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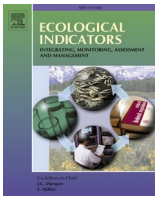

Impact of forest thinning on aboveground macrofungal community composition and diversity in Mediterranean pine stands

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ABSTRACT

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. 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. 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. Moreover, 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. Our results indicate that the post-treatment conditions following forest thinning may cause short-term successional changes in both ectomycorrhizal and saprotrophic fungal assemblages, benefiting, in turn, particular fungal species of socioeconomic interest by producing large amount of sporocarps. Furthermore, forest thinning with careful and low-impact removal of trees does not jeopardize sporocarp diversity.

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 et al., 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).

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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 et al., 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 et al., 2012). Moreover, the forest stand structure is another important factor in fungal dynamics that, unlike climate, can be modified by human activities (Tomao et al., 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 et al., 2017). Heavy forest disturbances may trigger reductions in ECM fungal diversity (Jones et al., 2003; Parladé et al., 2019) and changes in soil fungal community composition (Kyaschenko et al., 2017). Sterkenburg et al. (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 et al. (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 et al., 2010; Rayner and 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 et al., 2007). However, forest thinning has shown, in different ecosystems, contrasting effects on sporocarp 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 that higher thinning intensity had greater impact on the sporocarp community. In another tropical plantation, Lin et al. (2011) also detected higher saprotrophic sporocarp richness in light-thinned stands than in those heavily thinned plots. 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 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 disturbances 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 et al., 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 × 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 × 40 m) in order to prevent edge effects (Fig. S1) and were fenced to prevent trampling and disturbance from occasional visitors. 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 stand characteristics after forest thinning and experimental design can be found in Table S1 and Bonet et al. (2012), respectively.

2.3. Sporocarp sampling

A total of 89,153 epigeous sporocarps were collected from all plots 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 taxa collected over the study period were then classified into two functional guilds based on expert and current scientific knowledge (e.g., Agerer, 2006; Hobbie and Agerer, 2010; Tedersoo et al., 2014; Tedersoo and Nara, 2010): ectomycorrhizal (168 taxa in total) and saprotrophic (253 taxa in total, including both wood and soil saprotrophs). 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; Van den Brink and Ter Braak, 1998). 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). PRC produces a graphical output with the coefficient of the community response pattern on the y-axis and time along the x-axis. The plotted lines for each treatment group are named the response curves. The control treatment was the reference treatment and represented by the horizontal line at 0. Accompanying the curves of the treatment group coefficients are species scores which show the affinity of each species included in the analysis to the response shown. 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 et al., 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).

3.1.1. Thinning effects on abundance-based macrofungal community composition

PRC showed an immediate total sporocarp compositional effect two

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

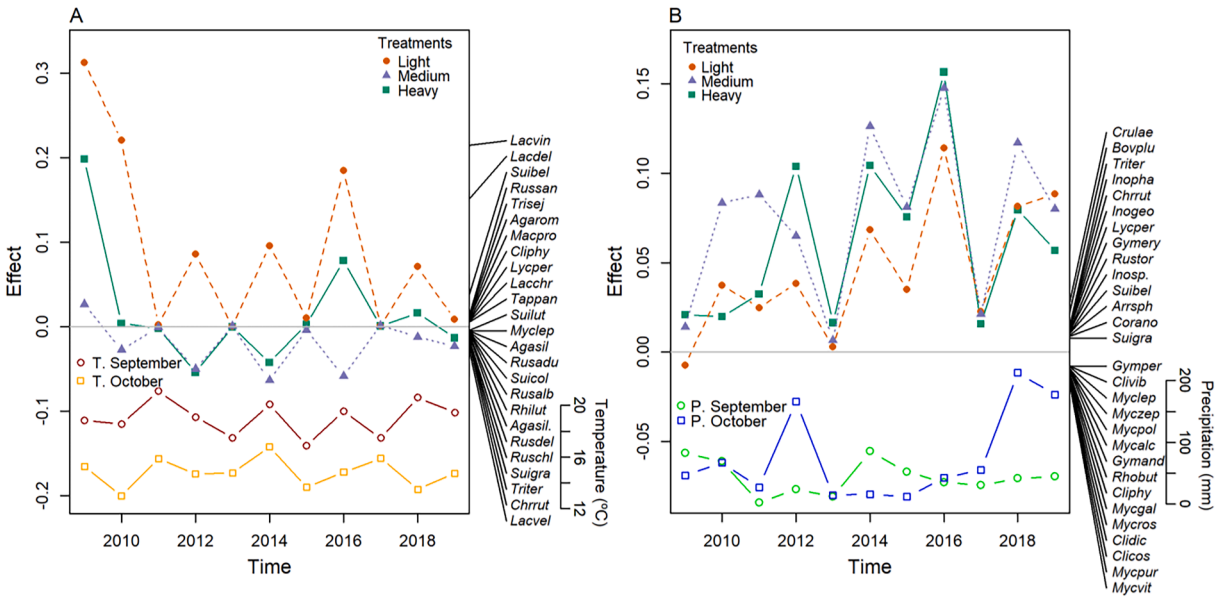

Fig. 1. Principal response curves (PRC) analysis showing the effect of thinning intensity on total sporocarp community composition (including both ECM and saprotrophic species) over 11 years after the thinning conducted in 2009 for (A) quantitative (i.e., species abundance) data and (B) qualitative (species 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*.

