitida*, Entpap = *Entoloma papillatum*, Ganluc = *Ganoderma lucidum*, Hypfas = *Hypholoma fasciculare*, Lepmag = *Lepiota magnispora*, Mycaet = *Mycena aetites*, Mycbry = *Mycenella bryophila*, Mycepi = *Mycena epipterygia*, Panate = *Panaeolus ater*, Parfla = *Paralepista flaccid*, Ramstr = *Ramaria stricta*, Tappan = *Taminella panuoides*.

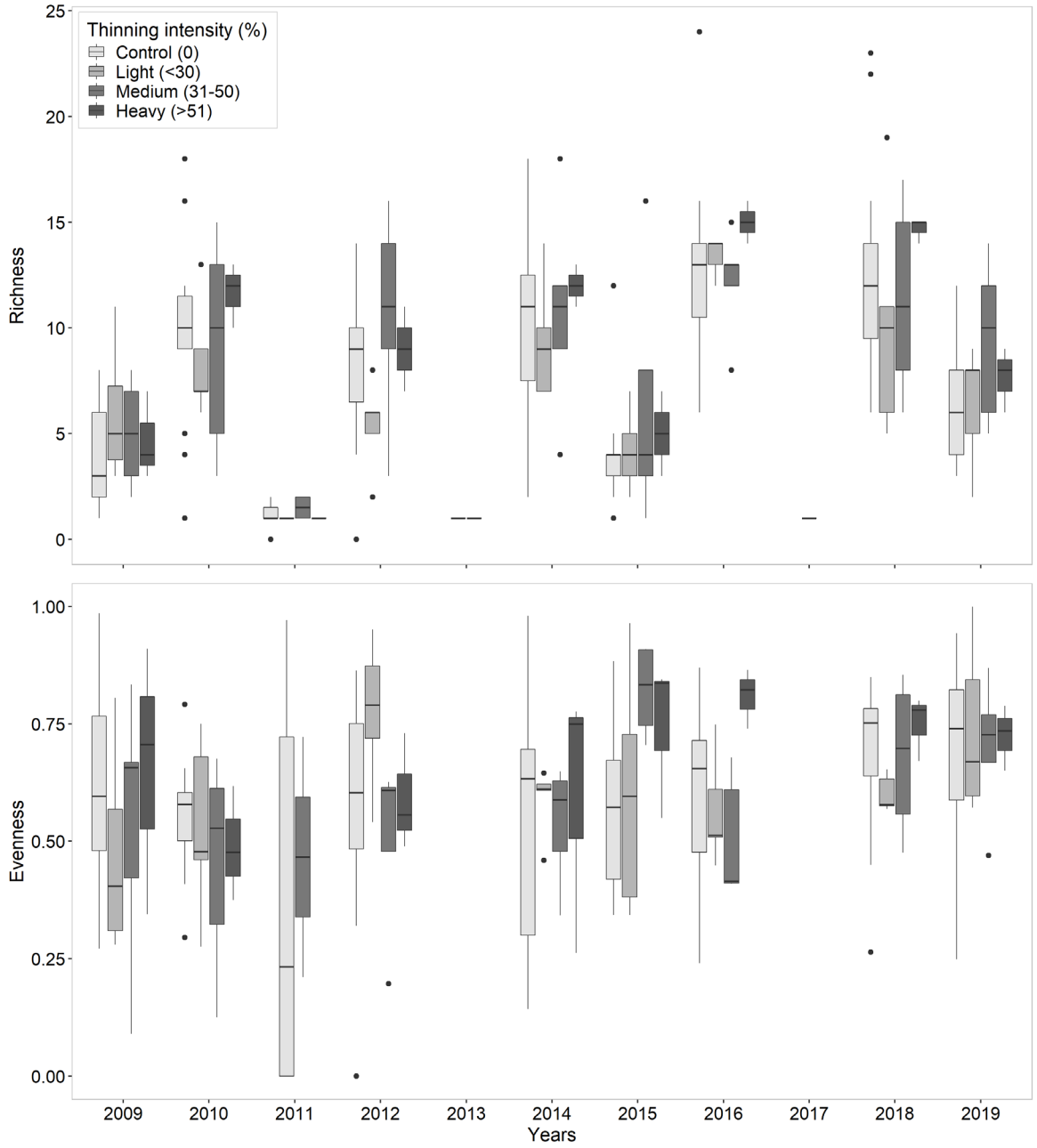

Figure S8: Ectomycorrhizal sporocarp richness and evenness under different thinning intensities in stand basal area: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). Dots denote outlier values (i.e., values that fall below Q1 – 1.5 IQR or above Q3 + 1.5 IQR).

