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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.

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 (Orwin et al., 2011; Mohan et al., 2014). 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 (Rayner & Boddy, 1988; Ferris et al., 2000).

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

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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	Treatment	Alt (m)	Asp (°)	Slo (%)	Initial	After thinning*	Thinning intensity (%)	ECM	Saprobic	Earlywood	Latewood	IADFs (%)*
301	Control	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	Control	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	Control	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	Control	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	Control	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	Control	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	Control	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	Control	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	Control	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	Control	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	Control	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	Control	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	Control	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	Control	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)
301c	Thinned	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)
302c	Thinned	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)
303c	Thinned	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)
304c	Thinned	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)
305c	Thinned	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)
306c	Thinned	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)
307c	Thinned	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)
308c	Thinned	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)
309c	Thinned	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)
312c	Thinned	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)
313c	Thinned	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)
315c	Thinned	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)
316c	Thinned	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)

Note: Plots with letter 'c' 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.
* Values are averaged by years (n = 7 years in control plots, and n = 6 years in thinned plots).

importance worldwide (Boa, 2004). Indeed, forest mushrooms are of significant importance for both recreation and trade (Martínez de Aragón et al., 2011; Gorriz-Mifsud et al., 2017), 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 & 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.