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: $F\text{-value}_{[2,261]} = 7.08$, $p = 0.394$). 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 ($F\text{-value}_{[1,200]} = 4.21$, $p = 0.84$; 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 total 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 ($F\text{-value}_{[3,217]} = 2.32$, $p = 0.002$; $F\text{-value}_{[3,217]} = 2.31$, $p = 0.001$, respectively). The interactions of total sporocarp composition with accumulated precipitation of September and October were not significant ($F\text{-value}_{[3,217]} = 0.95$, $p = 0.539$; $F\text{-value}_{[3,217]} = 0.57$, $p = 0.928$, 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 ($F\text{-value}_{[3,165]} = 2.33$, $p = 0.002$; $F\text{-value}_{[3,165]} = 2.31$, $p = 0.002$, 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

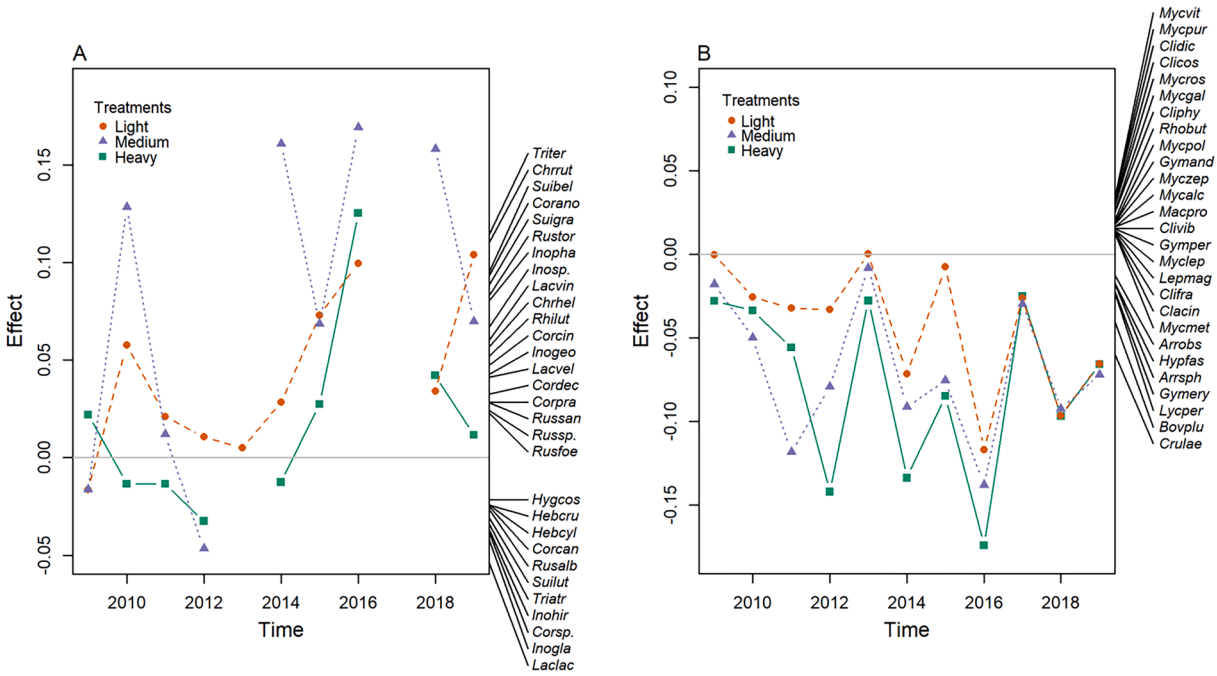

Fig. 2. Principal response curves (PRC) analysis showing the effect of thinning intensity on ectomycorrhizal (A) and saprotrophic (B) sporocarp community composition over 11 years after the thinning conducted in 2009. Macrofungal community composition was described based on qualitative data (i.e., presence-absence 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*.

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: $F\text{-value}_{[1,259]} = 3.23$, $p = 0.369$; 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 ($F\text{-value}_{[3,217]} = 1.70$, $p = 0.001$; $F\text{-value}_{[3,217]} = 1.71$, $p = 0.001$, respectively). In the saprotrophic sporocarp community composition, the mean temperature of September and October interacted with the treatment effect ($F\text{-value}_{[3,215]} = 1.83$, $p = 0.001$; $F\text{-value}_{[3,215]} = 1.84$, $p = 0.001$, respectively), as did the accumulated precipitation of October ($F\text{-value}_{[3,215]} = 1.43$, $p = 0.026$). 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).

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

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				
	Trophic group	Intercept	Thinning intensity	Time	Thinning intensity x Time	Plot Intercept	Residuals 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: '**' $p < 0.001$; '*' $p < 0.01$.