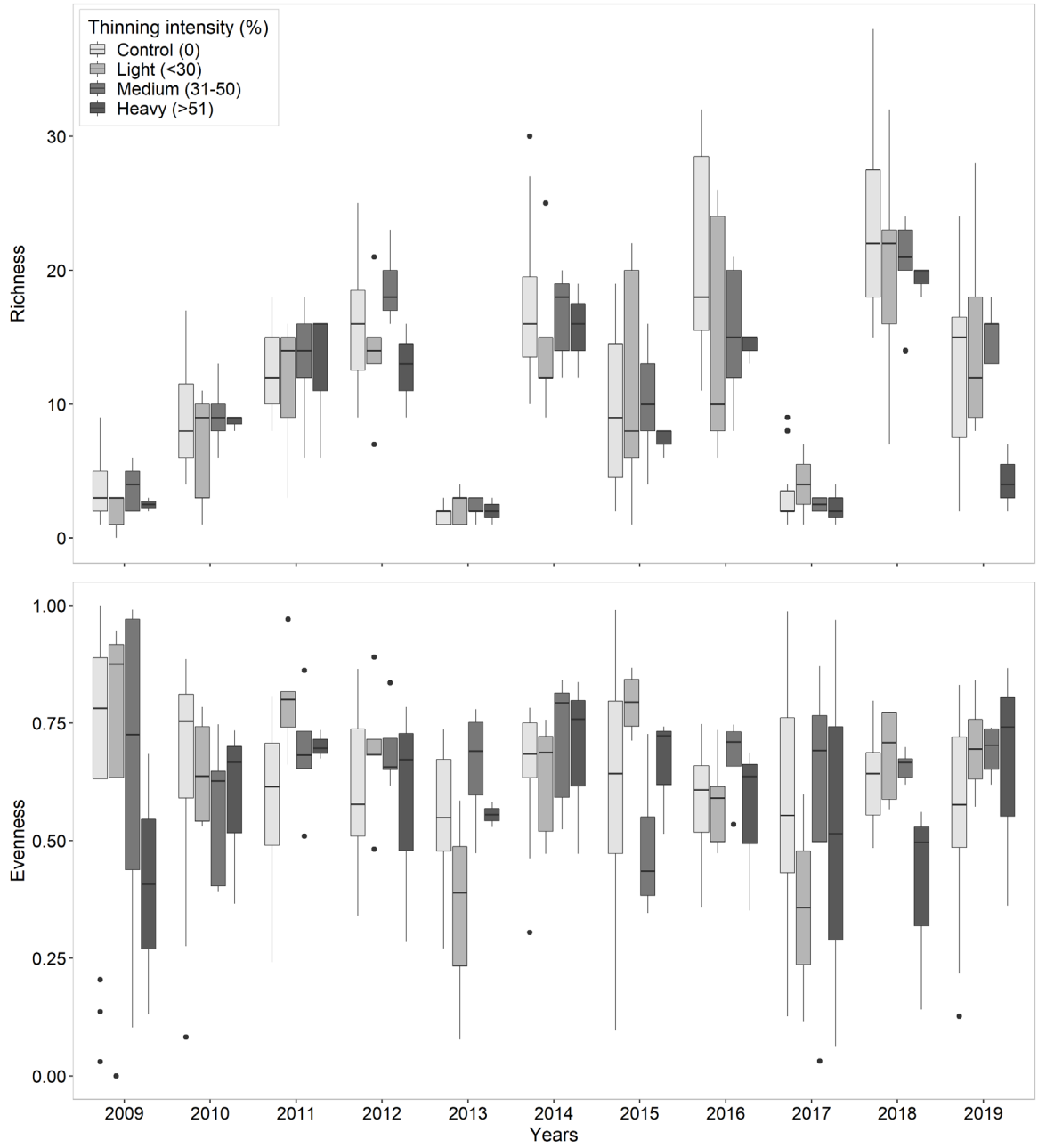

Figure S9: Saprotrophic sporocarp richness and evenness under different thinning intensities in stand basal area: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). Dots denote outlier values (i.e., values that fall below Q1 – 1.5 IQR or above Q3 + 1.5 IQR).

GENERAL DISCUSSION

The existent literature has amply demonstrated the significant role of fungi in forest ecosystem processes, as well as their relationships, directly or indirectly, with manifold organisms (Dighton, 2016; Morris and Robertson, 2005). Ectomycorrhizal fungi behave as an interface between soil and plant, being critical for the survival of most forest trees. In this sense, elucidating questions on complex fungi – tree interactions (e.g., carbon allocation patterns) that are, in turn, strongly mediated by climatic factors are highly relevant. Also, such interactions under environmental stressors deserve further attention, inasmuch as fungi may act as factors contributing to ecosystem stability and resilience or as agents of successional change. Furthermore, numerous uncertainties in the interaction between aboveground (sporocarps) and belowground (mycelium) fungal structures and their response to the aforesaid environmental stressors still remain. In particular, there are weak evidences on how belowground fungal biomass cope with disturbances and how fungi, afterwards, reallocate carbon into different fungal structures. Indeed, one of the fungal responses to stress factors is to perpetuate themselves, either vegetatively (mycelium) or reproductively (sporocarps), although fungi may react differently according to the functional guild and species. Therefore, changes in sporocarp communities (composition and diversity) may arise from forest disturbances. In this context, long-term experimental studies are required to deal with stochastic fruiting dynamics.

This thesis has aimed at shedding light on the interactions between fungal productivity, diversity and community composition and tree growth dynamics as mediated by anthropogenic disturbance (i.e., forest management) and environmental drivers (i.e., climatic and meteorological conditions) in different forest ecosystems and biomes (i.e., Mediterranean, temperate and boreal). One key result was the observed positive relationships between mushroom production (particularly ECM fungi) and radial tree growth (i.e., LW width) only in Mediterranean regions (Chapter II). This is partly due to the fact that, under water-limited climate conditions, both tree growth and mushroom yields are more sensitive to precipitation events during the late growing season. This resulted in higher synchrony between tree growth and mushroom yield as a function of water availability in late summer and early autumn. Likewise, Büntgen et al. (2015) observed a significant positive relationship between tree growth (TRW) and fungal fruiting in a Mediterranean pine ecosystem, while Büntgen et al. (2013) did not find any significant correlation under more temperate climatic conditions in Switzerland. All this previous research was based on the idea that mycorrhizal mushroom production is linked to tree growth, through the carbon allocation from the host trees to mycorrhizal fungi (Högberg et al., 2008), which also depends on climate conditions.

These findings were further confirmed by the results obtained from the long-term experimental set-up of 28 Mediterranean *P. pinaster* plots (Chapter I). Indeed, tree growth and, mostly, the intra-annual density fluctuations were shown to be correlated with mushroom (saprotrophic and ECM) production. Such tree growth – mushroom production – climate relationships are partly explained by their biological and ecological synchrony: the starting point of the mushroom fruiting season in late summer is related to the maximum LW growth rates and the occasional formation of latewood IADFs as a response to summer/autumn storms. Similarly, Primicia et al. (2016) found some positive associations between LW production and ECM yield in xeric sites. However, the relationship between tree growth and ECM mushroom production was mediated, not only by such precipitations, but also by forest thinning effects. In particular, the relationship

between LW width and ECM mushroom yield was only positive in those plots under low to moderate forest thinning intensities (i.e., ca. 30% in stand basal area) (Chapter I). Namely, the remaining trees of the plots that were strongly thinned increased their radial growth because of the reduced competition for water and nutrients, while the ECM fungi may be strongly affected by a drastic decrease in the number of host trees, resulting in reduced mushroom yield. Indeed, the remaining trees from the thinned plots could have allocated more carbohydrates to the associated fungi, as a result of colonization and trophic strategies of a few species. Unexpectedly, saprotrophic mushroom production was also related to LW formation, as a possible result of the alterations caused by high-intensity thinning (Tomao et al., 2017), namely, shifts in micro-climatic conditions and the additional litter supply from the enhanced tree growth. Likewise, Egli et al. (2010) found positive relationships between increased radial growth after thinning and both subsequent production of ECM and, to a lesser extent, saprotrophic fungi. The latter study also detected 2-year lagged effects between the tree-ring width and the current mycorrhizal mushroom production, whereas this thesis has shown 2-year lagged effects only between the current saprotrophic mushroom production and latewood width (Chapter I). The explanation of our lagged effects may lie in the fact that the litter follows a decomposition process that may take some time until the saprotrophic fungi can use it for sexual reproduction (Straatsma et al., 2001).