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.

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 which showed that forest management reduces 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 during harvest, since the trees were felled by chainsaw and removed manually from the plots to minimize soil disturbance. For instance, the soil compaction caused by mechanical

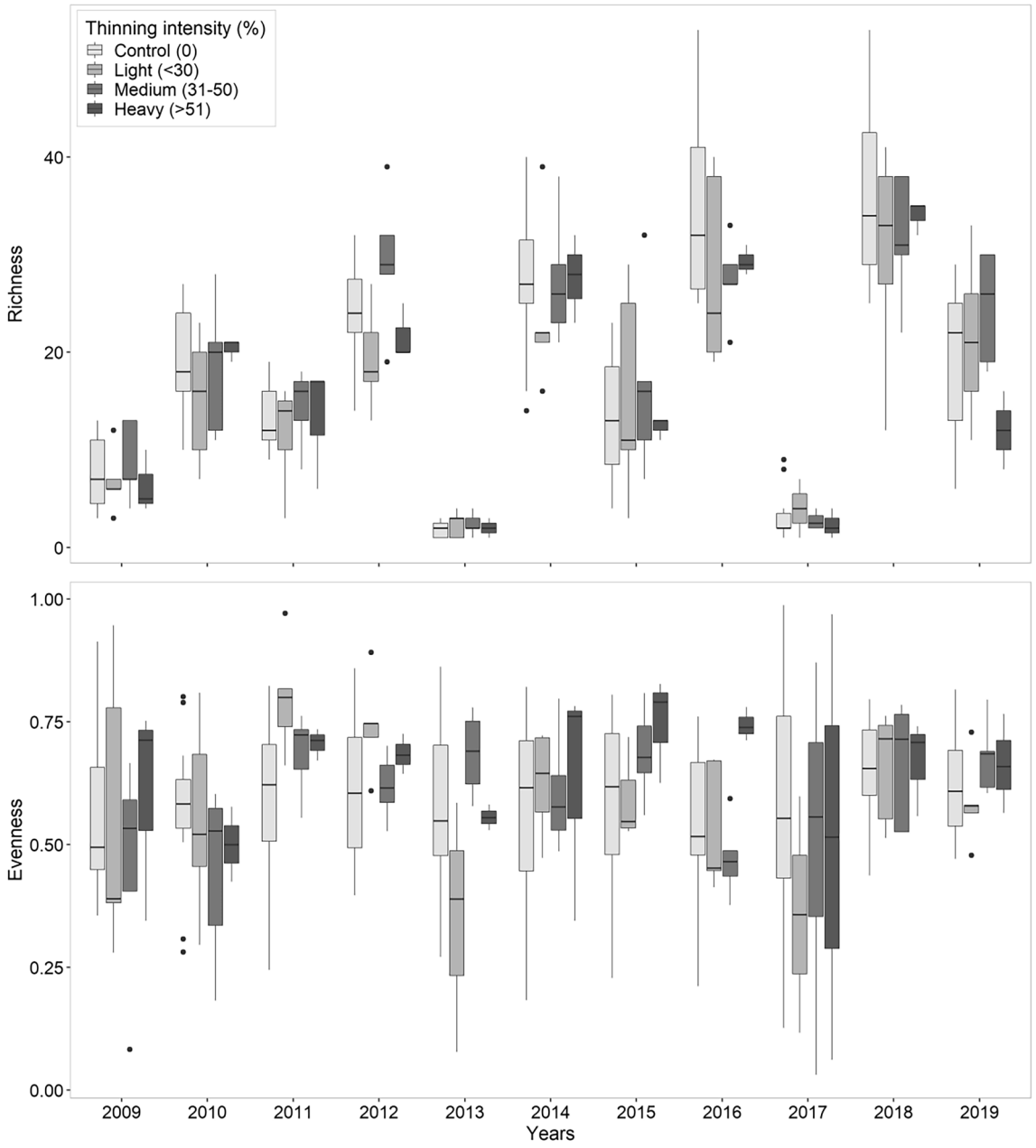

Fig. 3. Total sporocarp species richness and evenness under different thinning intensities in stand basal area: light (20 – 30%), medium (31 – 50%) and heavy (51 – 70%). Dots denote outlier values (i.e., values that fall below Q1 – 1.5 IQR or above Q3 + 1.5 IQR).

harvesting reduces the water infiltration and nutrient availability over at least 5 years (Page-Dumroese et al., 2006) and likely increase the physical damage to fungal hyphae and propagules (Brundrett, 1991), resulting in changes in fungal communities (Hartmann et al., 2012). In this sense, 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 sporocarp 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 sporocarp 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 et al., 2015). In this context, the soil of the study area 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 et al. (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 sporocarps (i.e., qualitative abundance), indicating that the same ECM species fructify regardless of thinning intensity. Actually, the increase over time in fungal sporocarp 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 et al., 2008; Gebauer and 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 et al., 2011; Parisi et al., 2018). For instance, Müller et al. (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 et al., 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 sporocarp 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 sporocarp 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.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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