Nevertheless, the relationship between ECM mushroom production and LW width may not be completely obvious due to several factors. For instance, the carbon allocated from the host tree to ECM may not necessarily be invested to promote mushroom fruiting but to mycelium growth belowground (Diez et al., 2013). In this sense, this thesis has shown that thinning reduced the total belowground fungal biomass in *P. pinaster* stands, as an effect of reduced belowground ECM biomass (Chapter III). Namely, ECM fungi is the only functional guild that has been clearly shown to be sensitive to host tree disturbances, as also found in Chapter I on the relationship between mushroom yield and tree growth dynamics. This thesis has also demonstrated that higher thinning intensities were related to a long-lasting reduction of total and ECM biomass (Chapter III). Reduced belowground biomass was observed both between different years and within the same year, from spring 2013 (four years after thinning) to spring 2014 (five years after thinning). Our inter-annual results are consistent with the findings of previous studies focused on single fungal species, in different forest ecosystems and under other disturbance intensities (Mediavilla et al., 2017; Parladé et al., 2017). It seems that the remaining trees after thinning, acting as a 'refuge', may suffice to support the belowground ECM fungi (Amaranthus and Perry, 1987; Sterkenburg et al., 2018; Varenius et al., 2016). Reductions in belowground fungal biomass may be also explained by alterations in the soil microclimatic conditions (Castaño et al., 2018; De la Varga et al., 2013), as an indirect effect of forest thinning. On the other hand, thinning did not only cause a negative effect on the mycelial biomass of both total and ECM fungi but also triggered an initial positive effect on the production of sporocarps which faded over time. Differences between the above- and below-ground biomass increased with higher thinning intensities, indicating a possible shift in the fungal biology from vegetative growth to reproduction under disturbances (Suz et al., 2008). Similar to our findings, a negative relationship between the mycelial biomass and the productivity of *B. edulis* sporocarps was observed by De la Varga et al. (2013), when they compared their results with those obtained from a previous work (De la Varga et al., 2012).

Forest thinning did not only entail changes in the ratio between above- and belowground fungal biomass, but also in the aboveground fungal community composition and diversity (Chapter IV). In *P. pinaster* stands, the total fungal sporocarp community composition showed short-term (< 2 years) changes mainly under heavy and light thinning intensities compared to unthinned stands, while there was no effect of thinning on sporocarp species diversity (i.e., richness and evenness). The unexpected compositional change caused by light thinning intensities has been exclusively related to a specific fungal genus (*Lactarius*). After excluding the *Lactarius* group *deliciosus* from the total and ECM quantitative sporocarp composition (based on dry weight), only the heavy thinning intensity induced the greatest and most long-lasting changes. This may be explained either by the high alteration of microclimatic conditions after reducing drastically the canopy cover (e.g., Santos-Silva et al., 2011) and/or by the interference in the carbon flux from trees to fungi as a result of very few standing trees (Högberg et al., 2001). However, climate conditions may disguise the reduction of carbon flow caused by thinning. In this sense, the short-term thinning effect on the community composition interacted with the mean temperature (September and October). The interaction enhanced or diminished the effect caused by thinning.

Moreover, forest thinning did not impact on the presence-absence of ECM species in *P. pinaster* stands, indicating that the same ECM species occur regardless of thinning intensity (Chapter IV). Actually, the increase over time in fungal species evenness indicates a gradual reduction of dominance in the fructification of particular ECM species, such as the initial short-term dominance of *Lactarius* group *deliciosus*. A plausible reason behind these findings may be that this study site is characterized by a similar tree species composition in both control and thinned plots, and therefore all plots are capable to harbor the same ECM community composition (Tedersoo et al., 2012). Nevertheless, forest thinning together with climatic factors led to short-term effects on the presence-absence of saprotrophic species (Chapter IV). In particular, the medium and heavy thinning intensities caused the largest alterations in the community. This may be explained by the fructification of less-abundant specialist fungal species facilitated by the new conditions established in the thinned stands after treatment: (i) the new microclimate (Pilz and Molina, 2002); and (ii) the additional available resources (Krah et al., 2018; Tomao et al., 2020). Namely, fructification of macrofungi –especially saprotrophic species– relies on water availability (particularly in Mediterranean biomes) and on the quality and quantity of resources, which may possibly be altered by anthropogenic disturbances (Krah et al., 2018; Tomao et al., 2020).

From a forest management point of view, this thesis has shown how different thinning intensities trigger different fungal responses, altering in turn the fungal-related ecosystem services. For instance, light thinning intensities with a careful and low-impact removal of trees have demonstrated in *P. pinaster* stands to be suitable in terms of conservation and production. Namely, such thinning intensities did not jeopardize sporocarp diversity, showed a limited effect on belowground total and ECM biomass and strongly increased the sporocarp production of particular commercial fungal species (*Lactarius* group *deliciosus*). For example, almost 500,000 kg year^{-1} of *L. vinosus* are sold at the three most important Spanish markets, with an estimated market value of €5.3 million year^{-1} (Voces et al., 2012). Therefore, this forest management is of great importance to maximize the benefits from Mediterranean pine forests by taking advantage of both timber and mushrooms, without forgetting the conservation of fungal communities and their vital role in forest ecosystems.

In short, this thesis has attempted to contribute to those unresolved questions on fungi – tree interactions and above- and belowground fungal dynamics under forest disturbances. To this end, huge amount of dataset from different disciplines has been compiled during several years (mid- to long-term) and at different spatial scales, covering in turn manifold approaches: mycological data, dendrochronological information, climatic data and forest stand parameters. Dendrochronological techniques have recently allowed to approach the poorly understood relationships between fungi and tree host, although systematic crossdisciplinary efforts are still scant. As this thesis has shown, such interactions are largely mediated, among others, by climatic factors and thus it becomes necessary to deepen this new and promising interdisciplinary perspective as Büntgen and Egli (2014) stated: (i) combining mushroom productivity with continuous high-resolution dendrometer measurements of cell formation and sap flow, or (ii) applying isotopic labelling to trace nutrient, water and symbiotic carbon fluxes and pathways for different species and biomes. Moreover, anthropogenic disturbances have been used in this thesis as a tool to observe changes in mushroom productivity (according to the functional guild) and tree growth, as well as to detect divergent responses of above- and belowground fungal communities. This has been possible here by combining, as very few studies have addressed (e.g., Hagenbo et al., 2018), different molecular and biochemical techniques (e.g., Pacific Biosciences sequencing and ergosterol quantification, respectively) to assess belowground fungal biomass together with fungal community composition. Such a combination of techniques may in the future yield complementary information on the biology and ecology of fungal species and guilds. However, not only these novel approaches have characterised this thesis, but also the longitudinal data. Namely, belowground fungal biomass was estimated by mid-term data (~5 years and 12 consecutive months), while aboveground fungal biomass was quantified by a continuous monitoring of sporocarps during up to eleven years. Although compiling such long-term data requires great effort, the potential benefits are numerous, such as: (i) elucidating how long the effects of forest disturbances persist on sporocarps community composition and diversity, (ii) showing more accurately the impacts of meteorological fluctuations and climate change on fungal dynamics, or (iii) shedding light on the occurrence and abundance of threatened and rare fungal species in managed stands. Therefore, all of these techniques applied during several years have allowed to shape this thesis, contributing to improving scientific knowledge on: fungal ecology, fungal response to anthropogenic disturbances and environmental drivers within the larger framework of the overall role of fungi in ecosystem functioning and services.

FINAL CONCLUSIONS

- Tree growth (earlywood and latewood) and, mostly, the intra-annual density fluctuations were correlated with saprotrophic and ectomycorrhizal mushroom yield in *P. pinaster* stands.
- 2-year lagged effects were found between the current saprotrophic mushroom production and latewood width in *P. pinaster* plots, while ectomycorrhizal mushroom yield was more correlated with current latewood.
- The relationship between tree growth and ectomycorrhizal mushroom production in *P. pinaster* stands was mediated, not only by precipitation from late summer to early autumn, but also by forest thinning intensity.
- The relationship between latewood width and ectomycorrhizal mushroom yield was positive in those *P. pinaster* plots under low to moderate thinning intensities (i.e., ca. 30% in stand basal area), the relationship becoming negative at heavy intensities.
- In *P. pinaster* stands, saprotrophic mushroom yield did not react to the thinning treatment and showed a more erratic pattern along time.
- The models on the interaction between tree growth and mushroom productivity may be used to reconstruct past mushroom production based on dendrochronological information.
- The models on the interaction between tree growth and mushroom productivity may be also used to predict future mushroom yield based on climate-sensitive tree and stand growth projections.
- At the European level, positive correlations between latewood growth and mycorrhizal mushroom biomass were only observed in some Mediterranean sites, this relationship being mainly mediated by summer and autumn precipitation.
- Weak or no significant synchronies between mushroom yield and climatic and dendrochronological variables were found in the boreal and temperate regions.
- Forest thinning in *P. pinaster* stands had a prolonged negative effect belowground, inter- and intra-annually, on total fungal biomass and on the biomass of ectomycorrhizal fungi, but not on saprotrophic fungi.
- In the *P. pinaster* plots, total and ectomycorrhizal mushroom yields were negatively correlated with the total and the ectomycorrhizal mycelial biomass, respectively.
- Forest thinning in the *P. pinaster* stands also correlated positively with the aboveground/belowground ratio of both total and ectomycorrhizal fungal biomass.
- Sporocarps community composition responded in short-term to the thinning intensity applied in *P. pinaster* stands, due largely to an immediate high production after thinning of *Lactarius* group *deliciosus*.
- Thinning intensity in the *P. pinaster* stands did not cause any effect on the sporocarps diversity (i.e., richness and evenness).

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